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Maturation of male and female North Sea plaice (*Pleuronectes platessa* L.)

A. D. Rijnsdorp

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The maturation of North Sea plaice is studied on the basis of two research-vessel surveys and market-sampling data from the commercial fisheries. In female plaice the juvenile–adult transition occurred between May and September. Development of the female gonad took place between July and December, although the gonad did not gain weight before October. Gonad weight reached a maximum of circa 17 % of the gutted body weight between January and March. The average female plaice was in spawning condition for about five weeks from late January to early March. Male plaice were in spawning condition for at least 11 weeks from the second half of December to the second half of March. In females the start of spawning was earlier in older fish, but the end of spawning did not differ between age groups. In males spawning ended later in older fish. The time that mature plaice were in spawning condition increased with the age of the fish in males and females. During the spawning season mature plaice hardly fed. Spent fish resumed feeding in January. The cessation of feeding in mature plaice was not related to the absence of food.

Male plaice became sexually mature as II- and III-group, females as IV- and V-group. Length at 50 % maturity (L_{50}) was 22 cm and 34 cm for males and females respectively. L_{50} and age at 50 % maturity (A_{50}) differed between geographical areas, increasing from south to north. Annual differences were observed in L_{50} and A_{50} which were related to annual differences in growth rate. Slower-growing plaice reached maturity at a smaller length but higher age than faster-growing plaice. Comparison with published data shows that at present both male and female plaice mature at a younger age and at a smaller size than at the beginning of this century.

A. D. Rijnsdorp: Netherlands Institute for Fishery Investigations, RIVO, P.O. Box 68, 1970 AB IJmuiden, The Netherlands.

Introduction

North Sea plaice have attracted the interest of both fishermen and fishery biologists for almost a century. Reviews of much of the earlier research are given by Wimpenny (1953), Simpson (1959), and Bannister (1978). The main spawning occurs in the southern and southeastern North Sea between late December and early April (Simpson, 1959; Harding *et al.*, 1978a). Males predominate on the spawning grounds and are thought to spend several months there – in contrast to female plaice which remain for a few weeks (Hefford, 1916), although a precise estimate of the duration of spawning is not available. During the spawning period plaice almost cease feeding (Todd, 1914; Lande, 1973), but it is not known whether this is caused by the absence of food or by behavioural changes associated with spawning. Data on the annual maturity cycle, which could yield information on the time of the year when maturation starts and on the duration of the spawning process, are not available for North Sea plaice, although LaHaye (1972) and Deniel (1981) present qualitative data for plaice along the coast of Brittany.

Data on the length and age at first maturity in North Sea plaice are given by Kyle (1900), Wallace (1914, 1916), and Hefford (1916). These studies showed that males became mature at a smaller length (30–37 cm) and a younger age (age group V–VI) than females (32–43 cm; age group V–VII) and that the onset of sexual maturity differed between the southern and southeastern North Sea. Simpson (1959) concluded that female plaice of the 1943 and 1944 year classes became mature as IV–V-group. More recent information is lacking.

This paper is the first of a series dealing with the changes in biological parameters of plaice such as growth, onset of maturity, and fecundity (Bannister, 1978; Rijnsdorp *et al.*, 1983; Horwood *et al.*, 1985) and will focus on the following aspects of the reproductive biology of plaice: 1) annual maturity cycle; 2) duration of the spawning process; 3) relation between the reproductive state and the level of feeding; 4) spatial distribution of immature and mature plaice; 5) length and age at first maturity in different parts of the southern North Sea; and 6) changes in the length and age at first maturity since 1900.

North Sea plaice

Tagging experiments with spawning plaice have shown the existence of four main spawning groups in the southern North Sea: Southern Bight, Transition area, German Bight, and Flamborough (de Veen, 1962, 1978). From the distribution map of egg-production (Fig. 1) the existence of several smaller spawning groups can be inferred along the east coast of England and Scotland (Lockwood and Lucassen, 1984) and in the Fisher Bank area.

The structure of the North Sea plaice population may therefore be visualized as a series of distinct spawning groups that partially mix on the summer feeding grounds (de Veen, 1962). Differences between the spawning groups in the southern North Sea have been shown in otolith and meristic characters (de Veen and Boerema, 1959) and in frequencies of abnormal pigmentation (de Veen, 1969), but not in serological or biochemical characteristics (de Ligny, 1967, 1969; Purdom *et al.*, 1976).

It is not fully understood from which nursery areas the adult fish of the different spawning groups originate. The results of tagging experiments with juvenile plaice reported by Hickling (1938), suggest that the Southern Bight spawners mainly recruit from the nursery grounds in the Dutch Wadden Sea and along the Frisian coast, whereas the German Bight spawners recruit from the nursery areas in the German Bight. Juvenile plaice along the English east coast mainly recruit to the Flamborough spawning population (Lockwood and Lucassen, 1984). However, the reported tagging experiments indicate that juveniles can recruit to other spawning populations than the main ones listed above. It is not established to which spawning group the juvenile plaice from the nursery area along the Jutland coast recruit.

The relative importance of the different spawning groups is indicated by their total egg production. In the 1960s the total production of fertilized eggs in the North Sea and English Channel was estimated at 25×10^{12}; of this total, 65 % occurred in the central and eastern North Sea, 20 % in the Southern Bight, less than 5 % in the western English Channel, and 10 % in the eastern English Channel. Spawning along the English and Scottish east coast was insignificant in relation to the total North Sea egg production (Harding *et al.*, 1978a), although in 1976 egg production in the Flamborough area was estimated at 3×10^{12} (Harding *et al.*, 1978b).

Another indication of the importance of the different spawning populations is given in Figure 2 by the relative catch per hour of plaice (⩾27 cm) in the International Young Fish Surveys of 1983, 1984, and 1985 (Anon., 1987). This result corroborates the importance of the German Bight subpopulation as indicated by the egg-production data.

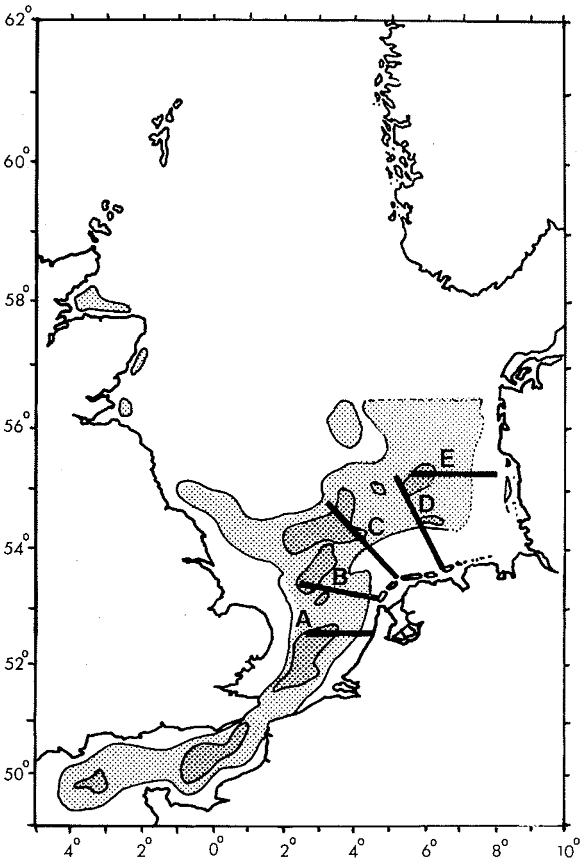

Figure 1. Map of lines A to E of sampling stations of the maturity survey in 1985 and 1986. The total spawning area (light shaded) and the main centres of egg production (dark shaded) are indicated according to Harding *et al.* (1978).

Sources of data

Maturity survey

Maturity surveys were carried out from 28 January to 6 February 1985 and from 27 January to 6 February 1986 by RV "Tridens" and RV "Isis". In both years the survey encompassed a total of 49 stations. The stations were distributed along 5 lines A to E as shown in Figure 1, more or less perpendicular to the coast at distances from the coast of 3, 6, 12, 18, 24, 36, 48, 60, 72, 84, and 96 miles. In 1986 the first four stations in line E had to be omitted owing to bad weather.

