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Changes in fecundity of female North Sea plaice (*Pleuronectes platessa* L.) between three periods since 1900

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Variations in size-specific fecundity were studied over a period of seven years between 1977 and 1985 and fecundity–body length relationships were compared between three periods: 1900–1910, 1947–1949, and 1977–1985. Significant differences were observed between years and areas. The average fecundity for a 40-cm female was 12% less in the German Bight than in the southern North Sea, but the annual variability was higher; 15% and 7% respectively. Length-specific fecundity showed a significant positive correlation with the pre-spawning condition factor, but not with the somatic growth in the preceding year. Fecundity appears to have changed since the early 1900s and 1947–1949. In 30-cm females the present fecundity was about 30–100% higher compared to the first two periods, depending on the area. Fecundity of larger females (50 cm) was similar to that in 1900, but was 30–60% higher than in 1947–1949. The substantial reduction in fecundity in the period 1947–1949 contrasted with the much smaller change in ovary weight, suggesting not a change in the energy allocation over reproduction and somatic growth, but in the energy allocation over a small number of large eggs versus a large number of small eggs. Both length- and weight-specific fecundity decreased with age. The effect was largest in young fish. Weight-specific fecundity decreased by 3.9% when age increased from 4 to 5 years, by 1.7% when age increased from 10 to 11 years, and by 0.8% when age increased from 20 to 21 years. Significant differences in length-specific ovary weight were also observed between years and geographical areas, but the variability between years was less than in fecundity. Ovary growth was not synchronous between age groups, the younger age groups lagging behind by about one month. Egg weight calculated from ovary weight and fecundity was lower than egg weight measured from ripe running females, suggesting that ovary growth continues after the start of spawning in an individual plaice. The differences in fecundity and ovary weight between the three time periods are discussed in relation to the question whether these are a phenotypic response due to changes in the conditions for growth or to a change in the genetical composition of the population.

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Introduction

Fecundity is defined as the number of eggs spawned by an individual female, and can be estimated by counting the number of developing oocytes in the ovary. For comparative purposes, fecundity is often reported as relative fecundity, defined as the number of eggs per gram body weight (Bagenal, 1973). In applying relative fecundity it is assumed that fecundity is proportional to body weight, which is not always the case. In the present paper, therefore, fecundity is given for females of a standard length, weight, or age in order to compare fecundity between areas and years. This will be referred to as length-, weight-, or age-specific fecundity.

Fecundity of female plaice has been studied by Fulton (1891), Reibisch (1899), Franz (1910a,b), Simpson (1951), Kändler and Pirwitz (1957), Kändler (1959), Bagenal (1966), Rijnsdorp *et al.* (1983), and Horwood *et al.* (1986). Bagenal (1966) showed a geographical pattern in length-specific fecundity increasing from a relatively low value in populations in the centre of the species distribution area to higher values in populations at the edge. He suggested that these differences "were related to the amount of food available, which in turn is related to population density". Rijnsdorp *et al.* (1983) and Horwood *et al.* (1986) reported higher fecundity values in the late 1970s and early 1980s in the North Sea than Simpson (1951) reported for the late 1940s and Reibisch (1899) and Franz (1910a,b) for the beginning of the century.

The reported change in fecundity of North Sea plaice since the late 1940s was questioned by Horwood *et al.* (1986), because of doubts about the comparability of the methods used. However, they concluded that the reported increase in fecundity must reflect a real change because

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ovary weights showed a corresponding increase. Although a comparison of ovary weights between the two periods offers the possibility of an independent test, such a comparison should take account of the fast growth in ovary weight in the months prior to spawning (Rijnsdorp, 1990). Since Simpson (1951) collected ovary samples between October and February, and Horwood *et al.* (1986) between December and February, the lower ovary weights in the 1940s might be related to the earlier sampling dates.

Changes in fecundity and ovary weight do not have to be proportional or to occur simultaneously, since concurrent changes in egg weight may occur. The question whether the fecundity or, more generally, the reproductive investment of plaice has increased therefore remains unanswered. This question is an important one, because it bears directly on two fundamental problems: (1) Is the total number of eggs produced annually by a population proportional to the biomass of female fish (Rothschild, 1986)? (2) Does a continued high level of fishing mortality cause changes in the genetic composition of the population with respect to reproductive parameters (Horn and Rubenstein, 1978; Allendorf *et al.*, 1986; Nelson and Soulé, 1986)?

Plaice has been exploited in the North Sea since the late 19th century at a level of fishing mortality that exceeds the natural mortality and, as a consequence, the age structure of the adult population must have changed towards younger age groups compared to the unexploited population. Certain biological parameters have been shown to have changed correspondingly: thus, length-at-age of juvenile plaice has increased while that of adult fish appears to have decreased (Bannister, 1978). And present maturity occurs at a younger age and a smaller length than at the beginning of this century (Rijnsdorp, 1989).

This paper analyses the changes in fecundity of female North Sea plaice between three periods: 1900–1910, 1947–1949, and 1977–1985, based on the literature data and new data. Changes in ovary weight between 1947–1949 and 1982–1988 are analysed. Egg weight, which links fecundity and ovary weight, is compared from estimates obtained both indirectly from ovary weight and fecundity and directly from running females.

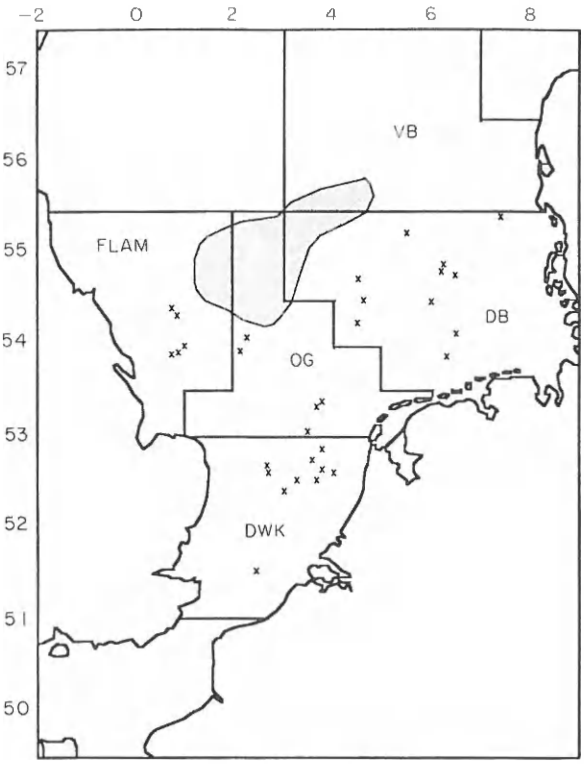

Figure 1. Sampling positions for fecundity (×) in 1982–1985 and the geographical area distinguished in the present study. The shaded area shows the Doggerbank.

Materials and methods

Notation

In this paper the following notation is used: A – age with 1 January as birthdate; DEW – dry egg weight (mg); %DEW – dry egg weight (%); EW – wet egg weight (mg); E – fecundity in thousands of eggs; G – ovary weight (g); RG – relative (length-specific) ovary weight = $100 \times G \times L^{-3}$; L – length in cm; W_t – total weight (g) including viscera and ovaries; W_g – gutted weight (g) excluding viscera; SW – somatic weight (g) = $W_g - G$; C – condition factor = $1000 \times W_t \times L^{-3}$; SC – somatic condition = $100 \times SW \times L^{-3}$; %dry – percentage dry weight.

Gutted weight in plaice is related to total weight according to $W_t = 1.07 \times W_g$ (Rijnsdorp and Ibelings, 1989).

Ovary samples

Ovary samples were taken from market samples of the landings of commercial beam trawlers at fish auctions as described in Rijnsdorp (1989). On board, the fish are stored on ice for less than one week before being sold, but some of the samples were deepfrozen at −20°C for some weeks before analysis. Market samples were taken randomly from various geographical areas (Fig. 1) and consists of four length strata. From each length stratum, ripening females, which had not yet started to spawn (maturity stage 2: Rijnsdorp, 1989), were randomly selected and total length (mm), gutted weight (g), and ovary weight (g) were recorded. Otoliths were collected for age-determination with 1 January assigned as the birthdate. Table 1 summarizes the sampling for fecundity and ovary weight and includes the new data as well as the data taken from the literature. The results for each fish sampled from 1982 to 1985 are tabulated in the Appendix.

Table 1. Number of ripening females (maturity stage 2) sampled for fecundity and ovary weight. Data sources: (1) Reibisch (1899), Franz (1910a,b); (2) Simpson (1951); (3) Horwood *et al.* (1986); (4) this study.

	Area code					
	DWK	OG	DB	FLAM	Total	Source
Fecundity						
1900/1910	–	–	108	–	108	1
1947/1949	221	–	–	33	254	2
1976/1977	29	37	65	–	131	3
1978/1979	46	64	37	–	147	3
1979/1980	68	49	137	88	342	3
1981/1982	31	24	26	21	102	4
1982/1983	17	33	65	38	153	4
1983/1984	45	8	34	42	129	4
1984/1985	38	14	52	0	104	4
Ovary weight (first quarter only)						
1947/1949	47	–	–	33	80	2
1982	44	92	104	82	322	4
1983	80	116	154	92	442	4
1984	111	98	171	14	394	4
1985	86	55	154	40	335	4
1986	88	49	174	49	360	4
1987	10	42	48	2	102	4
1988	27	28	63	29	147	4

Fecundity estimates

Female plaice in maturity stage 2 were selected randomly from all size classes in the market samples taken between December and February. Sampling information is summarized in Table 2 and the sampling positions are shown in Figure 1. The spatial distribution of the samples covers the main spawning areas of plaice in the North Sea except the southward extension in the eastern English Channel (Harding *et al.*, 1978; Heessen and Rijnsdorp, 1989; Rijnsdorp, 1989).

Ovary samples are stored in methanol (50–70%) for a period of between 2 and 12 weeks. The oocytes were separated from the connective tissue by washing in coarse- and small-meshed sieves under a gentle flow of water. The developing oocytes were finally cleaned of small fragments of connective tissue and small primary oocytes by decanting. This method is a further development of the one described in Reibisch (1899) and Leeuwen (1972) and serves as a suitable alternative for the traditional technique using Gilson's fluid (Simpson, 1951), which produces substantial amounts of toxic mercury waste products. Finally, the number of oocytes was counted using a wet counting device.

Fecundity was estimated by counting the number of oocytes from a subsample of the ovary tissue of known weight and raising this number to the total weight of the ovary. Weights were determined to the nearest 0.01 g. Ovary subsamples were taken from the middle region and had a weight of 1–4 g (about 2–10% of the ovary weight). Pilot counts showed that the egg densities of the two ovaries of an individual female did not differ significantly, neither did the egg densities of the various sections of one ovary. The variance of repeated estimates of relative egg density between ovaries was 9% ($n = 186$) and of repeated estimates of the various sections from the same ovary 5% ($n = 320$). The precision of the fecundity estimate of an individual female using two subsamples was estimated at $1.96 \times 9\%/\sqrt{2} = 12\%$, indicating that 95% of the measurements were within $\pm 12\%$ of the true egg density. Two ovary subsamples were taken per female in 1982, 1983, and 1984 and one subsample in 1985.

The number of oocytes was determined using a wet counting device (Philips PW4232) according to Parrish *et al.* (1960). The accuracy of this equipment was regularly tested by comparing the results with eye counts of test samples of 500–1000 oocytes. In a pilot experiment the deviation between the wet counting device and the eye count was observed to be $+0.5\%$ with a standard deviation of 2% ($n = 10$).

Egg dry weight

Sampling of ripe eggs for determining dry weights of eggs was carried out in area DWK in the second half of

Table 2. Dates and positions of the fecundity samples.

