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Fisheries as a large-scale experiment on life-history evolution: disentangling phenotypic and genetic effects in changes in maturation and reproduction of North Sea plaice, *Pleuronectes platessa* L.

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Abstract. This paper attempts to interpret the observed changes in reproductive strategy of female North Sea plaice since 1900 in the light of possible genetical selection exerted by the fisheries. Somatic growth of juvenile plaice increased between the 1950s and the 1980s, probably as a response to an increase in food availability. Adult growth rate was constant, except during a period of increased population abundance when somatic growth decreased. Both length (L_{mat}) and age at first sexual maturity decreased since 1900. No firm evidence was obtained for a change in total reproductive investment, although size-specific fecundity was reduced in the period of increased population abundance, suggesting a trade-off between egg numbers and egg size. Analysis of the phenotypic response of maturation to an increase in juvenile growth suggested that only a part of the decrease in L_{mat} could be ascribed to the observed increase in juvenile growth. The unexplained part of the change in L_{mat} corresponded with the predicted change due to genetical selection by the fisheries. This supported the hypothesis that fishing caused a genetical change in L_{mat}, although an unequivocal interpretation is not possible from a descriptive study.

Key words: Plaice – Life-history – Evolution – Maturation – Reproduction

Exploitation by the fisheries of natural populations can be considered a large-scale experiment on life-history evolution (Horn and Rubinstein 1984; Nelson and Soulé 1987; Stokes et al. in press). Life-history theory predicts that, due to the substantially enhanced mortality, genotypes coding for high fecundity or early maturation will be favoured over genotypes coding for low fecundity or delayed maturation (Gross 1985; Law and Grey 1989; Rowell in press; Rijnsdorp in press). However, since teleosts are well known for their phenotypic plasticity (Purdom 1979; Stearns and Crandall 1984; Roff 1992; Nelson in press), changes in reproductive parameters may also be due to phenotypic plasticity in response to an enhanced availability of food at reduced population sizes (Nelson and Soulé 1987).

A direct avenue to the study of genetical selection in natural populations is restricted to experiments with fish with a short generation time and small body size (Silliman 1975; Reznick and Endler 1982; Reznick et al. 1990), but is not readily available for commercial species which are in general characterized by a relatively large body size and a long generation time. An indirect approach, however, may be envisaged. The indirect approach explored in this study focused on phenotypic variability in reproductive parameters in response to variations in growth rate and temperature. Once the phenotypic plasticity is known, the phenotypic response can be predicted from the observed changes in growth and compared to the observed changes in reproductive parameters. If the observed change differs from the phenotypic response, a genetical explanation is likely. However, ultimate proof is not possible since changes in other environmental factors may always be suggested to have contributed to the observed changes in reproductive parameters.

A prerequisite of this approach is that the observed variability in reproductive parameters is mainly due to variability in environmental conditions. Heritability estimates for life history traits in teleosts indicate that about 24% of the phenotypic variability in a trait is due to genetical variability, fulfilling our prerequisite (Roff 1991, 1992; Policansky in press a). The assumption that the conditions for growth affect reproductive parameters is not unlikely since reproduction is intimately linked to the process of acquisition and allocation of energy (Jones 1976; Roff 1983; Rothschild 1986; Stearns and Koella 1986; Rijnsdorp and Ibelings 1989).

The species chosen for this study is plaice, *Pleuronectes platessa* L., a flatfish species which has been commercially exploited in the North Sea for more than a century. Current exploitation imposed an additional fishing mortality of about 40% above the annual mortality of 10% due to natural causes on fishes of 2 years and older

(≥18 cm) (Rijnsdorp et al. 1991; Rijnsdorp in press). The biology of plaice has been studied intensively since the late 19th century (Heincke 1908, 1913; Masterman 1914; Wimpenny 1953; Bannister 1978) and substantial changes have been documented in somatic growth (Beverton and Holt 1957; Bannister 1978; Rijnsdorp and van Beek 1991; Rijnsdorp and van Leeuwen 1992), onset of sexual maturity (Rijnsdorp 1989) and fecundity (Horwood et al. 1986; Rijnsdorp 1991).

This paper attempts to disentangle the phenotypic and genetic components in the observed changes in maturation and reproductive investment (fecundity, ovary weight) between three time periods: (I) around 1900; (II) 1946–1949, and (III) 1960–1990. The paper presents a new analysis of changes in the onset of sexual maturity between period I (Wallace 1909, 1914) and period III, reviews the changes in somatic growth and reproductive investment reported in previous papers (Rijnsdorp 1991; Rijnsdorp and van Leeuwen 1992) and reviews the phenotypic plasticity in maturation and reproductive investment in response to growth rate (Rijnsdorp 1990, 1993). Finally, the change in reproductive parameters, corrected for the phenotypic response, will be discussed against the background of the possible selective effects of fishing estimated by a simulation presented in Rijnsdorp (in press).