Catches were made with a 6-metre heavy beam trawl with four tickler chains as used by RV "Tridens" in the Demersal Young Fish Survey (mesh size: 40 mm; haul duration: 30 minutes; fishing speed: 4 knots). For each

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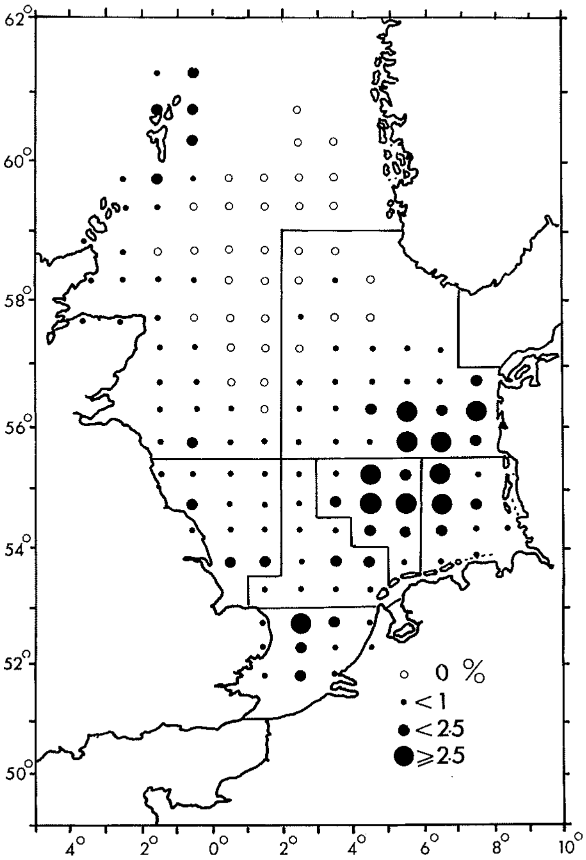

Figure 2. Distribution of plaice (≧27 cm) in the International Young Fish Survey in February (data 1983–1985) as indicated by the percentage of the total population present in each rectangle (from Anon., 1987).

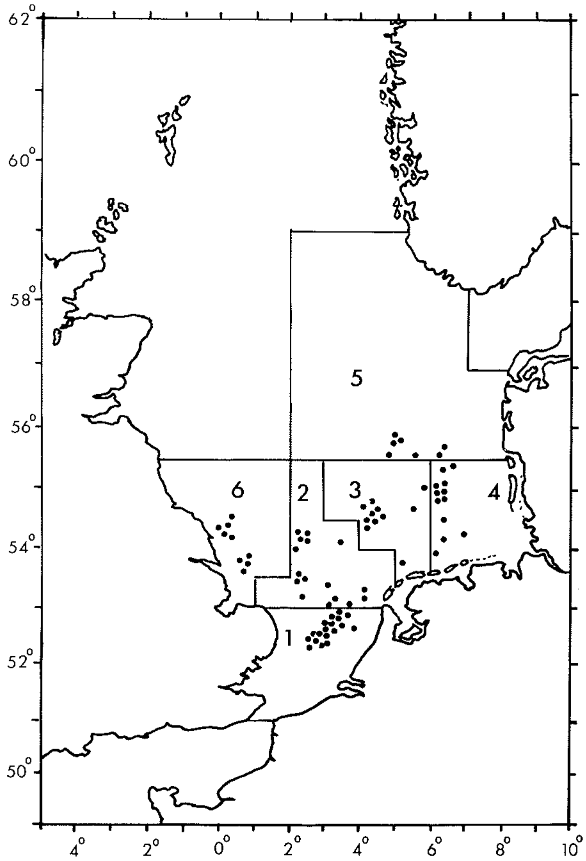

Figure 3. Distribution of market samples in the first quarter of 1985 and 1986 and the geographical areas used in the market-sampling program: area 1 = DWK, 2 = OG, 3 = DBW, 4 = DBO, 5 = VB, and 6 = FLAM.

haul the length-frequency distribution of plaice was recorded to the cm below and an otolith sample was taken. From each cm-group, four plaice, taken at random, were examined for age, sex, maturity stage, and feeding condition, giving a total over both years of 2772 male and 2270 female plaice.

Market sampling

The landings of plaice by commercial vessels in the Netherlands are sampled monthly on a routine basis for age, length, weight, sex, and maturity. The market samples (80 fish) were stratified according to geographical area and to the four market size categories in use in the Netherlands: 27–34 cm; 34–38 cm; 38–41 cm; >41 cm. Each market category consisted of 20 plaice taken at random. Comparison of the geographical distribution of market samples in the first quarter of 1985 and 1986 (Fig. 3) shows that they covered the whole North Sea plaice population except the smaller spawning groups along the British east coast north of Flamborough Head (Fig. 1).

Methods

Maturity staging

The maturity stages were recorded using the scale given in Table 1 (modified from Wimpenny, 1953). In female plaice staging was quite straightforward, but in male plaice problems arose in distinguishing spent males from immature males. Macroscopically no reliable diagnosis appeared to be possible. A preliminary attempt to facilitate the diagnosis by histological examination of the testis suggested that some of the bigger males recorded as stage 7 (spent) in January might have been immatures.

Duration of spawning

The annual maturity cycle was analysed on a monthly basis for the period 1981–1985 (n = 12 180) from the relative frequencies of maturity stages in the samples. The mean duration of the individual spawning activity was estimated following the method used by Iles (1964)

Table 1. Maturity stages of North Sea plaice.

		Males
1	Immature	Testis very small
2	Ripening	Testis bigger, colour grey
3*	Ripe	Testis big and white; milt can be expelled under pressure
4*	Spawning	As 3, milt freely running or can be expelled under slight pressure
5*	Nearly spent	Milt brownish, can be expelled under strong pressure
6	Spent	Small, form of half moon, colour brown
7	Spent	Shrunken, often going back to stage 1

*Milting males.

		Females
1	Immature	Lumen transparent, colour grey
2	Ripening	Colour orange, oocytes visible, vitellogenesis in progress
3*	Spawning	As 2 but with few ripe hyaline eggs
4*	Spawning	Ovary completely filled with hyaline eggs
5*	Spawning	Eggs partly shed
6	Nearly spent	Ovary contains only a small amount of hyaline eggs
7	Spent	Ovary small, flabby, and bloodshot, back to stage 2

*Running females.

for herring. In this method the duration of spawning is calculated as the time elapsed between the time when 50 % of the adult population has reached maturity stage 3 or higher and the time when 50 % of the adult population has become spent (stage $\geqq 6$). Market sampling data from the most intensively sampled period, 1974–1976 (n = 18 200), were analysed with a time unit of half a month. As spawning periods and spawning-stock sizes differed between geographical areas the relative frequency of each maturity stage in each market category and area were weighted by the monthly catch per unit of effort of the corresponding market category and geographical area to arrive at an estimate for the total North Sea population. This estimate for the total North Sea population is the most representative as it is based on all available data and is not affected by bias due to immigration or emigration of adult fish.

Maturity–length and maturity–age relationships

From the market sampling data the maturity–age relationship was determined for each market category separately and then summed over the categories after weighting them by the proportion of each market category in the total Dutch landings.

The maturity data from the surveys were analysed by taking account of the distribution of mature and immature plaice. First the proportion of mature plaice was determined for each station by length or age group. Then the average proportion of mature plaice was calculated for each line by weighting over the station abundance and the surface area of the zone sampled, approximated by the inter-station distance. So for the first two stations at 3 and 6 miles from the coast the weighting factor was 1, for the next three stations at 12, 18, and 24 miles the factor was 2, and for the remaining stations at 36, 48, etc. miles the factor was 4.

The length at which 50 % of the population reached maturity (L_{50}) was determined by a functional regression of the logit transformed maturity proportions (P) against length:

$$\text{Logit } P = 0.5 \log_n(P/1-P).$$

In age reading, 1 January was taken as the birthday.

Feeding condition

From the presence or absence of visible food remains in the gut, fish were classified as either "feeding" or "non-feeding". Information to test whether there was a relation between stage of maturity and feeding condition was available from the maturity surveys and from part of the market samples between 1983 and 1985. A total of 1356 plaice were investigated for feeding condition in these market samples and 5042 in the maturity survey samples.

Statistical analysis of feeding incidence in relation to maturity stage and distance from the coast was carried out with an ANOVA technique fitting a GLIM model (Baker and Nelder, 1978) with a binominal error distribution.

Results

Annual maturity cycle

In both sexes the resting (stage 7) and ripening stage (stage 2) dominated during the growing season between April and November (Fig. 4). In females visual inspection of the ovaries indicated that vitellogenesis started in July and continued until the spawning period. Substantial growth of the female gonad did not, however, occur before October (Fig. 5). The transition from juvenile to adult female took plaice between May and September and appeared to be slightly earlier in the older age groups. The percentage of adults increased between May and August in age group IV, between May and September/October in age group III, and between August and September in age group II (Fig. 6).