Sample no.	Date	Position	Number	Area code
Spawning season: 1981/1982				
82–1	21 December	5300 N 330 E	14	DWK
82–2	21 December	5130 N 230 E	5	DWK
82–3	7 January	5250 N 340 E	12	DWK
82–4	11 January	5400 N 200 E	11	OG
82–5	11 January	5445 N 630 E	8	DB
82–6	18 January	5403 N 215 E	13	OG
82–7	25 January	5420 N 100 E	10	FLAM
82–8	1 February	5445 N 530 E	12	DB
82–9	8 February	5425 N 050 E	11	FLAM
82–10	22 February	5410 N 630 E	6	DB
Spawning season: 1982/1983				
83–1	13 December	5415 N 415 E	20	DB
83–2	13 December	5320 N 230 E	33	OG
83–3	10 January	5355 N 050 E	38	FLAM
83–4	14 January	5430 N 420 E	20	DB
83–5	14 January	5450 N 610 E	25	DB
83–6	21 January	5245 N 345 E	17	DWK
Spawning season: 1983/1984				
84–1	9 December	5240 N 240 E	19	DWK
84–2	16 December	5240 N 240 E	20	DWK
84–3	22 December	5355 N 055 E	41	FLAM
84–4	20 January	5430 N 600 E	25	DB
84–5	13 February	5320 N 350 E	8	OG
84–6	27 February	5355 N 620 E	9	DB
84–7	9 March	5240 N 353 E	6	DWK
84–8	12 March	5400 N 100 E	1	FLAM
Spawning season: 1984/1985				
85–1	14 December	5230 N 355 E	4	DWK
85–2	14 December	5530 N 730 E	25	DB
85–3	18 January	5240 N 400 E	15	DWK
85–4	18 January	5225 N 300 E	14	DWK
85–5	20 January	5455 N 610 E	13	DB
85–6	25 January	5320 N 350 E	14	OG
85–7	28 January	5515 N 530 E	14	DB
85–8	8 February	5230 N 320 E	5	DWK

January 1990 on board a commercial beam trawl vessel. Ripe eggs were stripped from running females (maturity stages 3 to 6) directly on capture. Length, weight, age, ovary weight after the ripe eggs had been stripped, and percentage dry weight of the ovary were determined for each fish. Eggs were stored in 4% formaldehyde in sea water and the hydrated eggs separated from the non-hydrated eggs by sieving over a plankton gauge with a mesh size of 240 µm. After storing for 1–4 weeks the samples were washed in demineralized water; a subsample of about 400 eggs was counted and dried at 60°C and the dry weight determined to the nearest 0.1 mg. Replicates of weight estimates indicated that with 95% probability the measured weight per egg deviated by less than 0.006 mg of the real value.

Table 3a. ANCOVA results of the fecundity data 1982–1985 according to the GLM model: $\log_e E = \alpha + \alpha_{year} + \alpha_{area} + \beta.\log_e L + \gamma \log_e SC + \delta.\log_e A$; with E = fecundity; L = length; A = age; SC = somatic condition.

	SS	d.f.	MS	F	P
logA[1]	0.010	1	0.010	0.22	n.s.
logSC[1]	16.26	1	16.26	359.0	<0.01
logL[1]	29.84	1	29.84	658.8	<0.01
Area[1]	0.693	3	0.231	5.10	<0.01
Year[1]	0.870	3	0.290	6.40	<0.01
Error	21.56	476	0.045		
Total	170.2	485			

[1]After adjusting for main effects.

Table 3b. Parameter estimates of the significant parameters of the GLM model of Table 3a: $\log_e E = \alpha + \alpha_{year} + \alpha_{area} + \beta.\log_e L + \gamma \log_e SC + \delta.\log_e A$; with E = fecundity; L = length; A = age; SC = somatic condition.

Parameter estimate	
α	−6.872
β	3.220
γ	1.882
α1982	0.000
α1983	−0.0172
α1984	−0.0738
α1985	−0.1167
αDWK	0.000
αOG	−0.0954
αDB	−0.0407
αFLAM	−0.1041

Statistical methods

Analyses of covariance (ANCOVA) and backwards step-wise regression analyses were carried out with the NAG statistical package GLIM (Baker and Nelder, 1978). The basic GLM (McCullagh and Nelder, 1983) model to study the dependent variable (Y: fecundity, ovary weight), in relation to covariables (X: length, weight, somatic condition), and factors (F: age, geographical area, spawning season) was:

$$\log_e Y = \alpha + \beta \log_e X_1 + \gamma \log_e X_2 + F_i + F_j + \varepsilon$$

The assumption of the ANCOVA that the error term (ε) is normally distributed was tested by making a probability plot of the residuals. Parameter values were estimated: α for intercept, β and γ for the slopes of the main covariables, and α_i, α_j for the factorial effects of F_i and F_j. The multiplicative effect of a factor F was calculated as the antilog of the parameter estimate $\exp(\alpha_i)$.

Results

Fecundity

New data 1982–1985

The results of the ANCOVA for fecundity length relation with covariables, age and somatic condition, and factors, area and year (i.e. spawning season), are given in Table 3a. Variance in fecundity was explained by length of the fish (18%) and somatic condition (10%). The other factors, though statistically significant, contributed much less (area – 0.4% and year – 0.5%). Age was not significant. A substantial part of the variance in fecundity (59%) could not be ascribed to a single factor. A test of the interaction of the significant covariables, length, and somatic condition, with area and year showed that the secondary and tertiary interactions were all non-significant, just as the interaction between the factors geographic area and spawning season.

The parameter estimates for the covariables length and somatic condition and for the factors area and year are given in Table 3b. The slope of the fecundity–length relation ($\beta = 3.22$) is slightly but significantly larger than 3 ($p < 0.01$). The somatic condition of the females prior to spawning positively influenced fecundity ($\gamma = 1.882$), indicating that a 10% increase in somatic condition results in an approximately 10% increase in fecundity. The multiplicative effect of area and year, calculated as the antilog of the parameter estimates, indicated that fecundity decreased between area DWK in the south and the more northern areas OG (–9%), DB (–4%), and FLAM (–10%) and also by 11% between 1982 and 1985.

Distribution of the error term showed a slight skewness and kurtosis with parameters of –0.336 and 0.554, respectively ($n = 486$). Outliers were checked but there was no reason to suspect these observations; all were subsequently included in the analysis.

The relationship between fecundity and body weight was studied and the result of the ANCOVA is given in Table 4a. Only the primary factors are included since secondary and tertiary interaction terms were not statistically significant. The slope of the fecundity–weight relationship ($\beta = 1.241$) is significantly larger than one ($p < 0.01$). Overall, the results of this ANOVA are very similar to those of the fecundity–length relationship, except that the covariable age is also significant. The parameter estimates in Table 4b indicate that weight-specific fecundity decreases with increasing age. An increase in age from 4 to 5 years old reduces fecundity by 3.9%, from 10 to 11 years old by 1.7%, and from 20 to 21 years old by 0.8%. The age effect is thus particularly pronounced in the younger age groups.

Table 4a. ANCOVA results of the fecundity data 1982–1985 according to the GLM model: $\log_e E = \alpha + \alpha_{year} + \alpha_{area} + \beta \log_e W + \delta \log_e A$; with E = fecundity; W = weight; A = age.

	SS	d.f.	MS	F	P
logA[1]	0.728	1	0.728	14.6	<0.01
logW[1]	52.43	1	52.43	1054	<0.01
Area[1]	0.613	3	0.204	4.11	<0.01
Year[1]	1.086	3	0.362	7.28	<0.01
Error	23.71	477	0.0497		
Total	170.2	485			

[1] After adjusting for main effects.

Table 4b. Parameter estimates of the significant parameters of the GLM model of Table 4a: $\log_e E = \alpha + \alpha_{year} + \alpha_{area} + \beta \log_e W + \delta \log_e A$; with E = fecundity; W = weight; A = age.

Parameter estimates	
α	–2.658
β	1.241
δ	–0.172
α1982	0.000
α1983	–0.0523
α1984	–0.1114
α1985	–0.1314
αDWK	0.000
αOG	–0.0820
αDB	–0.0510
αFLAM	–0.1028

Data 1977–1985

A similar ANCOVA to that of Table 3 applied to the data of Horwood *et al.* (1986) for the areas DWK, OG, DB, and FLAM is shown in Table 5, except that the covariable somatic condition could not be included because the information required is not available for the period 1977–1980.

ANCOVA of the combined data set of 1106 female plaice showed again the significant effect of length, year, and area, but in this case also age contributed significantly to the variance in fecundity (Table 5). A study of the secondary interaction terms showed a significant interaction of Area.Year, logL.Area, and of logA.Area. None of the tertiary interaction terms was found to be significant. The parameter estimates of the model including all significant terms indicate that the slope of the fecundity–length relationship is steeper in area FLAM (Table 5). The estimated age effect was lowest in area DB and highest in area FLAM. In area DB an increase in age from 4 to 5 years old reduces fecundity by 1.5%, whereas in area FLAM this was 9.0%.

Table 5a. ANCOVA results of the fecundity data 1977–1985 according to the GLM model: $\log_e E = \alpha + \alpha_{year} + \alpha_{area} + \beta.\log_e L + \delta \log_e A$; with E = fecundity; L = length; A = age.

	SS	d.f.	MS	F	P
logA[1]	5.21	1	5.21	57.2	<0.01
logL[1]	112.3	1	112.3	1233.0	<0.01
Area[1]	2.59	3	0.863	9.48	<0.01
Year[1]	7.52	6	1.254	13.77	<0.01
Error	99.64	1094	0.0911		
Area.Year	2.209	15	0.147	1.70	<0.05
logL.Area	1.671	3	0.557	6.43	<0.01
logL.Year	0.265	6	0.044	0.51	n.s.
logA.Area	0.941	3	0.314	3.62	<0.05
logA.Year	0.583	6	0.097	1.12	n.s.
Error	91.84	1061	0.0866		
Total	374.3	1105			

[1] After adjusting for main effects.

Table 5b. Parameter estimates of the ANCOVA of Table 5a according to the model: $\log_e E = \alpha + \alpha_{year} + \alpha_{area} + \beta.\log_e L + \delta \log_e A$; with E = fecundity; L = length; A = age; $\alpha_{area.year} = \alpha + \alpha_{year} + \alpha_{area}$.

	DWK	OG	DB	FLAM
β	3.593	3.343	3.016	4.425
γ	−0.313	−0.267	−0.070	−0.425
$\alpha_{area.year}$				
1977	−7.650	−6.813	−6.062	–
1979	−7.705	−6.921	−6.308	–
1980	−7.550	−6.834	−5.904	−10.496
1982	−7.534	−6.783	−5.916	−10.494
1983	−7.699	−6.771	−6.054	−10.653
1984	−7.669	−7.049	−6.199	−10.707
1985	−7.679	−7.081	−6.118	–

The fecundities for three size classes (30, 40, and 50 cm) and four geographical areas (DWK, OG, DB, FLAM), predicted from the parameter estimates in Table 5, fluctuated in concert with relatively low values in 1979, 1984, and 1985 and relatively high values in 1980 and 1982 in all areas (Fig. 2). No differences appear in the level of or the variability in fecundity between the data sets for 1977–1980 (Horwood *et al.*, 1986) and for 1982–1985 (present study). Table 6 shows that the between-year variability, expressed as the coefficient of variation (C.V.) of predicted fecundity, appears to be lowest in area DWK (C.V. = 7%) and highest in area DB (C.V. = 14%), the other areas being intermediate (FLAM: C.V. = 11%; OG: C.V. = 12%).

Comparison of 1947–1949 data with data for 1977–1985
Simpson (1951) studied fecundity in area DWK in 1947/1948 and 1948/1949 and in area FLAM in 1948/1949. The log–log scatter plots of fecundity against fish length are shown in Figures 3(a–d). ANCOVA of the data for both areas separately showed that the slopes of the regressions were significantly different between both periods in area DWK, but not in area FLAM (Table 7). Comparison of the predicted fecundities for three size classes from the parameter estimates of Table 7 showed that fecundity increased by 26% in area FLAM. In area DWK the increase in fecundity was between 62 and 103%, depending on fish size (Table 8).

Comparison of 1900–1910 data with data for 1977–1985
From the fecundity data collected around 1900 by Reibisch (1899) and Franz (1910a,b), plaice with hyaline eggs were excluded from the analysis, leaving a total number of fecundity estimates of 108 for these years. The samples originated mainly from the German Bight and were therefore compared with the data for this area (DB) from the period 1977–1985. The log–log scatter plots of fecundity against fish length are shown in Figure 4. The regression slopes differed significantly between both periods (Table 7). At a fish length of 50 cm, present fecundity was 4% higher than in 1900–1910, but the difference increased to 35% at 40 cm and 90% at 30 cm (Table 8). Comparison of the 1900–1910 data with the individual years between 1977 and 1985 showed significant differences between slopes for all years except 1979.