Observed changes in somatic growth, maturation and reproductive investment

Somatic growth

Although changes in somatic growth of plaice have been reported by various authors (reviews in Bannister 1978; Rijnsdorp and van Beek 1991), the interpretation of the data remains complicated. Samples may not always be representative because the mean length of a particular age group increases with increasing distance from the coast (Heincke's law; Wimpenny 1953). Other uncertainties are due to possible inconsistencies in the age determinations of different authors over a long time.

In order to circumvent these methodological problems, we apply the results of Rijnsdorp and van Leeuwen (1992), who reconstructed changes in somatic growth of female plaice between 1930 and 1985 from the growth patterns of otoliths. The back-calculation method was validated by Rijnsdorp et al. (1990). This approach has the advantage that representative samples were taken from fully recruited age groups that were collected during the reproduction period when the fish gather on the spawning grounds in the southern North Sea.

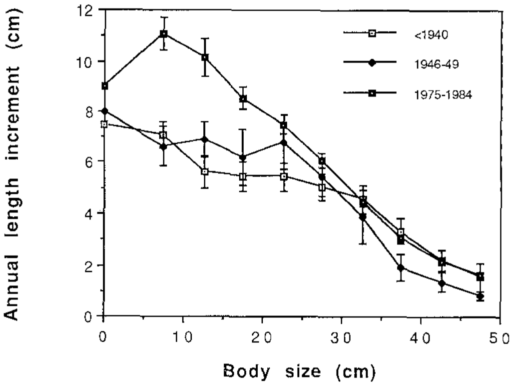

Fig. 1. Average annual growth (length increment in cm) of female plaice in relation to the body size (cm) at the start of the year in three periods (I, 1930–1940; II, 1946–1949; III, 1975–1985) as obtained by back-calculation from otoliths. The growth at body size *zero* refers to the size attained after the 1st year of life. *Vertical bars* indicate ± 2 SE

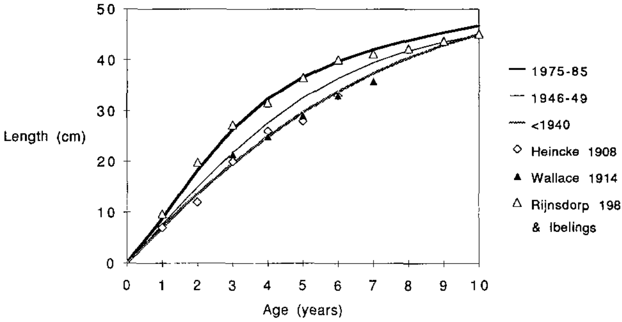

Fig. 2. Growth curves of female plaice for three time periods (I, 1930–1940; II, 1946–1949; III, 1975–1985) reconstructed from the back-calculated length increments shown in Fig. 1 in comparison with the observed lengths at age in period I (Heincke 1908; Wallace 1914) and period III (Rijnsdorp and Ibelings 1989)

Figure 1 illustrates substantial changes in somatic growth that have occurred since 1930. Somatic growth in period III was higher than in the other periods in size classes smaller than 25–30 cm. Somatic growth of size classes > 30 cm did not differ between period I and period III, but was lower in period II. From the relationship between the annual growth increments and body length, a growth curve can be reconstructed for the three periods studied. Because the historic reconstruction back-calculated from the otoliths did not go back before 1930, we assumed that growth in period I (around 1900) was similar to growth in 1930–1939. This assumption is supported by the correspondence of back-calculated and observed growth rates in both historic (Heincke 1908; Wallace 1914) and recent data sets (Fig. 2).

The reduction in somatic growth of the size classes > 30 cm in period II followed a threefold increase in the plaice stock in the southern North Sea during the 1939–1945 war when fishing was substantially reduced (Baerends 1947; Margetts and Holt 1947; Jenssen 1947; Beverton and Holt 1957; Simpson 1959; Rijnsdorp and van Leeuwen 1992). The increase in growth rate of the smaller size classes between period II and period III is probably related to an increase in the availability of food (de Veen 1976, 1978; Rijnsdorp and van Beek 1991).