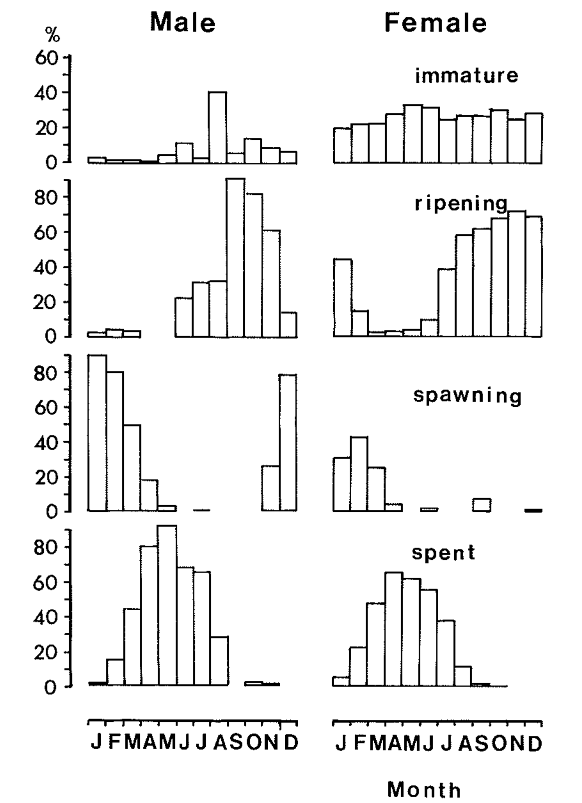

Figure 4. Monthly percentage of immature (stage 1), ripening (stage 2), spawning (stages 3, 4, and 5) and spent (stages 6 and 7) male and female plaice in the market samples of 1981–1985.

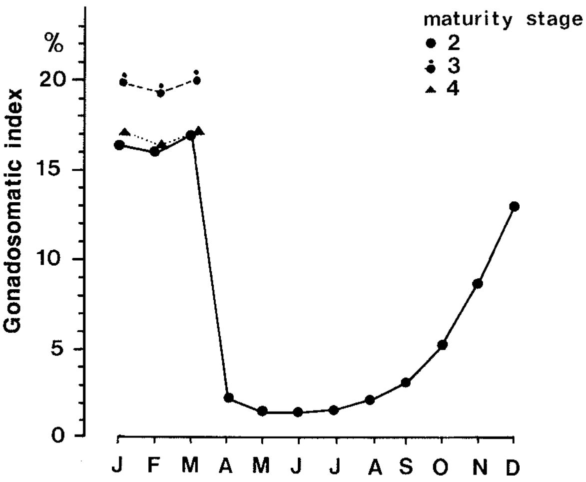

Figure 5. Gonad weight of female plaice as percentage of the gutted body weight (including gonads) by month for maturity stages 2, 3, and 4 in the market samples of 1981–1985.

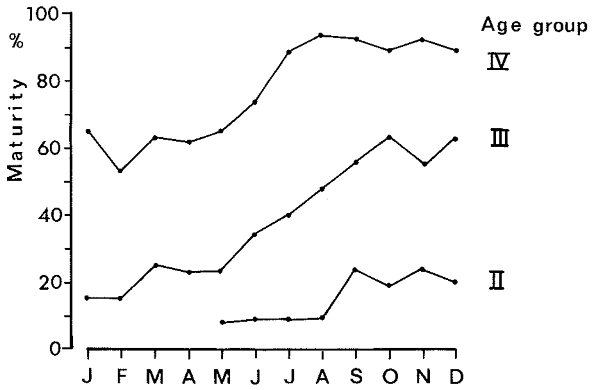

Figure 6. Time of the juvenile–adult transition in female plaice as indicated by the increase in the percentage of mature fish (stage ≧2) in age groups II, III, and IV in the market samples of 1981–1985.

Duration of spawning

Spawning females (stages 3, 4, and 5) were observed from January until April with a peak in February, but their proportion never exceeded 50 % (Fig. 4). Spawning males (stages 3, 4 to 5) were observed from November until May and predominated in the total population between December and March. Male plaice thus started their spawning activity at an earlier date and continued for a longer time. The few male and female plaice that were recorded as being in spawning condition outside the main spawning period were probably due to errors in the maturity staging.

In Figure 7 the cumulative proportions of maturity stages within the adult population (maturity stages 2–7) are shown. The descending lines, which connect the cumulative proportions of the successive maturity stages (2, 2+3, 2+3+4, etc.), demonstrate the transition of adult fish through successive maturity stages. The shaded area in Figure 7 indicates the proportion of fish within the adult population that were in a spawning stage (stages 3–5). The distance between the two lines encompassing the shaded area at the points where 50 % of the population had reached at least maturity stage 3 and 6 indicates the duration of spawning of an average individual plaice. Thus estimated, the average male plaice was in a spawning stage (maturity stages 3–5) for a minimum of 11 weeks ending in mid-March. The start of the spawning in December could not be determined precisely. The average female was in a spawning stage (maturity stages 3–5) for about five weeks from late January to the beginning of March. The time that plaice were engaged in the spawning process increased with the age of the fish (Fig. 8, left and right). In females that increase coincides with an earlier start of spawning in older fish and a longer duration of maturity stage 3. The end of the spawning in females is remarkably similar between age groups. In males the end of spawning is later in older age groups.

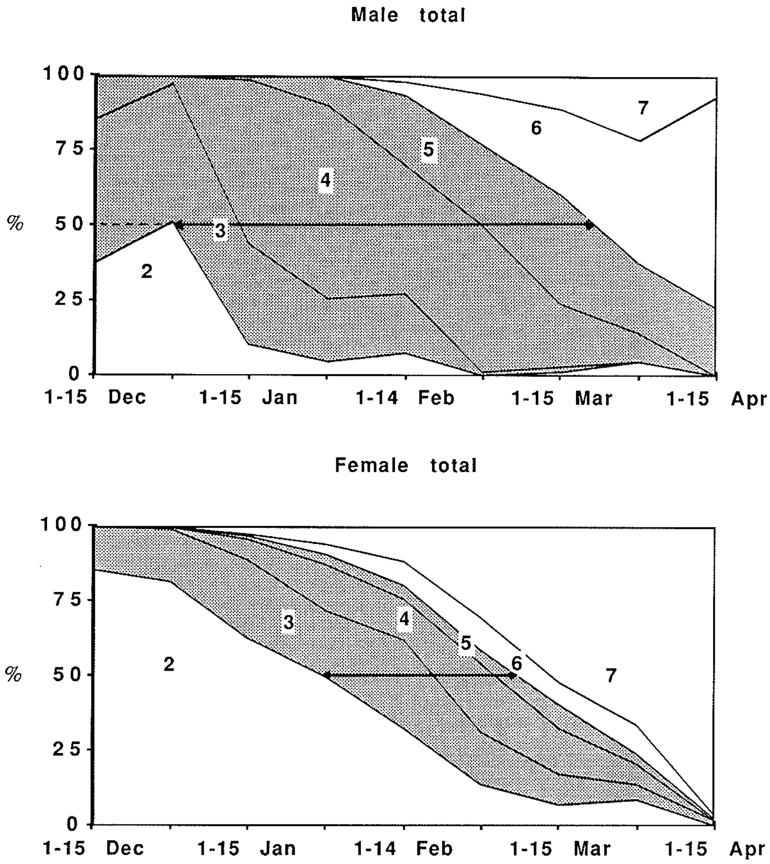

Figure 7. Cumulative percentage of the adult maturity stages 2 to 7 of male and female plaice by half-monthly period. The spawning stages 3–5 are shaded. The estimated spawning duration is indicated by the horizontal line at 50 % encompassing the spawning stages. Data: pooled market-sampling data of the areas DWK, OG, DBW, and DBO between 1974 and 1976.

Feeding condition and reproductive state

The lower incidence of feeding during the spawning period was apparent in both immature and mature fish, but was most pronounced in fish of maturity stages 2–5, that is, fish that are (nearly) engaged in spawning (Fig. 9). After spawning the spent fish resumed feeding as early as January.