Ovary weight

New data for 1982–1988
The relationships between ovary weight and the covariables length and somatic condition, and the factors age, spawning season, and geographical area, were studied in first-quarter samples of pre-spawning females (maturity

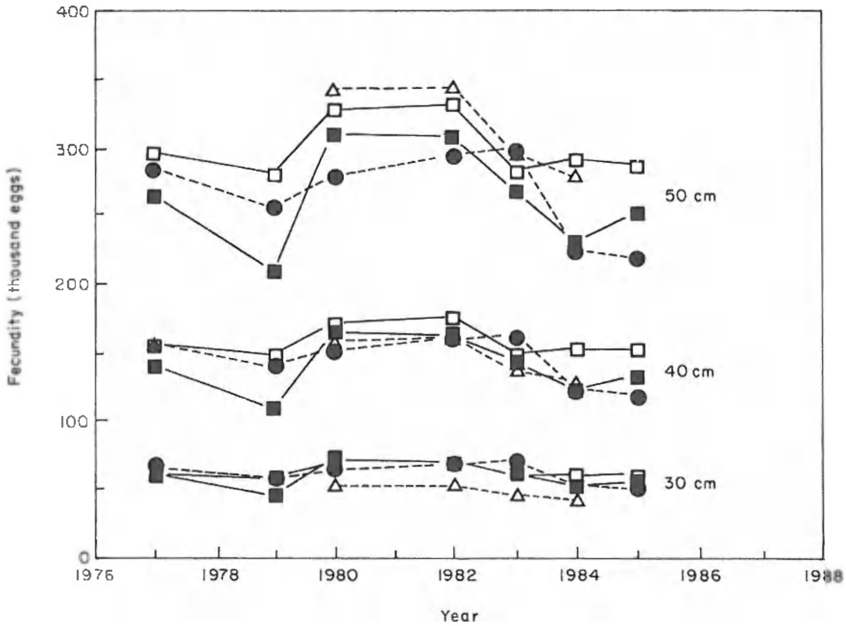

Figure 2. Annual variability in predicted fecundities for three size classes (30, 40, and 50 cm) by geographical area from parameter estimates in Table 5. —□— = DWK, —●— = OG, —■— = DB. —△— = FLAM.

Table 6. Mean, standard deviation, and coefficient of variation of predicted fecundities according to the parameter estimates of Table 5 for three size classes and age groups of plaice.

	30 cm age 4		40 cm age 6		50 cm age 10		
	Mean	s.d.	Mean	s.d.	Mean	s.d.	C.V.
Area							
DWK	63	4.5	157	11.2	298	21.4	7.3
OG	61	7.5	144	17.6	264	32.4	12.3
DB	60	8.5	138	19.8	259	37.4	14.3
FLAM	48	5.2	145	15.7	310	33.9	10.8

stage 2). Table 9 shows that length was the main covariable explaining 75% of the variance in ovary weight. Somatic condition explained 0.3%, area – 1.4% and year – 0.2%. Age was not found to be significant. The analysis was complicated because there was a significant heterogeneity in the slopes of the regressions of ovary weight with length and somatic condition between areas and between years. However, this heterogeneity explained only 1% of the variance in ovary weight. The significant interaction logL.Area indicates that the slopes of ovary weight on length were slightly steeper in the more northern areas.

The annual variability in ovary weight was studied by comparing the predicted ovary weight of female plaice of 30, 40, and 50 cm in area DWK and DB (Fig. 5). The C.V. was generally below 10% (Table 10). The variability in ovary weight was less in area DWK and increased in more northern areas. For the size class of 40 cm, which is close to the average length in the sample, the C.V. was 2% in DWK and 6% in areas OG, DB, and FLAM. These values are substantially lower than those for fecundity.

Comparison of 1947–1949 data with data for 1982–1988

Simpson (1951) reported ovary weights of ripening females from areas DWK and FLAM between October and February in 1947–1949. Since ovary weight increases rapidly in the month prior to spawning a comparison was made between ovary weights for January and February only. Figure 6(a and b) shows the log–log scatter plots of the ovary weight against fish length for area DWK (January) and area FLAM (January–February), respectively. ANCOVA of the data for both areas separately showed that about 70% of the variance in ovary weight was explained by $\log_e L$ (Table 11). The factor Year,

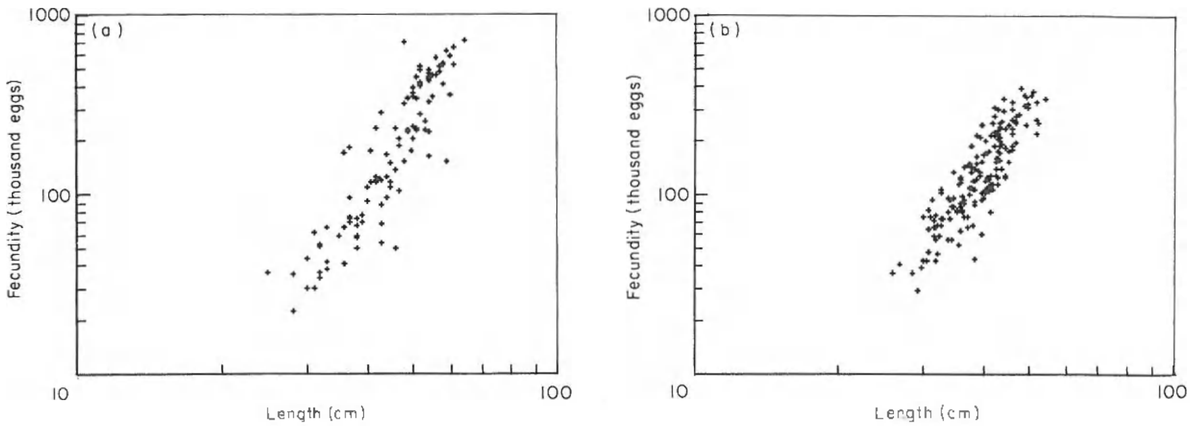

Figure 4. Scatter plots of fecundity (thousand eggs) against fish size (cm) for area DB in the periods 1900–1910(a) and 1982–1985(b). Data from Reibisch (1899), Franz (1910a,b), and the present study.

Table 8. Predicted fecundity in thousand eggs for three size classes of plaice and three time periods according to the parameter estimates of Table 7. The percentages at the bottom of the table indicate the percentage change from the historic period to the present period.

	30 cm		40 cm		50 cm	
Period: 1900–1910						
DB	33.6		104.8		252.8	
Period: 1947–1949						
DWK	35.9		89.3		181.1	
FLAM	40.9		108.9		232.5	
Period: 1977–1985						
DB	63.8	+90%	141.4	+35%	261.9	+4%
DWK	72.8	+103%	159.8	+79%	294.0	+62%
FLAM	51.7	+26%	137.6	+26%	293.8	+26%

This decrease in egg weight coincides with a decrease in size-specific ovary weight and a decrease in percentage ovary dry weight as the successive batches of eggs are released (Table 15). To estimate the average weight of the total number of eggs spawned during the spawning period, this decrease in egg weight during the spawning period of individual females must therefore be accounted for. A weighted average egg dry weight (DEW) can be calculated from the observed stage-specific egg weight (DEW_i) if the proportion of eggs (P_i) spawned at the various maturity stages i is available: $DEW = \Sigma P_i \times DEW_i$. Estimates of maturity stage duration (D_i), available from Rijnsdorp (1989), can be taken as a crude approximation of the number of eggs spawned at each stage, assuming constant batch size and inter-batch spawning interval. The result of this calculation is given in Table 14 and yields an estimate of the average egg dry weight of 0.264 mg.

No clear relationship was evident between egg weight and age of female plaice, although the samples were confined to age-group 5 and older (Table 16). Figure 10 shows the relationship between egg size (ES) and dry egg weight (DEW). The predictive regression is: $ES = 1.288 + 2.151$ DEW ($r = 0.801$, $n = 42$, $p < 0.01$).

Discussion

Methodology

In comparing the results of various fecundity studies carried out at different times and by different methods, care has to be taken that the methods are comparable (Schmitt and Skud, 1978). In the various fecundity studies of plaice which have been carried out over the last century, different methods have been applied to: (a) isolate the oocytes from the ovaries; and (b) subsample and count the

Table 9a. ANCOVA results of ovary weights in the period 1982–1988 according to the GLM model: $\log_e G = \alpha_{area,year} + (\beta + \beta_{year} + \beta_{area}) \log_e L + \gamma_{area} \log_e SC + \delta \log_e A + Area + Year$; with G = ovary weight; L = length; A = age; SC = somatic condition. Data FLAM in 1987 excluded.

	SS	d.f.	MS	F	P
logA[1]	0.149	1	0.149	1.81	n.s.
logSC[1]	2.570	1	2.570	31.20	<0.01
logL[1]	570.8	1	570.8	6930	<0.01
Area[1]	10.29	3	3.43	41.64	<0.01
Year[1]	1.793	6	0.299	3.63	<0.01
Error	171.9	2087	0.0824		
Area.Year	2.789	17	0.164	2.05	<0.01
logL.Area	0.799	3	0.266	3.32	<0.01
logL.Year	1.694	6	0.282	3.52	<0.01
logSC.Area	1.062	3	0.354	4.41	<0.01
logSC.Year	0.959	6	0.160	1.99	n.s.
Error	164.7	2053	0.0802		
Total	760.5	2099			

[1]After adjusting for main effects.

Table 9b. Parameter estimates according to the GLM model of Table 9a with all significant interaction terms: $\log_e G = \alpha_{area,year} + (\beta + \beta_{year} + \beta_{area}) \log_e L + \gamma_{area} \log_e SC + \delta \log_e A + Area + Year$; with G = ovary weight; L = length; A = age; SC = somatic condition. Data FLAM in 1987 excluded.

$\alpha_{area,year}$ Area:	DWK	OG	DB	FLAM
1982	−7.048	−8.470	−7.710	−8.659
1983	−8.603	−9.964	−9.184	−10.319
1984	−8.687	−9.983	−9.186	−10.318
1985	−8.620	−9.973	−9.219	−10.392
1986	−9.383	−10.791	−9.969	−10.980
1987	−9.816	−11.225	−10.353	–
1988	−10.447	−11.711	−11.066	−12.091

	β	β_{year}	Area:	β_{area}	γ_{area}
1982	3.213	0.000	DWK	0.0000	0.3201
1983	3.213	0.433	OG	0.3613	0.8986
1984	3.213	0.436	DB	0.1109	0.1673
1985	3.213	0.422	FLAM	0.3887	0.4747
1986	3.213	0.627			
1987	3.213	0.752			
1988	3.213	0.921			

oocytes. These differences could affect the comparability of the results and will now be discussed.

Franz (1910a,b), Simpson (1951), and Horwood *et al.* (1986) preserved the ovaries in Gilson's fluid. Reibisch (1899) boiled the ovaries for 15 min to harden and isolate the oocytes. A small number of oocytes were isolated from the ovary wall using a spatula and brush. In the present study the oocytes were hardened in methanol and isolated from the connective tissue by gently washing above a fine meshed sieve. Because the oocytes hardened sufficiently, it is unlikely that the method of preparation of oocytes could have significantly affected the fecundity estimation.

In all studies the oocytes were separated from the debris of connective tissue by decanting. This step could have resulted in some loss of the smallest developing oocytes,

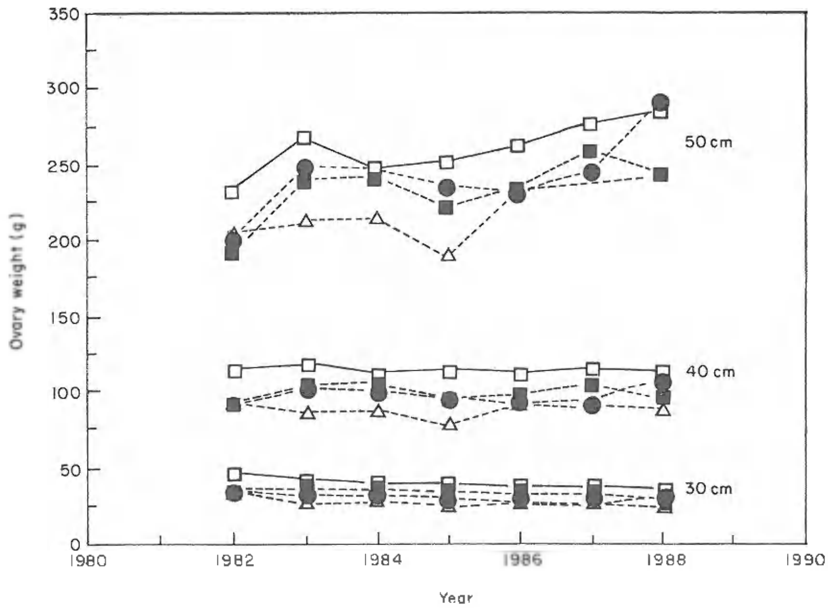

Figure 5. Annual variability in predicted ovary weights for three size classes of plaice (30, 40, and 50 cm) according to the parameters in Table 11. —□— = DWK, —●— = OG, —■— = DB, —△— = FLAM.

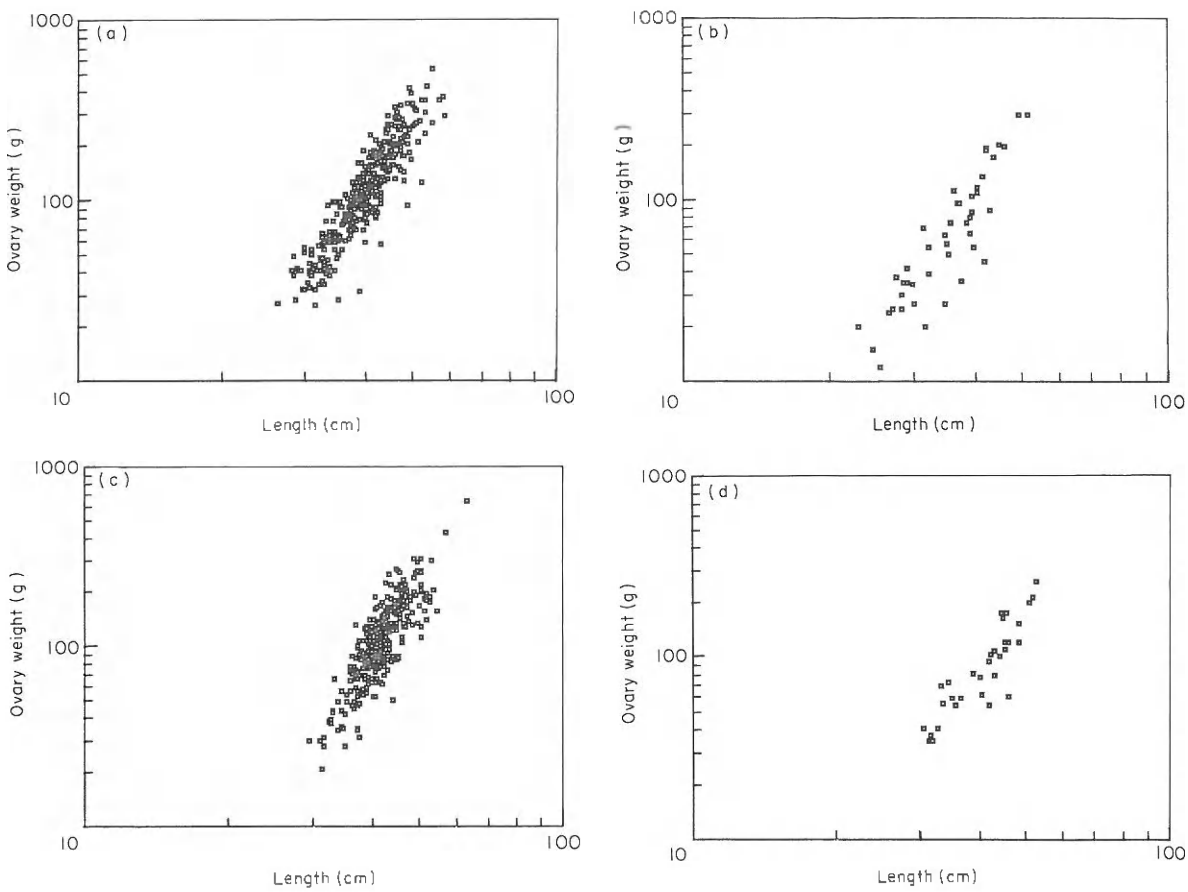

Figure 6. Scatter plots of ovary weight (g) against fish size (cm) in the periods 1947–1949 and 1982–1988 for areas DWK (a and b) and FLAM (c and d). Data from Simpson (1951) and the present study.

Table 10. Means, standard deviations, and coefficients of variation of predicted ovary weights according to the parameter estimates of Table 9 for three size classes of plaice and with a somatic condition of 0.800.

	30 cm			40 cm			50 cm		
	Mean	s.d.	C.V.	Mean	s.d.	C.V.	Mean	s.d.	C.V.
Area									
DWK	39	3.5	8.9	113	2.7	2.4	261	17.7	6.9
OG	30	2.4	7.8	97	5.9	6.2	243	26.2	11.2
DB	33	2.7	8.0	99	5.2	5.2	233	21.3	9.2
FLAM	27	3.1	11.1	87	5.4	6.2	217	19.7	9.3

Table 11a. ANCOVA results of the ovary weight data 1982–1988 (present study) and those of 1947–1949 (Simpson, 1951) for areas DWK and FLAM separately according to the GLM model: $\log_e G = \alpha + \beta.\log_e L$; G = ovary weight; L = length.

	SS	d.f.	MS	F	P
Area: DWK (January data only)					
logL[1]	128.5	1	128.5	1718	< 0.01
Year[1]	0.588	1	0.588	7.86	< 0.01
Error	30.75	411	0.0748		
logL.Year	0.0181	1	0.0181	0.24	n.s.
Error	30.73	410	0.0750		
Total	174.1	413			
Area: FLAM (January and February data)					
logL[1]	66.30	1	66.30	752.0	< 0.01
Year[1]	0.290	1	0.290	3.28	n.s.
Error	28.39	322	0.0882		
logL.Year	0.3934	1	0.393	4.51	< 0.05
Error	26.00	309	0.087		
Total	96.43	324			

[1] After adjusting for main effects.

Table 11b. Parameter estimates of the GLM model of Table 11a of ovary weight data 1982–1988 (present study) and those of 1947–1949 (Simpson, 1951) for areas DWK and FLAM separately: $\log_e G = \alpha + \beta.\log_e L$; G = ovary weight; L = length.

Period	Parameter	DWK	FLAM
1947–1949	α	−9.007	−7.081
	β	3.691	3.118
1977–1985	α	−8.884	−9.720
	β	3.691	3.859

especially in the samples of the smaller females taken early in the season, as ovary development in these fish lags behind. This probably did not affect the results for the period 1977–1985, as the sampling did not start before December, but could have affected Simpson's (1951) results, which included samples collected in October and November. However, comparison of the fecundity–length relationships for Simpson's October–November and December–February samples did not indicate a significant difference in slopes or intercepts. This effect cannot be tested for Franz's (1910a,b) data as sampling dates were not specified.

Table 12. Predicted ovary weight (grams) for three size classes of plaice and two time periods according to the parameter estimates of Table 11. The percentages at the bottom of the table indicate the percentage from the historic to the present period.

	30 cm		40 cm		50 cm	
Period: 1947–1949						
DWK	34.7		100.3		228.7	
FLAM	33.9		83.2		166.8	
Period: 1977–1985						
DWK	39.1	+13%	113.5	+13%	258.6	+13%
FLAM	30.1	−11%	91.4	+10%	216.3	+30%

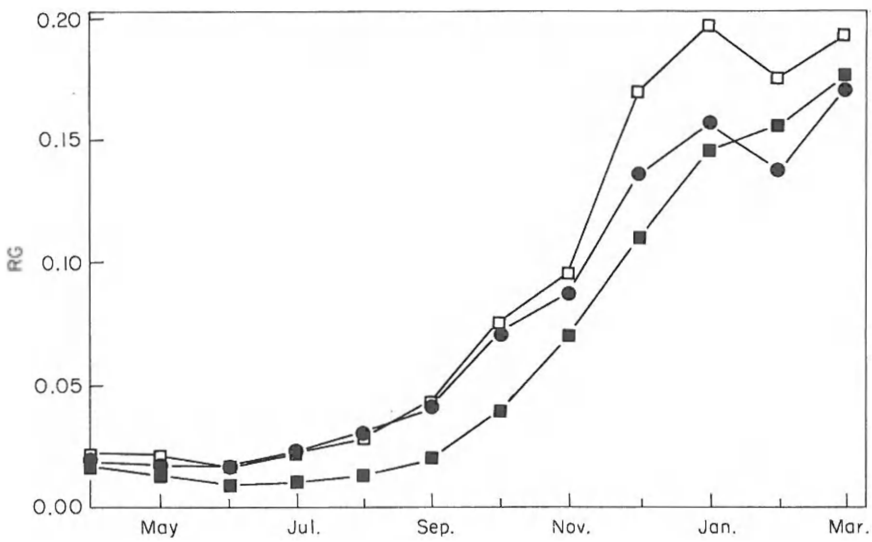

Figure 7. Increase in size-specific ovary weight ($RG = G \times L^{-3}$) for various age groups of female plaice. Data 1982–1988. —■— = age 3–4, —□— = age 5–14, —●— = age 15+.

Table 13. Coefficients of the predictive regression of first-quarter ovary weight (g) against body size (cm) in stage 2 plaice according to the GLM model $\log_e G = \alpha + \beta \log_e L$; where G = ovary weight and L = length. Pooled market sampling data 1981–1985.

	α	s.e.	β	s.e.	r^2	N
October	−14.5	0.455	4.89	0.124	0.692	699
November	−12.2	0.353	4.39	0.095	0.706	885
December	−11.3	0.363	4.26	0.098	0.753	623
January	−9.56	0.205	3.85	0.055	0.773	1411
February	−7.86	0.382	3.38	0.104	0.687	487
March	−6.93	1.458	3.14	0.394	0.523	60

Oocytes were generally subsampled before being counted. In the present study subsampling was done by counting all the eggs from a subsample of the ovary from the middle region. Total fecundity was calculated by raising the weight of the sample to the total ovary weight. Replicate samples from the individual fish showed no systematic difference in egg density between various parts of the ovary, nor between the left and right ovaries. Equal egg densities in both ovaries were also reported for Pacific halibut (*Hippoglossus stenolepis*) (Schmitt and Skud, 1978) and pike (*Esox lucius*) (Kipling and Frost, 1969).

Franz (1910a,b) and Simpson (1951) suspended the oocytes and used a stemple pipette to obtain a volumetric subsample. This method was criticized by Kändler and

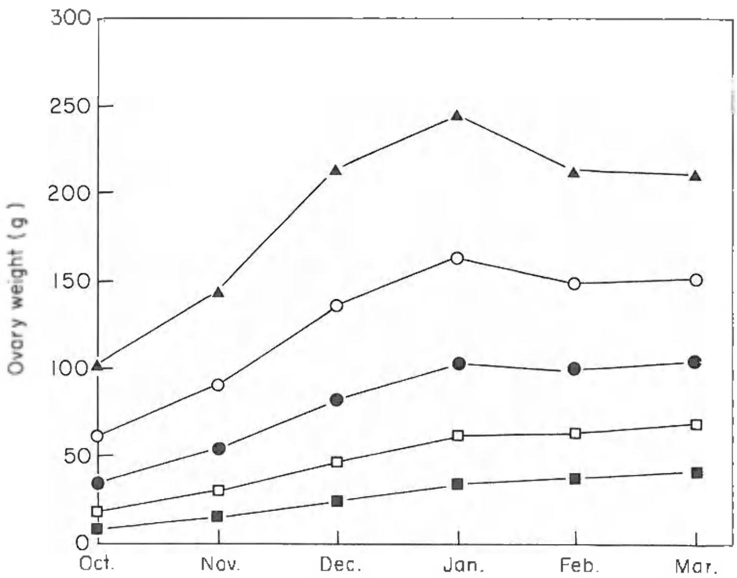

Figure 8. Increase in ovary weight (g) during the spawning period. Data 1982–1988. —■— = 30 cm, —□— = 35 cm, —●— = 40 cm, —○— = 45 cm, —▲— = 50 cm.

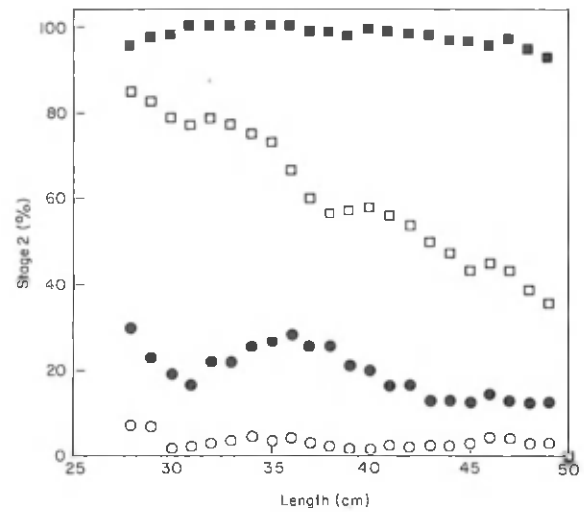

Figure 9. The proportion of pre-spawning female plaice (maturity stage 2: ripening ovaries) within the adult population between December and March. Data 1982–1988. ■ = December, □ = January, ● = February, ○ = March.

Table 14. Mean and standard deviation of dry weight per egg after fixation in 4% formaldehyde in sea water in relation to maturity stage. N denotes the number of observations. The overall mean was weighted over the stage durations of each stage.

Maturity stage i	Dry weight (mg)	s.d.	N	Proportion of total spawning time P_i
3	0.274	0.025	73	0.49
4	0.266	0.024	14	0.28
5	0.241	0.020	16	0.10
6/7	0.240	0.020	23	0.13
Overall mean	0.264	0.025		

Pirwitz (1957) and by Bagenal and Braum (1978) because the oocytes quickly sink to the bottom and might result in undercounting. Witthames and Greer Walker (1987) compared the volumetric method of fecundity determination as used by Franz and Simpson with fecundity estimates counting all oocytes with an automatic particle counter; they found that the volumetric method underestimated the fecundity by about 6%. The actual fecundity–body size relation might therefore be underestimated by the volumetric subsampling method over the entire size range of fish, but this bias is probably small compared with the observed difference in fecundity between the time periods.