Because the distribution of mature and immature plaice differed it is possible that this might be the cause of differences in feeding condition. Therefore the relation between maturity and feeding condition was studied in more detail during the maturity surveys in 1985 and 1986 with reference to the distance from the coast (Table 2). ANOVA showed that both maturity stage (males: $F = 22.6$; d.f. = 2,14; $P < 0.01$; females: $F = 48.2$; d.f. = 2,16; $P < 0.01$) and distance from the coast (males: $F = 5.88$; d.f. = 8,14; $P < 0.01$; females: $F = 6.89$; d.f. = 8,16, $P < 0.01$) were significantly related to the feeding incidence. Overall feeding incidence was highest between 6 and 18 miles from the coast. Spawning fish showed a lower feeding incidence than immature or spent fish irrespective of the distance from the coast. Ripe female plaice were hardly feeding at all wherever they were caught. The same applies to ripe males in the centre of the spawning areas. However, the smaller ripe male plaice at the edges of the spawning areas did show some feeding activity. The differences in feeding incidence between the maturity stages are apparently not caused by a lack of suitable food, because immature and spent plaice were observed feeding at stations where ripe plaice did not feed.

Spatial distribution of plaice in the spawning period

In Figure 10 the catch per hour of age groups I to V and the percentage of immature plaice are shown in relation to the distance from the coast. Data for lines C+D only are shown. The distribution patterns on the other lines were essentially the same. The location of spawning grounds, as indicated by the presence of "running" females, is shown by black bars at the top of Figure 10. "Running" females (maturity stages 3–5) were first observed at 18 miles from the coast. From 24 miles onwards, on average 34 % of the mature females were in "running" condition (range 24–47 %). The distribution of plaice eggs indicated that around line C+D the main

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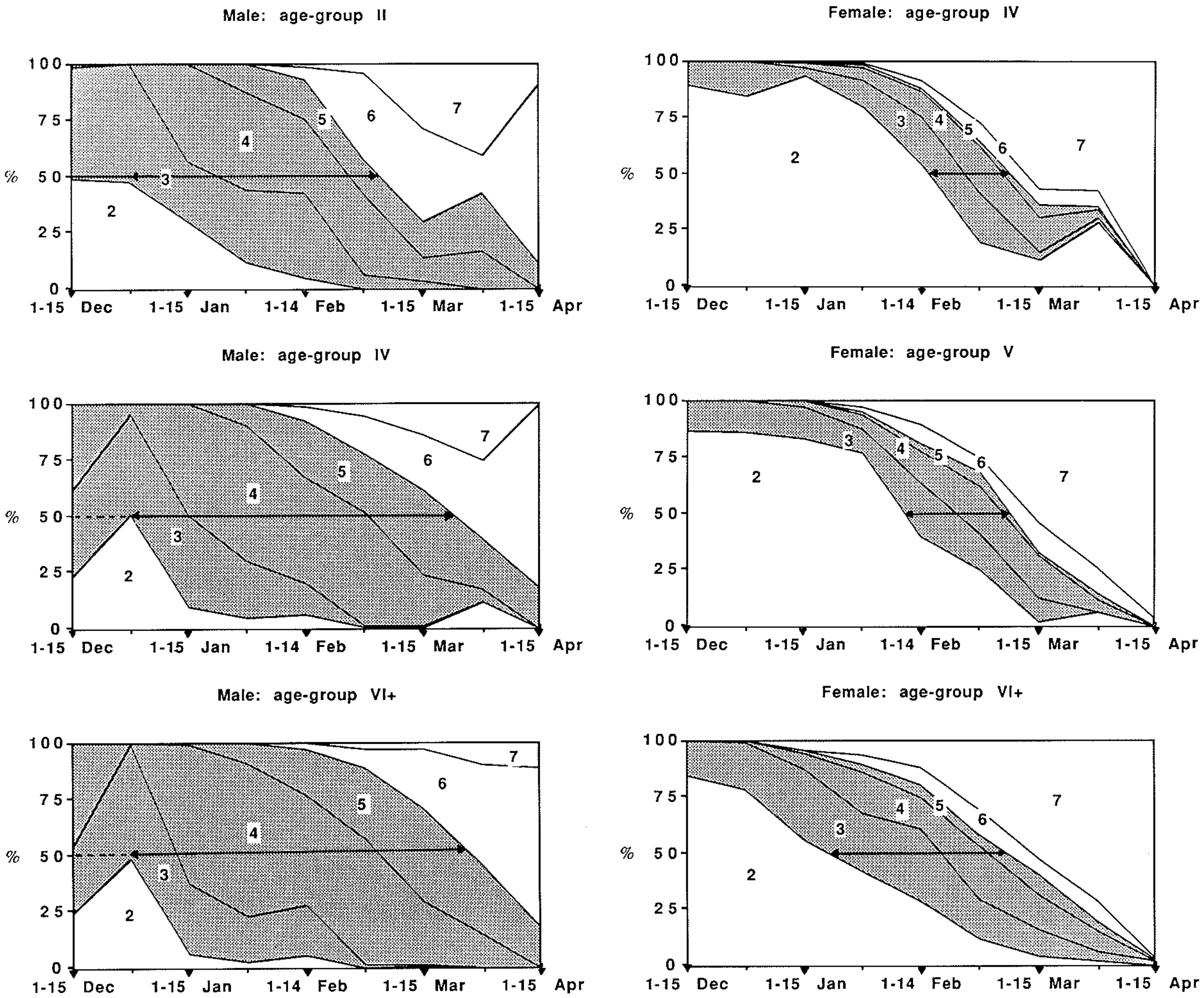

Figure 8. Cumulative percentage of the adult maturity stages 2 to 7 by half-monthly period for (left) males: age groups II, IV, and VI+, and (right) females: age groups IV, V, and VI+. The spawning stages 3–5 are shaded. The estimated spawning duration is indicated by the horizontal line at 50 % encompassing the spawning stages. Data: pooled market-sampling data of the areas DWK, OG, DBW, and DBO between 1974 and 1976.

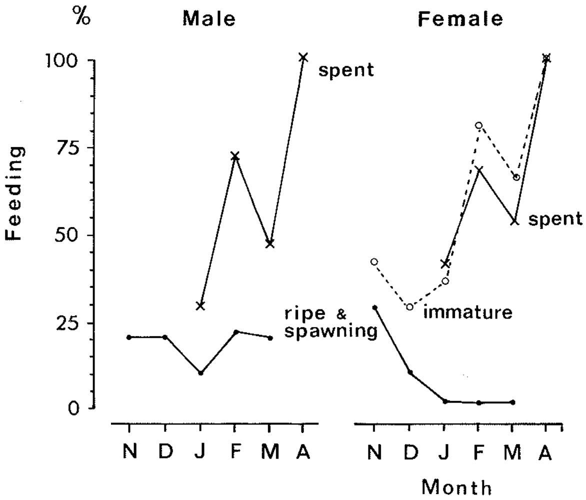

Figure 9. Percentage of feeding fish of immature (stage 1), ripe and spawning (stages 2–5), and spent (stages 6 and 7) male and female plaice by month as observed in market samples and the maturity surveys.

Table 2. Feeding incidence of plaice in relation to the maturity stage and the distance in miles from the coast as observed in the maturity surveys in 1985 and 1986.

	Males Stage 1			Males Stages 2–5			Males Stages 6–7		
	Feeding	Total	%	Feeding	Total	%	Feeding	Total	%
Distance									
3	59	229	25.9	2	26	7.7	–	–	–
6	64	175	36.6	9	72	12.5	–	–	–
12	48	123	39.0	25	105	23.8	2	6	33.3
18	45	105	42.9	23	195	11.8	1	3	33.3
24	36	160	22.5	41	253	16.2	16	32	50.0
36	15	74	20.3	32	432	7.4	7	31	22.6
48	10	51	19.6	5	180	2.8	3	16	18.8
60	4	39	10.3	2	154	1.3	6	29	20.7
≧72	4	17	23.5	5	249	2.0	2	16	12.5
Total......	285	972	29.3	144	1666	8.6	38	134	28.4

	Females Stage 1			Females Stages 2–5			Females Stages 6–7		
	Feeding	Total	%	Feeding	Total	%	Feeding	Total	%
Distance									
3	83	244	34.0	1	3	33.3	1	1	100.0
6	90	209	43.1	0	1	0.0	1	1	100.0
12	91	161	56.5	1	15	6.7	3	3	100.0
18	85	182	46.7	1	33	3.0	1	1	100.0
24	120	319	37.6	2	75	2.7	5	9	55.6
36	39	233	16.7	1	130	0.8	4	5	80.0
48	35	134	25.9	0	48	0.0	2	5	40.0
60	32	117	27.4	2	40	5.0	3	11	27.3
≧72	71	200	35.5	1	74	1.4	1	16	6.3
Total......	646	1799	35.9	9	419	2.1	21	52	40.4

spawning occurred in an area between 40 and 100 miles from the coast (Fig. 1).