Horwood (1990), studying plaice fecundity in the Irish Sea, could not find a significant difference compared with the results of a similar study of Simpson (1957) in the 1950s. This suggests that the methodological differences between Simpson's and Horwood's studies cannot have played a major role in explaining the fecundity increase in the North Sea. Finally, the agreement between the results of the present study and those of Horwood *et al.* (1986) with regard to both the general level of fecundity and the residual variance is further support of the conclusion that methodological differences have not seriously distorted the fecundity–body size relationships reported here.

Table 15. Average percentage and standard deviation of dry weight of ovary samples and relative ovary weight ($RG = G.L^{-3}$) in relation to maturity stage. N denotes the number of observations.

Maturity stage	%dry	s.d.	R.G.	s.d.	%dry RG.	s.d.	N
2	33.3	0.7	0.165	0.057	0.055	0.019	43
3	26.2	3.4	0.194	0.057	0.052	0.019	73
4	19.4	3.2	0.133	0.036	0.026	0.009	14
5	18.8	4.4	0.049	0.026	0.014	0.007	16
6/7	14.4	1.6	0.034	0.017	0.005	0.003	23

Table 16. Average and standard deviation of dry weight per egg after fixation in 4% formaldehyde in sea water for maturity stage 3 females. N denotes the number of observations.

Age	Egg dry weight (mg)	s.d.	N
3	0.286		1
4	–	–	–
5	0.278	0.031	10
6	0.267	0.024	17
7	0.267	0.028	12
8	0.281	0.023	16
9	0.279	0.025	9
10+	0.274	0.023	9

Long-term changes in fecundity

In these circumstances it is concluded that the observed differences in size-specific fecundity between the three time periods are so large that they must reflect real changes between 1900 and the present.

The historic changes in fecundity–length relationship can be summarized as follows. Fecundity in 1947–1949, as compared to 1900–1910, had not changed in females up to about 40 cm, but was substantially lower in larger females, especially in area DWK (Fig. 11a). By 1977–1985 fecundity had increased substantially in females of 30–40 cm, but not in larger-sized females (50 cm). The substantial change in the fecundity–length relationship between 1947–1949 and the present was not reflected in the ovary weight–length relationships, which showed no change (area FLAM) or at most a marginal increase only (area DWK; Fig. 11b).

Changes in ovary weight

A puzzling result is the discrepancy between the changes in fecundities and ovary weights between 1947–1949 and 1977–1985 (Fig. 11a and b). For area DWK, fecundity increased by 70–100%, whereas the ovary weights increased by only 13%. For area FLAM, fecundity increased by 26% whereas ovary weight did not change.

If these discrepancies between changes in fecundity and ovary weight are real and the proportion of connective tissue in the ovaries is constant, they imply that the egg weights between both periods were different. The average dry egg weight of a 40-cm female in area DWK can be estimated from the predicted fecundity (159 800) in Table 8, ovary weight (113.5 g) in Table 12, and ovary dry weight (33.3%) in Table 15 as $0.333 \times (113.5/159.8) = 0.237$ mg. The average dry weight of eggs stripped from spawning females was estimated at 0.264 mg after fixation, corresponding to 0.352 mg after correction for the loss in dry weight by 25% due to fixation (Hislop and Bell, 1987).

The substantial discrepancy between observed and calculated egg weight indicates that the reallocation of matter continues after the start of spawning (Dawson and Grimm, 1980; Rijnsdorp and Ibelings, 1989; Rijnsdorp, 1990).

As the reallocation from soma to ovary continues into the spawning season an accelerated ovary growth in 1948–1949 could in theory explain the discrepancy between the changes in fecundity and ovary weights between 1947–1949 and the present. However, the seasonal egg production curves given by Simpson (1959) and Harding *et al.* (1978) showed that the peak of spawning in 1948 was only two weeks later than in an average year. The low between-year variability in first-quarter ovary weights between 1982 and 1988 is a further indication that the difference in timing of ovary development between years is small.

Assuming that the substantial increase in fecundity and the only marginal increase in ovary weight between 1947–1949 and the present is real, the corresponding change in egg weight can be predicted from the ratio of ovary weight and fecundity. For a 40-cm female in area DWK this difference is – 1947–1949: $100.3/89.3 = 1.12$; 1977–1985: $113.5/159.8 = 0.71$. Thus, egg weight should have declined by 37% (0.71/1.12). Similarly, for a 40-cm female in area FLAM, the predicted decrease in egg weight is 13%. From the positive relationship between egg size and egg weight (Fig. 10) it can be calculated that 13% and 37% decreases in weight of an average egg of 0.28 mg (1.89 mm) correspond to decreases in egg size of 4%

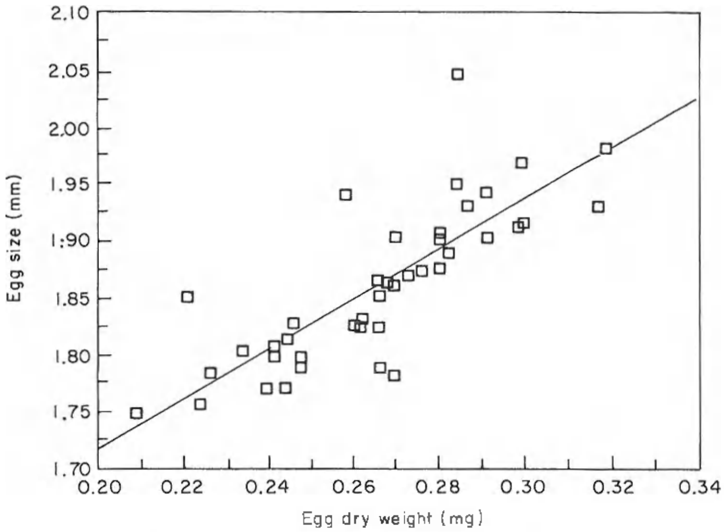

Figure 10. Relationship between the egg size and dry weight of formaldehyde preserved eggs. The predictive regression is given by $Y = 1.288 + 2.151X$ ($r^2 = 0.642$, $n = 42$; $p < 0.01$).

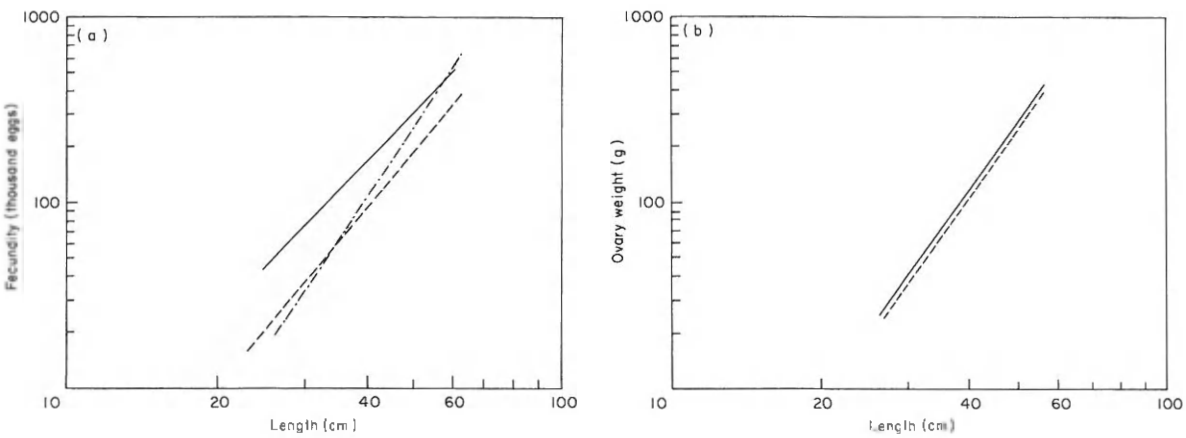

Figure 11(a). Fecundity–size relationships for 1900 (area DB), 1947–1949 (area DWK), and 1977–1985 (area DWK). – · – = 1900, – – – = 1947–1949, —— = 1977–1985. (b). Ovary weight–size relationships for 1947–1949 (area DWK) and 1982–1988 (area DWK). The regression parameters are given in Tables 7 and 11. – – – = 1947–1949, —— = 1982–1988.

(1.81 mm) and 12% (1.67 mm). The latter decrease seems fairly large compared with the coefficient of variation in egg size of 5% as observed in the sea (mean = 1.87; s.d. = 0.09), but falls within the range of egg sizes observed (Rijnsdorp and Jaworski, 1990).

Fecundity and growth

We now consider how the changes in fecundity between the three time periods are related to changes in growth. Wallace (1914) and Heincke (1908) give data on growth of plaice for the beginning of the 20th century for the same area as the fecundity data. Wallace (1914) has reported the average length-at-age of plaice from commercial samples taken in the eastern North Sea (our areas DB and VB) in the period 1906–1909. Heincke (1908) gives similar data for the youngest age groups in the area DB. Length-at-age data for the period 1985–1986, reported by Rijnsdorp (1989), are compared to the historic data in Figure 12. In Figure 13 the weights-at-age of plaice (sexes combined) in the late 1940s, given by Beverton and Holt (1957), are compared with similar data for the period 1980–1985 (Anon, 1990).

A study of the growth of plaice is complicated because the mean length of a particular age group increases with increasing distance from the coast, i.e. Heincke's law (Wimpenny, 1953). Another factor which might influence the estimated growth is the accuracy and precision of age

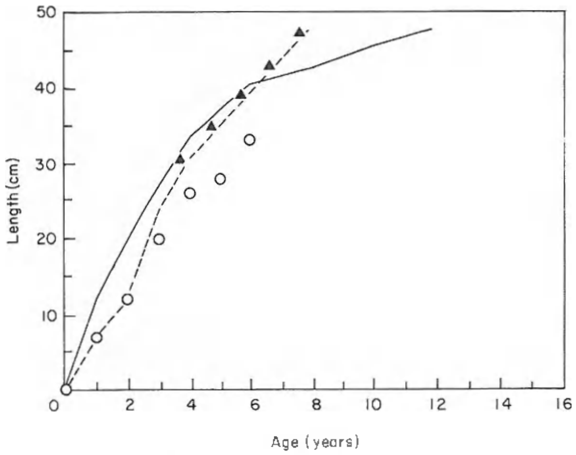

Figure 12. Comparison of the length-at-age of female plaice in 1900–1910 and 1980–1986 in the southeastern North Sea. The dotted line shows the estimated growth in 1900–1910 from data of Heincke (1908) – coastal areas around Heligoland – and Wallace (1914) – mainly offshore grounds in areas DB and VB. The full line refers to the area DB in the period 1980–1986 from Rijnsdorp (1989) and Rijnsdorp and Ibelings (1989). ○ = *Heincke (1908)*, ▲ = *Wallace (1914)*. ---- = *1900–1910*, —— = 1980–1986.

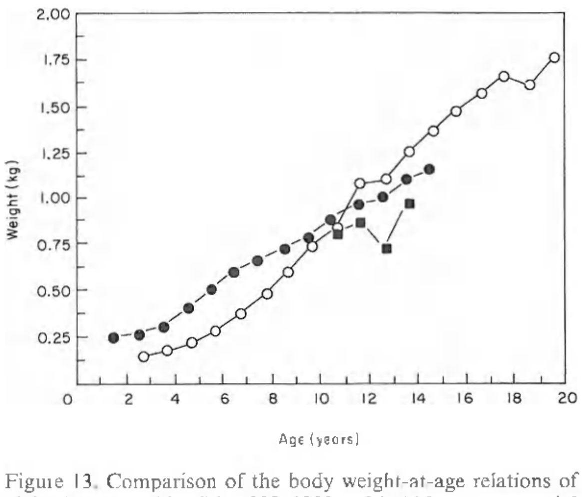

Figure 13. Comparison of the body weight-at-age relations of plaice (sexes combined) in 1928–1939 and 1946 from commercial samples of UK fleet (Beverton and Holt, 1957) and 1980–1985 from commercial samples (Anon, 1990). —○— = 1929–1938, —■— = 1946, —●— = 1980–1985.

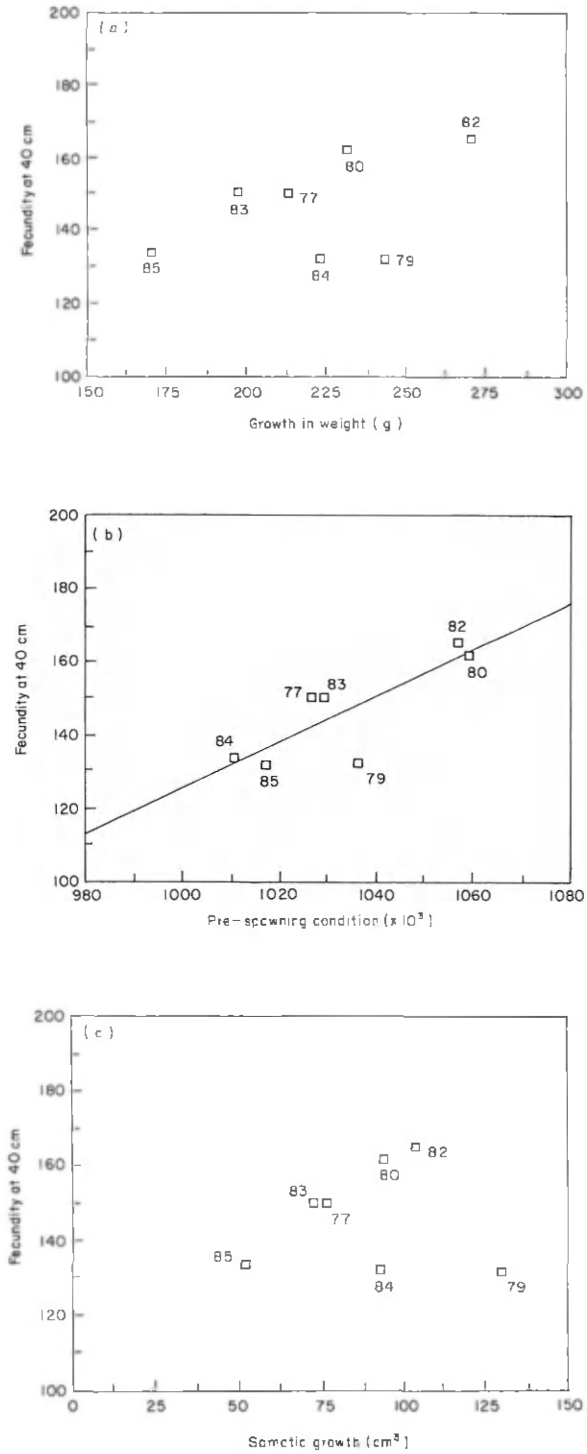

Figure 14. Relations between the predicted fecundity for a 40-cm female plaice with various growth parameters. (a) growth in weight ($W_i - W_{i-1}$) of age-groups 5–7, $r^2 = 0.21$; (b) pre-spawning condition factor (gutted), $r^2 = 0.67$; (c) somatic growth ($L_i^3 - L_{i-1}^3$) for age groups 5 to 7 between present year i and previous year i – 1, $r^2 = 0.001$.

determinations. Van Leeuwen and Groeneveld (1988) showed that the age determination in plaice, when carried out from untreated otoliths, is less precise and may even be biased for age groups older than 8 years (see also page 96 in Heincke, 1908). Finally, the mean length or weight of the younger age groups may be overestimated due to partial recruitment or discarding of undersized fish.

Table 17. Condition factors (C) of adult plaice at the start of the spawning period. Values were converted from gutted (including ovaries) to whole weight by multiplying by 1.07. For the period 1970–1988 the mean, standard deviation, and coefficient of variation of the annual condition factors of pre-spawning female plaice (maturity stage 2; length range 30–55 cm) are given for different areas in the North Sea. N denotes the number of observations, except for 1970–1988, where it denotes the number of years.

Period		Size group	c	N	Source
1990	Female	40–55	1.07	5	Reibisch (1899)
	Male and female	30–55	1.07	–	Borley (1909)[1]
1948	Female	25–55	1.11	82	Simpson (1951)

[1]areas B1, B2, B4, C1, C2, C3, D2

Area	c	s.d.	C.V.	N
DWK	1.114	0.023	2.1	19
OG	1.084	0.028	2.6	19
DB	1.068	0.029	2.7	19
FLAM	1.099	0.028	2.5	19

All these factors may have affected the comparison of the growth data presented in Figures 12 and 13.

Comparison of the growth data of Heincke (1908) and Wallace (1914) suggests that the former may have underestimated the length of the older age groups due to the restricted sampling area in the German part of the North Sea, while Wallace may have overestimated the length of the youngest age groups sampled due to the extension of the sampling area over the offshore grounds of the Doggerbank and the central North Sea. The dotted line in Figure 12 subjectively connects the most likely values of Heincke and Wallace and may be taken tentatively as an indication of the growth in the period 1900–1910. This line now can be compared to the full line representing present growth, which was based on first-quarter samples and took account of the relationship between length-at-age and distance from the coast (Rijnsdorp, 1989). Comparison of the growth between both periods in the eastern North Sea suggests that the growth rate of the youngest age groups (up to age-group 3 or 4) has increased between 1900 and 1985, but growth in older plaice has not changed.

Growth data of plaice for the late 1940s are restricted to weight-at-age of sexes combined from commercial samples taken from the English fleet and showed that growth was substantially reduced between 1939 and 1945 when stock size increased at least threefold due to the almost complete closure of the fishery during the Second World War (Beverton and Holt, 1957). Figure 13 shows the decrease in mean weight-at-age of age-groups 11–14 that lived through this period and were sampled in 1946 as compared to the average weight-at-age of similar age groups in the period 1929–1938. This figure also compared the average weight-at-age from the market samples taken from the fishery and indicates that the growth of the youngest age groups may have increased, whereas that of the older age groups has remained the same or has decreased. The differences in weight-at-age of the older plaice between the two periods may have been influenced to some extent by inaccuracies in age determination and should be treated with caution. However, age-groups 11–14 in 1946 would have had to be overestimated by 2–4 years to explain the differences. This is not in the direction in which errors are likely.

The observed increase in fecundity of smaller size groups of plaice since 1947–1949 (Table 8) seems to correspond to the inferred increase in growth of the youngest age groups (up to age 3 or 4). For the moment it remains unresolved which way these changes in fecundity are related to the reported advance in the onset of sexual maturation (Rijnsdorp, 1989). The decrease in fecundity for the larger females in 1948–1949 corresponds to the substantial decrease in growth during the Second World War. The decrease in fecundity was restricted to the DWK spawning group, suggesting that the increase in plaice density was particularly pronounced on the feeding grounds of this spawning group, but less on that of the FLAM group. De Veen (1978) showed that the DWK plaice are distributed in the southern and southeastern North Sea during the feeding period, whereas the FLAM group is distributed in the western North Sea.

Further indications that the conditions for growth might affect size-specific fecundity were obtained when analysing the annual variability between 1977 and 1985. The predicted fecundities of a 40-cm female appeared to be correlated with some growth parameters of age-groups 5 to 8 estimated from first-quarter market sampling data. These age groups dominate the mature population, are well-sampled, and their average length ranges between 35 and 40 cm (Rijnsdorp *et al*., 1991). Figure 14(a) indicates that fecundity is associated positively with the increase in weight in the preceding year, although the correlation is not significant. The positive relation was mainly due to the positive correlation with pre-spawning condition factor ($p<0.05$; Fig. 14b) and not with the preceding increase in the cube of length (Fig. 14c). These results suggest that favourable conditions for growth will result in an above-average growth in length and consequently an increase in absolute fecundity, but only a slight increase in pre-spawning condition and size-specific fecundity.

The literature on the relation between fecundity and growth rate, food ration, or population density is not unequivocal. Increased food ration has been shown to enhance fecundity in a number of experimental studies (brown trout (*Salmo trutta*), Bagenal, 1969; cod (*Gadus morhua*), Waiwood, 1982; *Cichlasoma nigrofasciatum*, Townshend and Wootton, 1984; rainbow trout (*Oncorhynchus mykiss*), Springate *et al*., 1985; plaice, Horwood *et al*., 1989). However, field studies on the relation between fecundity and growth or population density have not usually shown a clear interdependence (haddock (*Melanogrammus aeglefinus*), Hislop and Shanks, 1977; Pacific halibut, Schmitt and Skud, 1978; North Sea sole (*Solea solea*), Millner *et al*., 1991). Kipling and Frost (1969) found an increase in size-specific fecundity of 10–20% in the pike (*Esox lucius*), but could not find a clear relation with adult growth rate over the same period. De Veen (1976) showed that in the period 1960–1975 growth rate and length-specific ovary weight of North Sea sole increased substantially, in conjunction with an increase in pre- and post-spawning condition factor. However, ovary weight as a percentage of body weight did not change during these years (van Beek, 1988; Rijnsdorp *et al*., 1991).

The observed annual and geographical differences in slope of the relationships of fecundity and fish size and of ovary weight and fish size suggest that environmental conditions for growth (e.g. temperature, availability, and quality of food) of small and large plaice were different both within and between geographical areas, as well as within and between years. This is reasonable, since there are considerable differences in spatial distribution between size groups of plaice, small fish concentrated close to the coast, and larger fish dispersed over deeper water (Heincke, 1908; Wimpenny, 1953; Rijnsdorp and van Beek, 1991). The reproduction of the smaller fish, mainly recruit spawners, would largely be determined by the feeding conditions on the nursery grounds, whereas reproduction of larger size groups, mainly repeat spawners, would be determined by the conditions on the feeding grounds of the adult fish.

Tagging experiments suggest that the population in the nursery areas inside the west Frisian Islands recruits mainly to areas DWK and OG, whereas juveniles from the nursery areas along the German and Danish coast mainly recruit to area DB (Hickling, 1938; unreported results of tagging data RIVO). The spawning fish in area FLAM derive from a local nursery area along the English east coast (Lockwood and Lucassen, 1984). The summer feeding grounds are widespread in the southern and central North Sea, including both stratified waters, where bottom temperature is about 7°C, and non-stratified waters, where the maximum summer temperature reaches 14–17°C (Tomczak and Goedecke, 1964).

Since extensive migrations of adult fish occur during the months prior to spawning (de Veen, 1978; Arnold *et al*., in prep.), the time and place of sampling can affect the observed geographical differences in reproduction–body size relationships. Samples could include both fish that will spawn locally and fish that are still migrating, particularly when samples are taken just before or early in the spawning season. This should include mainly data for repeat spawners.

Egg weight

Horwood *et al*. (1986) showed that length-specific fecundity decreased with age. A similar result was obtained in this paper (Tables 4 and 5), although this effect disappeared when the covariable somatic condition was included in the analysis (Table 3). The decline in fecundity with increasing age leads immediately to the question whether it is compensated for by an increase in egg weight. The absence of an age effect on ovary weights (Table 9) suggests that egg weight indeed increases with age. The egg dry weights collected in this study, however, did not reveal a significant relation with age (Table 16), but this might be due to the restricted sampling period in the first half of the spawning season and the fact that hardly any 3- and 4-year-old females were sampled. In haddock, Hislop (1988) observed that egg size in the youngest age groups, mainly recruit spawners, was significantly lower than in older age groups.

The fecundity of individual plaice of a given size varies considerably, and the question arises as to whether also the level of fecundity in individual fish is in some way related to egg weight, i.e. do females with a relatively high fecundity produce smaller eggs and those with a low fecundity larger eggs?

This question was tackled by examining the relation between the egg weight and size-specific fecundity. Only first-quarter samples were analysed to reduce the influence of the continuous ovary growth. Egg weight was estimated by the quotient of ovary weight and fecundity. Size-specific fecundity was calculated by analysis of covariance (Table 3). Egg weight and size-specific fecundity showed a significant negative correlation ($r=-0.36$; $n=308$; $p<0.01$; first-quarter samples only), suggesting that females with relatively high fecundity produce on average smaller eggs. However, this result could be an artefact if the timing of ovary development of females with a relatively high size-specific fecundity is delayed. On the population level an inverse relationship between egg number and egg size was observed in herring (*Clupea harengus*) (Parrish and Saville, 1965), rainbow trout (Bromage *et al.*, 1990), and Pacific salmon (*Oncorhynchus kisutch*) (Fleming and Gross, 1990).

A complicated picture emerges from the few experimental studies that deal with the relationship between egg numbers and egg sizes with respect to food intake. Experimental restriction of food before the spawning period resulted in a reduction in size-specific fecundity and lower egg weight (haddock: Hislop *et al.*, 1978; rainbow trout: Springate *et al.*, 1985; Know *et al.*, 1988), a reduction in size-specific fecundity and constant egg weight (rainbow trout: Scott, 1962; stickleback (*Gasterosteus aculeatus*): Wootton, 1973, 1977), or a reduction in fecundity and increase in egg weight (brown trout: Bagenal, 1969). The duration and timing of starvation prior to spawning can explain part of the difference in experimental results (rainbow trout: Ridelman *et al.*, 1984). Again, factors other than food can influence the trade-off between egg size and egg number. Tanasichuk and Ware (1987) showed for Pacific herring (*Clupea harengus pallassi*) that ovary weight did not change with temperature, but in a year with high water temperature the size-specific fecundity was higher and the egg weight lower. The interaction between the growth and the allocation of the available reproductive resources in relation to egg size therefore remains an intriguing but rather unexplored territory.