The I-group males and females showed a strictly coastal distribution, and the centres of distribution of older age groups moved farther offshore. Mature males of age groups II and III (length range 15–30 cm) were concentrated on the edges of the main spawning grounds (18–36 miles from the coast) and occurred farther offshore than the immature fish of the same age. Older males (>30 cm) predominated in the central parts of the spawning grounds (>36 miles). II-group females, though still mainly immature, had already started to spread out from the coastal nursery grounds towards the offshore spawning grounds. In the older age groups the proportion of mature females increased, while the dispersion of the immatures over the offshore grounds was further advanced. The proportion of mature female plaice, mainly ripening females (maturity stage 2), was highest at the edges but decreased towards the centre of the spawning grounds. With the other lines (A,B,E), the proportion of mature females was also highest at the edges of the spawning areas. Although female plaice matured at an older age than male plaice the dispersion from the nursery areas towards the spawning grounds was similar.

Length and age at first maturity

In Figure 11 the length-frequency distribution of mature and immature plaice from the maturity survey is shown. From Figure 12 it can be seen that males reached sexual maturity over a range of length between 15 and 30 cm, with 50 % reaching maturity at a length of 21.9 cm (L_{50}) (Table 3). Females attained maturity between 24 and 37 cm, with 50 % reaching maturity at a length of 33.9 cm. In male plaice the maturity percentage did not increase continuously with fish length but levelled off between 20 and 27 cm before increasing again. This levelling off was observed in males on all lines but not for females.

The maturity–length relationships differed between

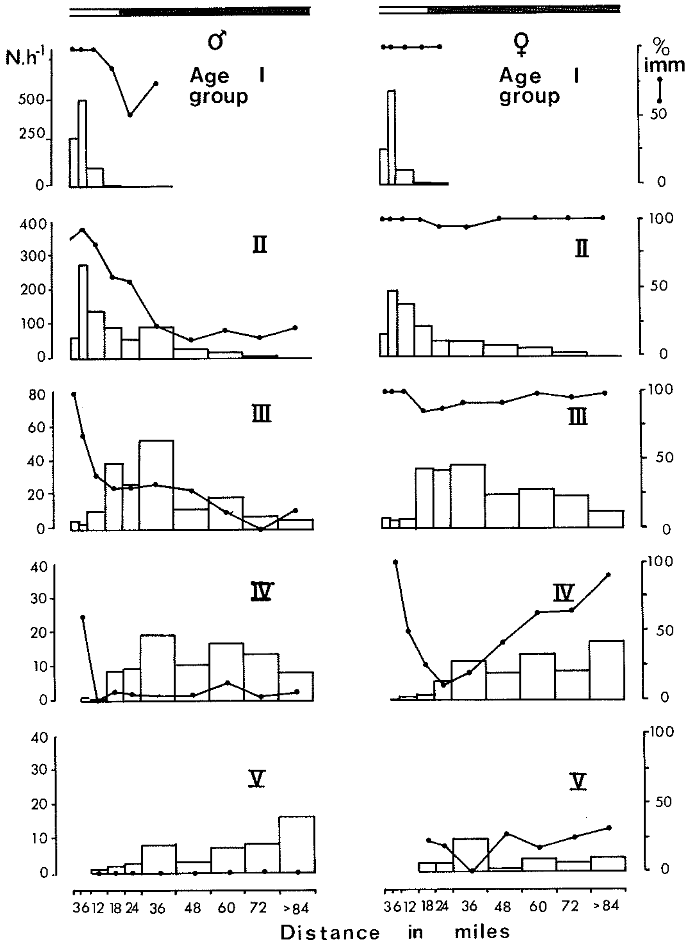

Figure 10. Density (c.p.u.e.) of plaice (histograms) and the percentage of immatures (dots) by age group in relation to the distance to the coast in lines C+D (survey data for 1985 and 1986). The bars at the top of the figure show the spawning areas as indicated by the presence of "running" females.

areas and years (Table 3). Going from south to north the L_{50} increased in males from 20 cm on line A+B to 22 on line C+D, and to 24 cm on line E; and in females from 33 cm on line C+D to 36 cm on line E. The market-sampling data also indicated an increase in the L_{50} in females from 30 cm in area DWK to 34–35 cm in area VB and FLAM. The L_{50} in males was 23 cm in the 1985 survey but only 20 cm in the 1986 survey. In females the L_{50} did not differ between these two years.

In general the maturity–length relationships obtained from the maturity survey were in agreement with those obtained from the market sampling, even though the market-sampling areas did not exactly coincide with the lines of the maturity survey. The maturity–length relation for the line C+D corresponded to that for areas OG, DBW, and DBO. The maturity–length relation for line A+B was based on a relatively small number of females, which were mainly taken at line B, and differed markedly from the relation for area DWK but only slightly from the relation for area OG. The maturity–length relation in line E was close to that of area VB.

The maturity–age relation based on the survey data is given in Table 4. The mean overall lines were calculated by weighting by the abundance per line. The majority of the male plaice became mature as II- and III-group. A very small proportion of males were already mature as I-group. As explained in the methods section some of the males recorded as spent (stage 7) could have been immature. To indicate the possible bias from this misinterpretation two values for the proportion of mature males are included in Table 4, one including and one excluding stage 7. The majority of female plaice became sexually mature as IV- and V-group. The youngest sexually mature females observed were of age group II.

Differences were observed in the age at which plaice became sexually mature between year classes and between areas. The 1983 year class as II-group fish contained a much higher percentage of mature fish than did the 1984 year class at the same age. Females of the 1983 year class also showed a slightly higher proportion of mature fish, particularly in the southern lines (A to C). These differences persisted when the 1983 year class

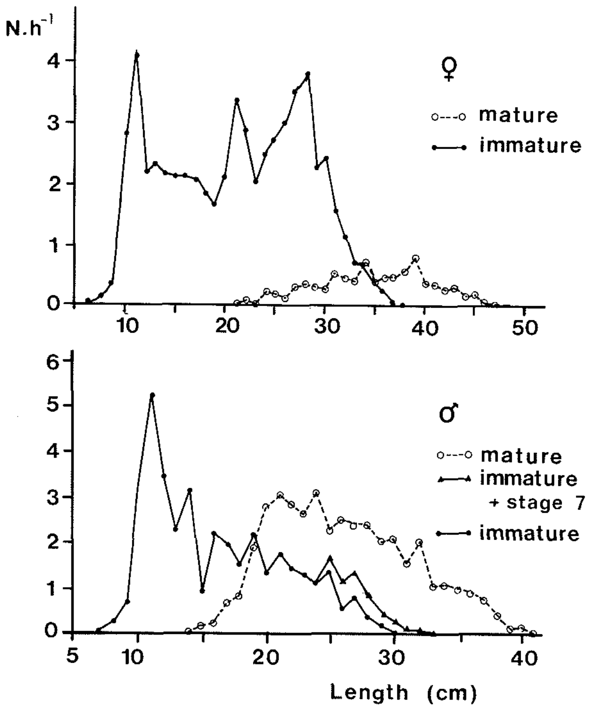

Figure 11. Length-frequency distribution of mature and immature plaice in the maturity surveys of 1985 and 1986. For male plaice the occurrence of stage 7 males is indicated.

was III-group. The percentage of mature fish declined from south (line A+B) to northeast (line E). Especially in line E both male and female plaice appeared to become sexually mature one year later than in the southern area.

For comparison, the maturity–age relationship derived from market sampling in the first quarter of 1985 and 1986 is given in Table 5. The average maturity percentage was calculated over the areas that included the lines of the survey. Because plaice abundance differed between these areas, the maturity percentage at age was weighted over the abundance in the lines of maturity survey by age group. Market-sampling results for males are not tabulated because the minimum landing size in use prevents the landing of plaice below 27 cm. In female plaice the market-sampling estimate was only slightly higher in age group III (9 % against 6 %) and IV (36 % and 29 %), but not in age groups II, V, and older. Comparison within market-sampling areas shows higher discrepancies, the market sampling data generally yielding higher estimates, especially in areas DWK+OG compared with the line A+B and area VB compared with line E. Areas DWB and DBO showed good correspondence with lines C+D.

For the partially mature age groups the maturity–length relations were studied by age group in the survey data and market-sampling data (Figs. 13a–c). In both male and female plaice the maturity percentage at a certain length generally increased with age. Consequently the L_{50} decreased with age.

Discussion

Annual maturity cycle

Gametogenesis in plaice extends over the major part of the reproductive cycle in accordance with the general pattern in teleosts (Scott, 1979). The cycle of vitellogenesis, gonad growth, and spawning of North Sea plaice is similar to that of plaice caught in the English Channel, although the timing is slightly different (LaHaye, 1972; Deniel, 1981; Houghton and Harding, 1976).