In this context Rijnsdorp (1990) proposed a hypothetical allocation model of energy over reproduction and somatic growth that was inspired by the observation that the body condition was fairly constant between years and was not related to the rate of somatic growth. According to this model an individual fish allocates the incoming energy to somatic growth and energy reserves for reproduction during the growing season in such a way as to maintain its body condition at a threshold level, which increases during the season. In the few months prior to spawning the body reserves are reallocated from the soma to the ovary (Dawson and Grimm, 1980; Rijnsdorp, 1990). Poor conditions for growth in the main growing period result in a reduced somatic growth but not necessarily in a reduced energy reserve for reproduction. Only if conditions for growth deteriorate in the later part of the growing period will a fish be prevented from allocating sufficient energy to its body reserves for reproduction, hence resulting in a lower pre-spawning body condition. Larger fish are more vulnerable in this respect since they allocate a relatively large proportion of their total surplus production to restoring their depleted energy reserves after the previous spawning period and only a small proportion to somatic growth (Rijnsdorp and Ibelings, 1989; Rijnsdorp, 1990). According to this hypothesis, the timing of energy intake therefore plays a significant role in determining the variability of pre-spawning energy reserves and size-specific fecundity.

The present study revealed that substantial changes in fecundity but much smaller changes in ovary weight had occurred between three historic periods. Further, comparison of condition factors of pre-spawning females in two periods, which gives a rough approximation of the energy reserves available for spawning (Rijnsdorp, 1990), does not suggest major changes (Table 17). Finally, the comparison of the weight–length relationship between 1947–1949 and the present period for the pooled data of areas DWK and FLAM did not show significant change in the slope ($F_{1,422}=2.45$) or intercept ($F_{1,424}=1.83$) between both periods. This suggests that the energy allocation to reproduction versus somatic growth has not changed, but rather that the reproductive energy has been allocated to a larger number of smaller eggs compared with a smaller number of larger eggs.

Effect of fishing on changes in fecundity

In the North Sea the total annual mortality in the adult population is about 40% (F = 0.4: Rijnsdorp *et al.*, 1991); this compares with a natural mortality of about 10% (M = 0.10: Beverton and Holt, 1957). The plaice population is now dominated by younger age groups and concurrently the growth rate of juveniles has increased. At present, plaice of a given length will on average be younger than at the beginning of the century. Since the length-specific fecundity decreases with age, it may be asked whether the age effect alone can explain the observed change in fecundity?

The present fecundity of a 4-year-old female of 30 cm is 63 000 (Table 6). Fecundity of a 30-cm female in 1947–1949 was 36 000. If lower fecundity in 1947–1949 was due to the age effect on fecundity and the present fecundity–length relation applies to the period 1947–1949, we can predict the age of a 30-cm female in 1947–1949 with a fecundity of 36 000 from the equation:

$$\log_e E = \alpha + \beta \log_e L + \delta \log_e A.$$

The parameter estimates for area DWK are given in Table 5: $\alpha = -7.640$ (average over years 1977–1985); $\beta = 3.593$; $\delta = -0.313$. Thus $\log_e 36 = -7.640 + 3.593 \log_e 30 - 0.313 \log_e A$. Giving an age of 24 years. Obviously the observed decrease in size-specific fecundity with age is much too small to account for the observed change in fecundity.

The basic question raised in the Introduction was whether the differences in fecundity of plaice or, more generally, reproductive energy, between years or areas are due to differences in the environmental conditions for growth or to changes in the population genetics due to fishing. As plaice is an iteroparous species which matures at an age of 3–6 years (Rijnsdorp, 1989) and has a maximum life span of at least 25 years (Wimpenny, 1953; Beverton, 1964), the spawning population will be largely composed of the same individual fish for a number of successive years. If the intensive exploitation of the adult stock has resulted in a change in the genetics of the population, we can expect a gradual increase in size-specific fecundity or size-specific reproductive investment over a number of years. The observed changes do not seem to be consistent with a gradual change of this kind, except perhaps with the increase in fecundity of the smaller size groups (about 30 cm). It is therefore concluded that they are most likely due to differences in the environmental conditions for growth.

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Appendix

Length, weight, gonad weight, age, and fecundity of each fish sampled between 1982 and 1985.

Fish no.	Length (cm)	Gutted weight (g)	Gonad weight (g)	Age	Fecundity (thousand eggs)
Sample 82-1					
1	47.3	930	139	13	169.7
2	45.7	980	120	7	217.8
3	41.9	830	166	5	210.8
4	41.5	870	137	5	284.6
5	42.3	940	148	6	207.8
6	43.7	940	164	6	268.2
7	38.1	650	81	4	201.5
8	35.2	510	72	4	130.8
9	38.9	610	59	4	134.4
10	35.6	460	52	4	112.7
11	30.3	300	19	3	58.4
12	28.4	240	22	3	54.3
13	29.1	270	18	3	71.9
14	29.3	270	34	3	80.3
Sample 82-2					
1	48.7	1220	263	13	368.2
2	61.3	2640	485	19	754.6
3	47.5	1250	243	13	317.0
4	42.3	750	87	4	256.0
5	44.4	890	157	9	201.9
Sample 82-3					
1	44.9	1140	262	9	339.2
2	50.2	1410	257	13	327.8
3	51.8	1520	274	12	373.5
4	53.1	1510	306	10	430.7
5	44.7	1230	189	6	350.4
6	36.9	540	64	4	128.1
7	39.2	780	185	5	297.1
8	42.7	790	101	6	146.3
9	36.8	550	78	3	125.5
10	36.9	570	65	4	98.5
11	37.8	610	133	5	133.8
12	30.5	270	45	3	73.2
Sample 82-4					
1	45.4	1150	217	9	305.5
2	42.9	900	95	5	260.2
3	45.6	950	212	6	307.5
4	46.0	1010	216	8	225.4
5	44.6	1150	270	7	297.4
6	40.7	740	67	6	132.6
7	38.7	690	116	5	172.2
8	43.3	830	133	5	190.2
9	35.3	420	53	5	80.9
10	37.6	600	94	5	135.9
11	33.7	410	49	5	93.0
Sample 82-5					
1	45.0	930	148	10	152.6
2	42.9	740	82	6	123.8
3	46.5	950	153	9	194.4
4	46.0	1090	225	10	327.8
5	44.1	960	157	10	339.0
6	38.5	530	46	4	87.6
Sample 82-5 (*Continued*)					
7	37.4	640	68	4	150.2
8	38.7	700	136	4	213.3
Sample 82–6					
1	29.7	270	36	3	81.3
2	28.4	250	36	3	77.5
3	36.1	450	58	7	68.7
4	35.8	410	77	6	93.8
5	36.1	550	100	6	124.4
6	40.7	800	147	6	218.4
7	38.3	500	49	6	60.7
8	42.5	730	120	8	176.6
9	46.5	1040	153	14	164.3
10	44.4	1010	177	7	234.5
11	52.2	1840	431	11	516.5
12	44.8	1090	177	5	310.1
13	47.3	1130	153	8	199.0
Sample 82-7					
1	46.9	940	177	9	146.0
2	46.5	1020	129	11	223.3
3	44.8	1050	122	8	278.7
4	45.3	1180	262	8	395.5
5	40.0	640	82	9	97.4
6	39.1	640	112	5	130.7
7	40.4	710	123	5	151.8
8	40.8	740	74	5	171.1
9	37.1	500	48	8	106.5
10	35.9	510	56	6	118.9
Sample 82-8					
1	44.0	910	209	9	290.1
2	43.4	910	99	7	252.3
3	41.6	830	131	9	248.2
4	44.2	850	135	8	183.1
5	45.9	870	137	6	232.7
6	42.1	780	136	8	221.6
7	40.6	650	95	7	170.4
8	39.7	630	111	7	152.6
9	37.9	580	86	6	119.3
10	38.8	670	106	4	162.4
11	36.4	540	98	5	143.9
12	35.8	440	31	5	62.0
Sample 82-9					
1	43.4	910	131	9	200.1
2	52.8	1350	187	15	371.0
3	42.6	880	155	10	201.0
4	54.8	1960	246	13	582.7
5	46.7	1300	219	13	365.9
6	40.8	740	118	9	164.4
7	45.0	920	87	9	158.8
8	42.0	740	108	7	117.2
9	40.6	740	111	10	178.8
10	38.1	520	75	5	92.9
11	36.5	530	77	6	154.4

Fish no.	Length (cm)	Gutted weight (g)	Gonad weight (g)	Age	Fecundity (thousand eggs)
Sample 82-10					
1	51.9	1600	271	9	260.1
2	47.6	1210	252	6	281.4
3	39.8	700	144	4	244.4
4	38.6	560	102	5	149.8
5	39.5	590	81	5	126.6
6	30.8	310	57	4	81.1
Sample 83-1					
1	42.1	900	62	7	188.9
2	43.9	1020	138	6	292.7
3	41.1	670	64	5	111.1
4	49.6	1270	225	14	318.9
5	42.7	840	118	8	229.5
6	52.3	1420	164	13	248.7
7	49.2	1280	181	11	242.9
8	40.9	660	86	6	105.4
9	43.2	810	157	7	186.7
10	46.0	930	178	11	220.3
11	42.3	910	187	6	274.3
12	41.3	850	100	5	215.3
13	43.7	990	161	6	254.2
14	42.3	900	109	7	306.9
15	37.6	560	73	5	188.7
16	40.5	620	94	9	107.7
17	39.6	650	87	5	153.9
18	40.3	780	109	5	169.6
19	32.1	350	34	4	66.5
20	30.7	270	23	4	47.5
Sample 83-2					
1	35.4	440	38	4	84.2
2	37.7	600	96	5	135.8
3	34.4	410	18	5	47.1
4	34.7	420	50	4	110.2
5	38.6	560	79	6	108.2
6	39.3	660	91	5	157.7
7	40.3	690	79	7	104.9
8	42.4	870	131	5	204.5
9	46.6	950	197	11	231.9
10	41.7	790	125	6	214.5
11	38.3	670	143	6	184.9
12	39.1	600	46	5	122.8
13	38.3	640	93	5	169.3
14	39.3	660	76	5	135.2
15	43.2	940	217	7	295.1
16	44.6	820	137	9	193.8
17	47.5	1220	177	11	260.5
18	41.7	850	175	7	219.6
19	54.0	2030	599	16	597.9
20	51.5	1610	263	12	337.7
21	63.9	2250	284	17	429.5
22	53.2	1420	297	14	365.0
23	54.7	1710	309	14	458.4
24	53.1	1750	195	17	446.2
25	51.1	1270	180	11	360.7
26	48.8	1230	176	9	255.6
27	47.4	1190	193	10	352.5
28	64.9	2510	335	15	560.5
29	54.5	1470	211	14	305.1
30	51.7	1470	251	13	330.8

Fish no.	Length (cm)	Gutted weight (g)	Gonad weight (g)	Age	Fecundity (thousand eggs)
Sample 83-2 (*Continued*)					
31	43.1	840	89	7	164.9
32	40.2	790	114	7	174.7
33	42.6	870	126	7	193.7
Sample 83-3					
1	52.1	1300	222	10	174.4
2	45.5	810	158	6	165.1
3	53.6	1570	183	9	231.8
4	43.3	800	175	5	203.8
5	50.4	1390	291	15	355.3
6	43.5	860	175	10	192.8
7	53.0	1380	323	11	379.9
8	45.5	840	198	10	181.1
9	42.5	840	138	6	145.7
10	50.6	1430	233	10	407.9
11	44.8	910	70	8	179.4
12	45.8	1020	62	10	216.9
13	49.6	1120	257	10	243.1
14	40.8	710	125	7	154.8
15	47.2	1180	181	6	345.9
16	39.3	610	72	5	121.3
17	40.2	610	80	5	92.1
18	37.0	540	52	5	125.8
19	41.8	870	141	6	240.7
20	38.1	540	89	6	85.2
21	40.8	590	82	5	134.5
22	44.0	730	146	5	137.4
23	41.8	740	157	4	231.0
24	37.6	620	105	4	141.5
25	43.2	900	134	10	249.2
26	39.8	680	109	4	169.8
27	43.6	750	150	10	181.8
28	41.7	820	116	6	218.7
29	41.8	810	155	9	194.7
30	36.1	530	94	4	148.1
31	34.3	390	36	4	70.9
32	32.8	370	47	4	68.7
33	39.4	560	84	5	133.2
34	37.0	520	104	5	117.6
35	37.5	580	111	5	159.8
36	34.4	410	39	5	75.4
37	34.9	390	31	4	60.0
38	31.4	300	30	3	53.2
Sample 83-4					
1	25.9	180	13	3	36.9
2	29.8	270	26	3	75.1
3	29.8	240	14	3	43.2
4	35.4	490	56	4	114.7
5	34.3	370	36	4	56.5
6	33.8	390	39	4	80.6
7	31.4	300	43	4	65.6
8	39.9	690	125	5	166.9
9	39.2	620	76	5	133.3
10	40.7	590	94	8	124.4
11	36.4	500	54	6	88.9
12	35.8	540	72	4	123.4
13	37.8	570	119	5	143.0
14	40.2	580	46	7	101.5
15	37.8	550	65	6	110.4