At the end of the growing season nearly all females have started to develop their gonads, as can be seen from the very small proportion of spent fish in November and December (Fig. 4). This indicates that in North

Table 3. Length (cm) at which 50 % of the plaice are mature (L_{50}) as estimated from the geometric mean regression of logit P = a+b length. Pooled data for 1985 and 1986.

	Maturity survey Male		Maturity survey Female			Market sampling Female	
	L_{50}	95 % CL	L_{50}	95 % CL		L_{50}	95 % CL
Line					Area		
A+B	19.8	18.9–20.7	34.0	32.5–35.5	DWK	30.1	29.5–30.7
C+D	21.6	20.0–22.2	32.8	31.9–33.7	OG	32.5	31.2–33.3
E	24.2	23.1–25.3	35.9	34.7–37.2	DBW	32.9	32.5–33.3
					DBO	33.2	32.4–34.0
					VB	34.6	33.7–35.5
					FLAM	33.8	32.9–34.7
Total	21.9	21.1–22.7	33.9	32.6–35.2	Total*	32.9	32.3–33.5

*Excluding FLAM.

ıreas that included ice abundance dif- ırity percentage at ıce in the lines of ɜt-sampling results he minimum land- g of plaice below sampling estimate p III (9 % against ıt in age groups II, arket-sampling ar- market sampling ates, especially in ıe line A+B and s DWB and DBO ıes C+D.

ıps the maturity– ɾoup in the survey . 13a–c). In both y percentage at a with age. Conse-

the major part of with the general cycle of vitelloge- : North Sea plaice he English Chan- ifferent (LaHaye, arding, 1976). nearly all females ;, as can be seen nt fish in Novem- ates that in North

. regression of logit

:et sampling Female
95 % CL
29.5–30.7
31.2–33.3
32.5–33.3
32.4–34.0
33.7–35.5
32.9–34.7
32.3–33.5

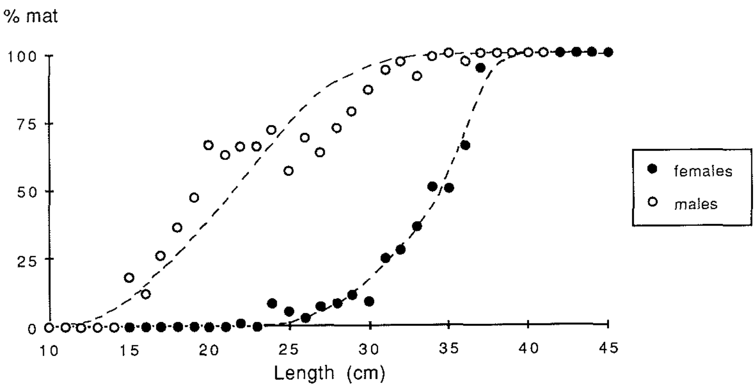

Figure 12. Percentage of mature fish in relation to length in male and female plaice in the maturity surveys of 1985 and 1986. The lines are drawn by eye.

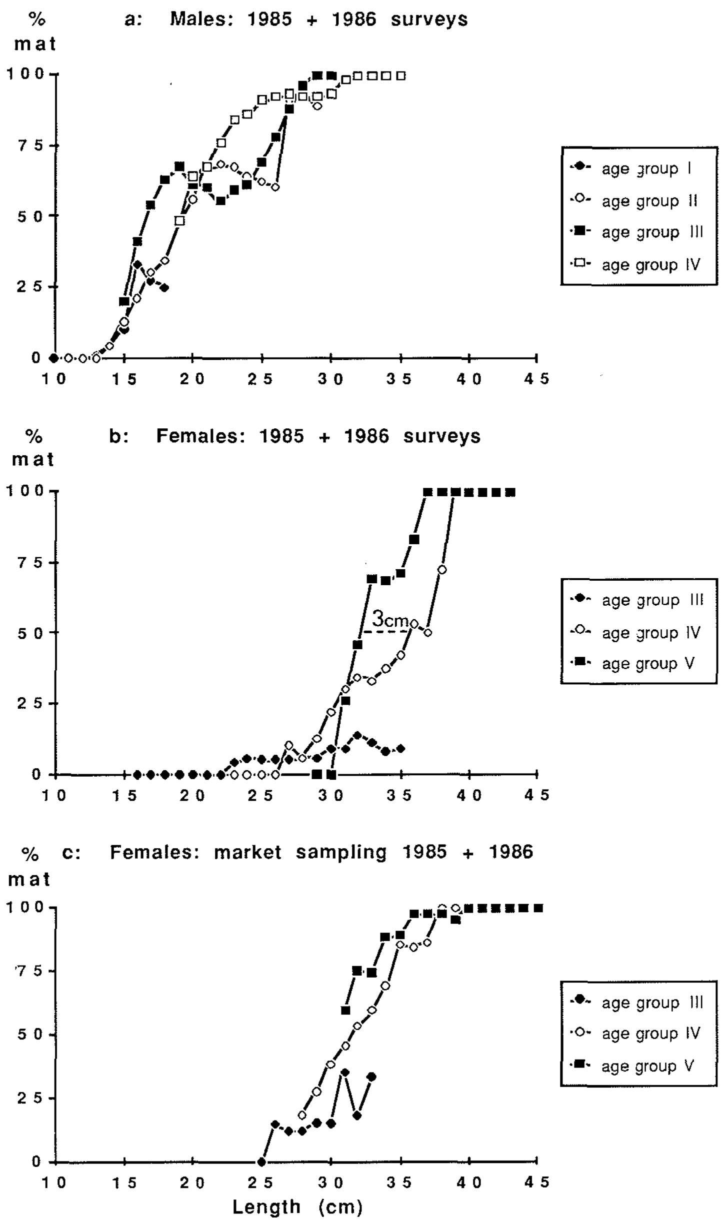

Figure 13. Maturity–length relation by age group for (a) male and (b) female plaice in the maturity surveys of 1985 and 1986 and (c) female plaice in the first quarter market samples of 1985 and 1986.

Table 4. Number of plaice caught per hour beam trawling (N/h), proportion of mature plaice by age group (mat), and mean length (L) of immature and mature plaice for line A+B, line C+D, and line E.

Males: 1985 survey

Line		Age group I	II	III	IV	V	VI
A+B	N/h	0.65	27.34	13.57	5.45	0.86	0.18
	mat	0.06	0.78	0.67	0.94	1.00	1.00
	mat*	0.06	0.76	0.57	0.94	1.00	1.00
	L_{imm}	12.40	21.27	24.74	24.50	–	–
	L_{mat}	16.50	21.66	27.05	31.57	33.33	36.08
C+D	N/h	0.85	40.50	14.00	12.00	4.87	1.28
	mat	0.00	0.57	0.57	0.91	1.00	1.00
	mat*	0.00	0.57	0.57	0.91	1.00	1.00
	L_{imm}	12.87	19.96	24.55	28.35	–	–
	L_{mat}	–	20.18	26.80	31.13	34.82	37.31
E	N/h	2.13	7.40	17.02	20.99	3.53	2.03
	mat	0.00	0.37	0.84	0.96	1.00	1.00
	mat*	0.00	0.37	0.42	0.79	1.00	1.00
	L_{imm}	11.61	18.64	26.50	29.30	–	–
	L_{mat}	–	19.05	26.50	29.91	34.33	36.60
Total	N/h	1.03	28.61	14.43	11.18	2.99	0.99
	mat	0.002	0.64	0.67	0.94	1.00	1.00
	mat*	0.02	0.63	0.53	0.87	1.00	1.00
	L_{imm}	12.22	20.15	24.85	27.92	–	–
	L_{mat}	16.50	20.84	26.81	30.75	34.58	36.85