Fish no.	Length (cm)	Gutted weight (g)	Gonad weight (g)	Age	Fecundity (thousand eggs)
Sample 83-4 (*Continued*)					
16	51.7	1600	319	9	218.9
17	43.4	700	144	6	157.6
18	48.8	1220	285	10	360.0
19	41.5	670	85	5	127.7
20	49.4	1170	205	9	307.1
Sample 83-5					
1	35.6	420	40	4	52.4
2	40.4	590	70	5	120.1
3	39.8	600	91	6	102.6
4	38.7	610	87	5	122.2
5	38.3	540	79	5	90.6
6	35.8	480	55	4	117.0
7	37.8	600	72	4	134.8
8	32.7	340	54	4	106.6
9	31.7	300	34	4	64.7
10	33.6	390	44	4	96.0
11	31.4	300	39	4	71.9
12	42.8	850	113	5	174.4
13	42.9	760	207	6	296.1
14	42.5	690	97	7	140.4
15	45.2	830	147	11	174.6
16	50.6	1270	279	10	359.1
17	41.2	670	81	4	121.5
18	42.4	700	106	10	161.6
19	43.0	660	123	7	115.4
20	42.4	680	113	6	126.7
21	43.7	750	97	9	138.8
22	43.0	630	131	8	160.0
23	47.8	1310	355	9	388.6
24	43.2	780	165	8	241.2
25	41.4	650	106	8	110.0
Sample 83-6					
1	32.9	410	80	4	116.9
2	33.9	420	103	4	151.0
3	43.0	900	207	7	257.1
4	50.2	1400	348	8	382.2
5	42.6	730	139	7	186.0
6	46.9	1010	170	7	241.3
7	40.4	720	154	5	175.3
8	49.2	1190	198	11	238.4
9	42.2	850	174	9	194.5
10	38.4	630	146	5	152.3
11	36.6	570	78	4	111.4
12	41.7	700	128	7	103.3
13	43.5	890	179	6	239.2
14	37.6	520	75	4	106.9
15	36.9	520	73	4	89.9
16	37.1	520	73	4	75.4
17	36.2	440	64	4	86.8
Sample 84-1					
1	44.6	980	161	9	247.6
2	48.5	1366	266	8	344.9
3	44.0	916	156	6	196.3
4	44.2	1149	162	6	240.0
5	46.4	1186	266	8	316.5
6	48.0	1340	302	7	384.0
Sample 84-1 (*Continued*)					
7	46.0	1171	163	9	208.3
8	56.3	1867	346	15	379.4
9	48.4	1439	281	5	351.2
10	46.9	1105	208	9	272.5
11	44.1	860	93	7	189.4
12	41.3	728	113	8	134.2
13	46.1	1111	200	7	254.0
14	43.9	1050	170	5	272.6
15	36.7	508	56	5	98.9
16	39.5	713	136	6	213.7
17	39.8	785	103	5	201.7
18	36.6	573	68	4	144.3
19	34.6	438	34	4	74.3
Sample 84-2					
1	55.9	1686	337	10	383.0
2	43.9	666	114	7	140.9
3	48.6	1221	292	12	304.0
4	49.2	1079	182	13	195.7
5	55.8	1490	257	14	358.0
6	43.3	741	151	5	212.9
7	45.9	1049	182	8	237.7
8	45.4	899	135	6	191.3
9	52.9	1481	336	10	377.7
10	55.4	1590	298	18	336.1
11	49.1	1206	241	7	409.8
12	38.7	569	60	6	116.1
13	42.6	679	101	6	136.8
14	44.0	810	165	10	181.2
15	37.3	543	72	5	96.5
16	37.5	631	80	4	135.3
17	40.2	637	114	5	177.7
18	39.5	564	100	6	122.4
19	34.5	390	67	5	85.9
20	35.6	509	62	6	78.8
Sample 84-3					
1	46.8	1259	229	7	251.5
2	43.7	925	173	5	206.3
3	44.1	923	205	8	258.2
4	43.0	723	110	8	137.3
5	34.8	421	38	5	55.2
6	40.2	600	89	5	95.6
7	42.8	742	92	9	135.0
8	44.1	893	115	8	172.8
9	43.3	896	121	6	168.8
10	34.0	425	57	6	73.7
11	44.8	985	148	7	224.9
12	37.0	512	74	4	170.5
13	47.8	1122	207	12	273.7
14	48.2	1143	253	12	275.5
15	38.2	602	100	6	131.6
16	32.3	321	22	5	28.8
17	47.9	959	132	10	129.3
18	37.5	495	35	5	57.2
19	41.2	712	108	5	121.4
20	39.3	699	107	5	175.8
21	34.5	436	55	5	84.5
22	34.4	388	50	4	67.2
23	39.5	622	103	7	105.0

Fish no.	Length (cm)	Gutted weight (g)	Gonad weight (g)	Age	Fecundity (thousand eggs)
Sample 84-3 (*Continued*)					
24	43.8	1033	213	8	244.0
25	47.8	1114	140	8	218.2
26	49.6	1327	247	10	299.0
27	47.3	1317	194	7	386.3
28	55.8	1668	201	–	270.8
29	40.3	602	104	8	118.3
30	41.5	814	105	7	169.3
31	33.5	382	41	4	67.9
32	45.3	838	94	6	120.6
33	58.8	1813	315	12	363.3
34	48.3	1117	149	12	199.4
35	41.2	688	107	8	184.0
36	50.4	1423	322	8	415.0
37	49.8	1513	222	8	390.5
38	51.4	1381	245	13	284.2
39	50.2	1290	270	–	273.8
40	40.5	681	82	5	156.2
41	38.5	558	94	6	91.0
Sample 84-4					
1	32.3	306	42	4	59.1
2	34.5	422	84	5	135.0
3	26.7	170	25	3	41.0
4	37.3	533	82	5	109.0
5	32.7	283	62	4	72.8
6	39.1	552	129	5	138.1
7	30.6	267	51	4	63.3
8	38.4	469	106	6	107.0
9	29.1	238	21	3	29.1
10	38.3	641	103	4	119.2
11	33.8	301	64	4	55.9
12	41.6	564	109	10	113.6
13	44.5	664	126	9	124.4
14	32.5	359	77	4	102.5
15	29.6	251	27	3	39.2
16	28.4	229	28	3	36.3
17	30.4	247	34	3	43.0
18	39.5	639	194	6	207.1
19	44.3	686	120	9	128.9
20	45.8	920	207	11	188.6
21	34.6	471	70	4	96.3
22	31.7	347	52	5	76.6
23	32.5	373	47	4	66.5
24	38.5	453	43	6	43.3
25	34.1	369	72	6	94.1
Sample 84-5					
1	38.3	587	97	5	107.8
2	26.0	191	35	3	40.4
3	43.8	784	178	4	228.7
4	36.3	389	56	5	67.8
5	29.2	277	51	3	66.5
6	44.1	946	185	7	255.3
7	35.7	495	67	5	91.0
8	38.2	462	42	5	50.7
Sample 84-6					
1	43.2	880	140	5	210.2
2	31.2	380	68	3	93.0

Fish no.	Length (cm)	Gutted weight (g)	Gonad weight (g)	Age	Fecundity (thousand eggs)
Sample 84-6 (*Continued*)					
3	35.1	434	64	4	81.2
4	41.6	620	79	5	107.1
5	37.5	494	65	4	100.2
6	40.1	654	83	6	95.3
7	37.0	544	94	4	145.1
8	36.2	451	75	5	97.5
9	39.6	586	98	5	94.0
Sample 84-7					
1	33.6	389	71	4	66.2
2	44.9	979	238	8	253.2
3	43.0	864	155	6	215.6
4	41.1	813	142	6	148.1
5	50.5	1370	331	10	414.0
6	46.1	956	205	7	256.5
Sample 84-8					
1	42.9	909	194	5	246.3
Sample 85-1					
1	42.6	877	141	6	242.3
2	51.3	1481	380	9	496.3
3	46.2	1093	156	7	283.6
4	44.2	1114	209	6	313.5
Sample 85-2					
1	45.7	896	97	9	178.8
2	42.5	694	94	8	152.4
3	46.7	1024	148	10	256.5
4	46.0	991	144	7	259.9
5	49.3	1325	229	11	353.4
6	46.0	1152	168	9	297.7
7	45.0	957	129	9	242.0
8	42.8	878	103	8	219.7
9	41.0	776	85	6	176.7
10	48.6	1290	197	9	314.7
11	50.9	1533	254	10	373.4
12	43.0	855	124	8	205.7
13	43.3	964	159	10	236.3
14	43.3	841	99	6	171.9
15	43.5	918	135	6	192.7
16	46.7	1113	130	9	271.9
17	41.4	746	54	4	111.7
18	41.5	750	74	8	113.8
19	44.3	973	187	9	231.8
20	36.2	510	45	5	92.2
21	35.8	513	39	5	86.4
22	35.8	563	63	5	125.9
23	36.0	494	40	4	81.5
24	35.9	506	45	4	89.7
25	31.0	340	33	4	74.2
Sample 85-3					
1	43.2	810	151	7	205.8
2	45.6	882	197	9	207.2
3	44.9	963	202	9	230.9
4	47.4	1064	209	6	222.4
5	45.1	911	172	9	166.8

Fish no.	Length (cm)	Gutted weight (g)	Gonad weight (g)	Age	Fecundity (thousand eggs)
Sample 85-3 (*Continued*)					
6	52.0	1267	126	16	155.0
7	39.0	648	160	6	214.1
8	41.8	632	116	5	119.2
9	39.6	533	78	5	103.7
10	41.2	661	127	7	133.3
11	32.8	346	41	4	77.3
12	34.1	398	77	4	111.7
13	32.1	324	49	4	87.0
14	29.7	283	49	4	71.3
15	28.6	215	43	3	62.4
Sample 85-4					
1	43.6	987	207	6	221.8
2	54.7	1772	269	16	311.4
3	49.1	1287	249	14	297.2
4	48.2	1157	231	10	264.2
5	46.6	1168	252	10	306.2
6	37.9	665	99	4	120.3
7	40.3	695	119	4	174.9
8	42.8	643	57	7	67.8
9	41.2	745	112	5	184.1
10	40.2	743	117	5	161.9
11	39.7	671	112	6	126.0
12	37.4	542	73	4	109.5
13	33.4	424	63	4	78.8
14	34.3	432	65	4	86.4
Sample 85-5					
1	42.0	850	124	7	214.3
2	40.8	700	77	6	109.0
3	40.4	752	98	7	199.1
4	41.5	634	66	9	80.2
5	37.2	511	65	5	66.1
6	37.2	469	69	7	75.0
7	39.9	625	72	6	105.5
8	38.1	502	50	6	66.2
9	39.6	557	43	5	59.9
10	38.2	543	99	9	140.6
11	33.9	365	41	4	73.9
12	32.9	350	57	4	73.8
13	31.7	285	26	3	55.3
Sample 85-6					
1	35.0	431	38	5	34.7
2	35.2	422	69	4	71.5
3	35.6	519	65	4	73.0
4	33.9	380	48	4	48.7
5	40.2	693	114	7	110.0
6	30.9	315	51	4	62.9
7	33.1	398	61	4	85.8
8	33.0	324	44	4	51.4
9	31.2	294	69	5	85.3
10	39.6	675	76	7	99.0
11	40.0	662	110	6	124.7
12	42.1	746	111	6	130.0
13	44.1	1006	194	9	263.2
14	42.1	819	185	7	289.5
Sample 85-7					
1	51.6	1384	262	13	324.6
2	43.5	851	112	6	200.7
3	46.7	992	176	9	248.7
4	54.0	1572	230	15	340.1
5	36.4	525	65	5	93.2
6	36.4	481	43	4	74.5
7	38.0	593	86	7	107.7
8	36.1	481	68	7	79.8
9	32.0	296	31	6	46.8
10	31.7	306	46	4	43.1
11	34.6	377	55	4	85.9
12	34.2	379	53	4	85.4
13	35.3	386	48	5	80.3
14	31.6	289	34	4	58.3
Sample 85-8					
1	37.9	544	86	4	121.2
2	36.0	535	112	5	161.5
3	34.7	417	73	6	103.0
4	43.6	873	222	6	282.9
5	42.4	791	150	7	213.3