Males: 1986 survey

Line		I	II	III	IV	V	VI
A+B	N/h	29.30	13.47	19.90	3.43	1.25	0.00
	mat	0.01	0.52	0.88	0.99	1.00	–
	mat*	0.01	0.50	0.83	0.99	1.00	–
	L_{imm}	10.47	20.90	25.57	28.50	–	–
	L_{mat}	15.66	21.70	26.17	31.51	32.20	–
C+D	N/h	79.81	66.08	26.56	9.90	8.87	3.37
	mat	0.01	0.34	0.78	0.94	1.00	1.00
	mat*	0.01	0.33	0.71	0.93	1.00	1.00
	L_{imm}	10.61	17.42	24.85	26.68	–	–
	L_{mat}	15.87	20.75	25.56	30.76	34.36	36.61
E**	N/h	11.67	6.60	27.58	8.08	12.17	2.25
	mat	0.00	0.29	0.53	0.95	1.00	1.00
	mat*	0.00	0.29	0.21	0.72	1.00	0.88
	L_{imm}	13.52	19.24	25.70	32.50	–	–
	L_{mat}	–	21.18	27.28	30.92	32.93	35.53
Total	N/h	45.98	33.14	24.10	6.95	6.48	1.80
	mat	0.007	0.37	0.76	0.95	1.00	1.00
	mat*	0.007	0.35	0.63	0.90	1.00	0.97
	L_{imm}	10.73	17.94	25.35	28.30	–	–
	L_{mat}	15.80	20.98	26.07	30.95	33.66	36.30

Cont'd

t), and mean length

VI

0.18
1.00
1.00
–
36.08
1.28
1.00
1.00
–
37.31
2.03
1.00
1.00
–
36.60
0.99
1.00
1.00
–
36.85
0.00
–
–
–
–
3.37
1.00
1.00
–
36.61
2.25
1.00
0.88
–
35.53
1.80
1.00
0.97
–
36.30

Cont'd

Females: 1985 survey

		Age group					
		I	II	III	IV	V	VI
Line							
A+B	N/h	0.36	7.90	12.93	2.10	1.58	0.65
	mat	0.00	0.004	0.05	0.32	0.98	1.00
	L_{imm}	11.75	21.81	26.57	32.38	32.50	–
	L_{mat}	–	22.48	27.89	33.79	39.61	41.24
C+D	N/h	0.97	30.53	17.56	10.05	2.27	3.20
	mat	0.00	0.02	0.07	0.46	0.94	1.00
	L_{imm}	12.54	20.95	26.29	31.73	32.20	–
	L_{mat}	–	23.36	27.60	33.59	36.65	39.26
E	N/h	2.03	8.15	25.06	19.59	1.94	1.03
	mat	0.00	0.00	0.02	0.07	0.64	1.00
	L_{imm}	11.61	18.68	28.69	32.01	34.05	–
	L_{mat}	–	–	29.92	32.84	39.41	38.40
Tot	N/h	0.94	17.00	17.21	8.78	2.13	1.74
	mat	0.00	0.02	0.05	0.27	0.90	1.00
	L_{imm}	11.94	20.89	27.09	31.95	33.38	–
	L_{mat}	–	23.43	28.00	33.53	37.97	38.96
Females: 1986 survey							
A+B	N/h	24.62	6.94	12.41	1.21	0.54	0.29
	mat	0.00	0.00	0.23	0.49	1.00	1.00
	L_{imm}	10.49	21.31	27.51	30.94	–	–
	L_{mat}	–	–	28.09	33.71	37.93	41.93
C+D	N/h	72.06	52.01	27.52	4.14	3.44	2.28
	mat	0.00	0.00	0.06	0.48	0.92	0.96
	L_{imm}	11.07	18.17	27.19	31.73	33.35	36.50
	L_{mat}	–	23.41	27.71	33.39	37.17	41.17
E	N/h	11.00	5.83	47.18	11.07	4.80	2.60
	mat	0.00	0.00	0.01	0.14	0.34	1.00
	L_{imm}	13.65	21.74	27.60	30.09	32.59	–
	L_{mat}	–	23.41	28.14	33.10	36.69	41.17
Tot	N/h	40.87	24.74	25.40	4.35	2.55	1.55
	mat	0.00	0.004	0.07	0.31	0.70	0.97
	L_{imm}	10.76	19.06	25.89	30.81	33.66	36.30
	L_{mat}	–	23.41	28.54	33.33	37.08	41.20

*Stage 7 males were considered to be immature.
**In 1986 the first four stations of line E were not fished.

Sea plaice almost all adult females will take part in spawning in each successive spawning season.

Duration of spawning

The duration of spawning was estimated using the pooled data over three years. This could lead to an overestimation if the timing of spawning and the level of sampling differed between the three years. Harding *et al.* (1978a) showed that the timing of spawning in plaice was fairly constant, so we can accept the estimated spawning times as a first approximation.

In this paper, females of maturity stage 3 were considered as taking part in spawning. During the final stage of maturation, the oocytes hydrate and greatly increase in volume. Egg diameter in plaice ranges between 1.66 and 2.17 mm, egg volume between 2.4 and 5.4 mm^3 (Russell, 1976). Given a relative fecundity of 220 eggs per g body weight (Rijnsdorp *et al.*, 1983), and assuming an equal specific weight of eggs and body of 1.0, the volume of eggs to be shed will be 0.86 cm^3 as compared with a gonad size of 0.17 cm^3 (gonadosomatic index = 17 %; Fig. 5), i.e., a fivefold increase. The mean gonadosomatic index of stage-4 females with a gonad completely filled with hydrated eggs is about equal to that of stage-2 females with ripening gonads. Thus at stage 4 only 20 % of the total volume of eggs can be accounted for; the other 80 % must already have been shed by stage-3 females, although it cannot be ruled out that a

Table 5. Proportion of mature fish at age derived from the market-sampling data in comparison with the average proportions as obtained from the survey. The market-sampling total was obtained by weighting over the female abundance by age group in the maturity survey.

	Age group I	II	III	IV	V	VI
Female plaice: market-sampling data 1985–1986						
Area						
DWK	–	0.00	0.26	0.86	1.00	1.00
OG	–	0.00	0.13	0.62	0.93	0.98
DBW	–	–	0.11	0.40	0.92	0.98
DBO	–	–	0.06	0.44	0.81	0.99
VB	–	–	0.00	0.19	0.68	1.00
FLAM	–	0.00	0.13	0.30	0.94	0.98
Total*	–	0.00	0.09	0.36	0.82	0.99
Female plaice: survey data 1985–1986						
Line						
A+B	0.00	0.00	0.14	0.41	0.99	1.00
C+D	0.00	0.01	0.07	0.47	0.93	0.98
E	0.00	0.00	0.02	0.11	0.49	1.00
Total	0.00	0.01	0.06	0.29	0.80	0.99
Male plaice: survey data 1985–1986						
Line						
A+B	0.03	0.65	0.78	0.97	1.00	1.00
C+D	0.01	0.46	0.68	0.93	1.00	1.00
E	0.00	0.33	0.69	0.96	1.00	1.00
Total	0.005	0.51	0.72	0.95	1.00	1.00

*Excluding FLAM.

small portion of the hyaline eggs were expelled during fishing or handling the fish on board. This also implies that female plaice will produce several batches of eggs during the spawning period.

The average male is in spawning condition for at least 11 weeks between the second half of December and mid-March, the average female for only five weeks between the end of January and the beginning of March. From this it can be inferred that an average male can fertilize eggs from early- as well as late-spawning females over nearly the complete spawning period.

Feeding condition

The incidence of feeding in plaice decreased in winter. Feeding incidence was already low by December when the water temperature was still relatively high and increased again in March when temperatures reached their seasonal low. In the laboratory also, food intake in plaice has been found to decrease in autumn under natural daylight (M. Fonds, pers. comm.). The decrease was therefore not related to the water temperature as suggested by Lande (1973). The difference in feeding condition between reproductive states suggests that spawning and feeding are mutually exclusive. Such mutual exclusion of feeding and spawning might stem from the limited metabolic scope of plaice that does not allow for both oxygen demands for spawning and related activities and feeding metabolism (Rijnsdorp and Ibelings, 1989).

Distribution

As juvenile plaice grow, they gradually disperse from the nursery areas in the estuaries and shallow coastal zone. The correspondence of the spatial distributions of male and female plaice (age groups I, II, and III), as observed in this study, corroborates the conclusion of Beverton and Holt (1957) that the offshore movement of plaice mainly results from a process of random diffusion. However, the difference in distribution between mature and immature females in age groups III and IV indicates that active behaviour must also be involved. Mature females of age groups III and IV were found to be distributed in a band 18–36 miles from the coast. Immature females of these age groups were, however, distributed over a wider area farther offshore. As the area of main egg production extends between 40 and

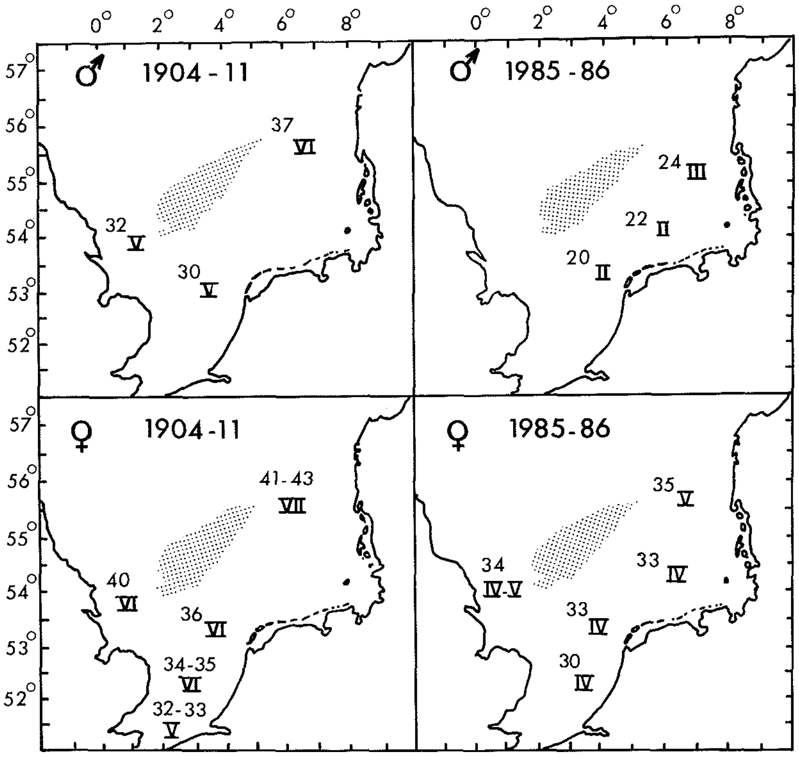

Figure 14. Comparison of the present length (L_{50}) and age (A_{50}) at 50 % maturity with those at the beginning of the century (from Wallace, 1914) in male and female plaice. The A_{50} in 1904–1911 have not been corrected for the different method of age determination (see footnote, page 50).

100 miles from the coast (Fig. 1), it can be inferred that the mature females of these age groups have to migrate to the actual spawning areas farther offshore to shed their eggs. Arnold *et al.* (in prep.) showed that in the spawning period especially, females of maturity stages 2 and 3 were caught in midwater on the spawning grounds. This suggests that the ripening females may migrate to the spawning areas to shed their eggs and that they avoid the spawning areas during the final stages of ripening just prior to spawning.

Length and age at first maturity

The maturity percentages of III- and IV-group females in the market-sample data were somewhat higher than in the survey data. The market samples were obtained from the beam-trawl fishery that mainly operates on offshore spawning concentrations of plaice (Fig. 3). The observed differences between survey and market-sampling results will be mainly due to the discarding of plaice smaller than the minimum landing size of 27 cm. In the survey nearly 100 % of the females of age groups I and II, 40 % of age group III, and 4 % of age group IV, were smaller than 27 cm. Because of differences in growth between areas these percentages will be lower in the south and higher in the northern areas.

From the distribution of mature and immature females in relation to the distance from the coast it can be deduced that sampling at the edges of the spawning areas will give lower values of the maturity percentage than in the centre. However, this will only slightly affect the maturity percentage in age groups II, III, and V, but will be more pronounced in age group IV, because this age group shows the biggest change in maturity percentage with distance from the coast. The error in the estimation of the maturity percentage from market samples due to differences in distribution of mature and immature fish will be relatively small if the market samples are taken over a wide area comprising the edges as well as the centre of the spawning grounds. The ripening females concentrated at the edge of the main spawning area will also migrate into the main spawning area to shed their eggs.

However, the maturity survey will not be free of bias. A survey in the first half of the spawning period, which does not take into account changes in the distribution during the spawning period and comprises only 49 stations, may not give an unbiased picture of the maturation of the plaice population in the southern North Sea. In particular, line A+B is assumed not to have given an unbiased sample of the Southern Bight spawning population, to judge from the low catches of female plaice (Table 4) in comparison with the amount of eggs produced in this area (Harding *et al.*, 1978a; Arnold *et al.*, in prep.). This can also be part of the explanation for the difference in maturity percentage in age group IV between line A+B and area DWK.

Furthermore, the survey did not encompass the estuarine area of the Waddensea, a major nursery area for 0- and 1-group plaice (Zijlstra, 1972). Although some juvenile plaice leave the estuaries in winter a considerable proportion will be distributed outside the survey area within the three-mile zone and the estuary (Fonds, 1978). Therefore the maturity percentage and also the mean length will be overestimated for 1-group plaice. From Demersal Young Fish Surveys in 1983, 1984, and 1985, the average length of 0-group plaice is estimated at 9.7 cm in September/October (unpublished RIVO data).

From the relatively small differences in the estimated maturity–length and maturity–age relations from the survey and market-sampling data it can be concluded that the market-sampling data will give a reliable estimate of the length and age at first maturity in female plaice, but for male plaice special surveys are needed to obtain representative data.

It is generally assumed that the onset of sexual maturity is determined by a constant threshold length (Roff, 1982), which can be affected by the growth rate of the fish (Alm, 1958; Nikolski, 1969). In this study the L_{50} decreased with age (Fig. 13a–c). Before we can conclude that the length at first maturity in plaice is affected by the growth rate we have to examine the possibility that differences in L_{50} between age groups were caused by the time interval between the onset of maturation and the spawning time. This could allow the younger and faster-growing plaice, after passing a threshold length for maturation out of season, to reach a greater length in the next spawning season than the older and slower-growing plaice.

This study showed that the juvenile–adult transition took place between May and September. In female plaice the difference in the L_{50} between age group IV and V was about 2–3 cm (Fig. 13b and c), whereas the difference in annual length increment between age group IV (increment = 5.4 cm) and age group V (increment = 4.8 cm) is only 0.6 cm (Table 4). Therefore differences in length increment after passing the assumed "maturity threshold" can only partly explain the decrease in L_{50} with age; we may therefore tentatively conclude that the maturity threshold length is not constant but decreases with the growth rate. Stears and Crandall (1984) interpreted the variability in length and age at first maturity as a reflection of the plasticity of the reproductive strategy of fish in response to environmental stress. Annual differences in growth can affect both the length and age at first maturity as shown by the differences in L_{50} in male plaice in 1985 and 1986 and the differences in maturity percentage of the year classes of 1982, 1983, and 1984 in both males and females.

In male plaice the maturity–length relation levelled off between 20 and 27 cm. This phenomenon can be partly explained by a year-class effect, the 1983 year class having a higher L_{50}. However, because it was also apparent in the maturity–length relations of individual year classes, it is possible that the male population consisted of two groups returning at different length thresholds.

Historic changes in the onset of sexual maturity

In Figure 14, the L_{50} and A_{50} obtained in the present study are compared with data from the beginning of this century as summarized by Wallace (1914). At the beginning of this century female plaice became mature as V- and VI-group at a length of 32–35 cm in the Southern Bight; and as VI- and VII-group at 40–42 cm in the region of the Dogger. Male plaice became mature as V- and VI-group at a length of 32–37 cm in the Dogger region. The onset of sexual maturity in males in the Southern Bight was unclear. However, some males were already mature as II-group and at a length of 18 cm.[1] Simpson (1959) estimated that female plaice of the 1943 and 1944 year classes became mature as IV- and V-group in the Southern Bight.

Compared with these historic data it is obvious that North Sea plaice now reach maturity about two to three years younger and also at a smaller size than at the beginning of this century. However, Rijnsdorp and van Leeuwen (1985) showed that the L_{50} of female plaice could vary by 2–3 cm between successive years, so the observed differences in L_{50} in the Southern Bight may not be real. It remains an intriguing question as to whether the change in length at first maturity is in any way related to the recent extension of the area inhabited by plaice in the northeastern North Sea (Bannister, 1978; Harding *et al.*, 1978a; Cushing, 1982) and whether the observed change in L_{50} is a reflection of phenotypic plasticity in response to changes in the environmental conditions (Stearns and Crandall, 1984) or reflects changes in the genetic composition of the plaice population. A future study of the variability in the onset of sexual maturity in relation to environmental conditions during the juvenile phase may give an indication of whether the phenotypic plasticity is sufficiently large to take account of the changes in length and age at first maturity as observed in North Sea plaice.

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[1]Our method of age determination, which assigns the birthday to 1 January, differs from that of Wallace, who allowed the birthday to vary between January and April depending on the formation of a new growth zone in the otolith. The A_{50} as determined by Wallace's method will therefore be on average 0.5 years too low compared with our method (see Appendix Table VI in Wallace, 1914). The data of Wallace given in Figure 14 have not been converted.

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