Maturation

Data on the onset of sexual maturity were available for period I (Wallace 1909, 1914) and period III (1960–1985;

Table 1. Results of the ANCOVA of the maturity – length relationships of female North Sea plaice for period I (1904–1911) and period III (1960–1990) according the GLM model: logit $Y = L + A + T + L.A + L.T + A.T + L.A.T$

	SS	*df*	MS	*F*	*P*
L[a]	2918	1	2918	1268.6	<0.01
A[a]	383.9	5	76.8	33.4	<0.01
T[a]	636.6	1	636.6	276.8	<0.01
L.A	91.47	5	127.3	55.3	<0.01
L.T	50.10	1	50.1	21.8	<0.01
A.T	0.4075	2	0.203	0.09	n.s.
L.A.T	2.343	2	1.171	0.50	n.s.
Multicolinearity	6438.4				
Error	174.4	74	2.357		
Total	10870	91			

Y = number of mature females; L = length; A = age; T = time period; $L.A$ = interaction of length and age; $L.T$ = interaction of length and time period; $A.T$ = interaction of age and time period; $L.A.T$ = interaction of length, age and time period. The table gives the marginal contribution of each covariable to the model. The multicolinearity term indicates the explained variance that can not be ascribed to a single covariable

[a] Neglecting the interaction terms

Rijnsdorp 1989, 1993). The number of mature females (Y) was studied as a function of length (L), age (A) and time period (T) employing a GLM model (Baker and Nelder 1978; McCullagh and Nelder 1983) with a binominal error distribution (ε) and a logit link function:

$$logit\ Y = L + A + T + L.A + L.T + A.T + L.A.T + \varepsilon \qquad (1)$$

where $L.A$, $L.T$, $A.T$ and $L.A.T$ denote the total set of interaction terms of the main independent variables. The logit link function corresponds to a logit transformation of the proportion of the population that is sexually mature. The independent variables were all tested for their marginal contribution to the explained variance. The model included all independent variables that had previously been shown to have a biological meaning. Onset of sexual maturity is expressed as the length at which 50% of the fish became mature (L_{mat}). L_{mat} can be estimated from Eq. 1 at logit $Y = 0$. The approximate SE of L_{mat} was calculated from the variances of the linear predictor, given by the NAG statistical package GLIM (Baker and Nelder 1978), at a value of the linear predictor of zero. At this value the confidence limits are approximately symmetrical.

The results of the ANCOVA showed that two of the three primairy interaction terms L.A and L.T were highly significant, indicating that the slope of the maturity-length relationship differed significantly between age-groups and time periods (Table 1). The lack of significance of the interaction term A.T indicated that the age effect is not significantly different between periods. The observed proportions of maturity and the fitted maturity-length relationships for period I and period III are shown in Fig. 3. The slope of the maturity ogives tended to increase with age. Further, the ogives were shifted to smaller length with increasing age, indicating that the maturation probability is higher for slower-growing fish.

The lengths at 10%, 50% and 90% maturity were estimated from the fitted maturity-length relationships and plotted in Fig. 4. The lines connecting the 10% and 90% length-at-age points form an envelope that encompasses the juvenile-adult transition points of individual fish in the population. Although the envelopes of both periods showed some overlap, the envelope of period I is shifted to smaller sizes, and more recently maturity occurred at a younger age and smaller size. In period III, L_{mat} is 5.8, 4.2 and 3.9 cm lower than in period I at ages 4, 5 and age 6, respectively. The shift in the maturation envelope coincided with an increase in growth rate (Fig. 4).

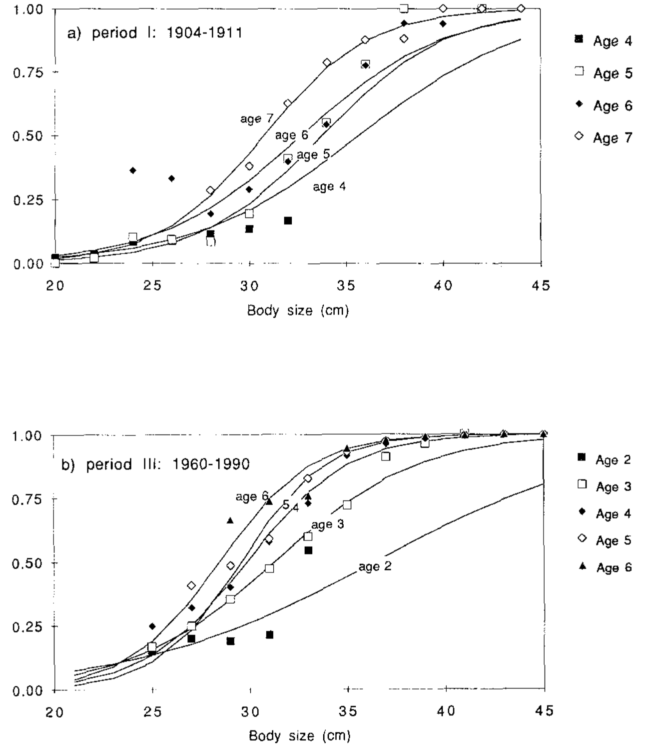

Fig. 3a, b. Proportion of mature female plaice in relation to length for **a** period I (1904–1911) and **b** period II (1960–1990). *Lines* show the fitted maturity ogives for separate age groups. The *data points* show the observed proportions of mature females

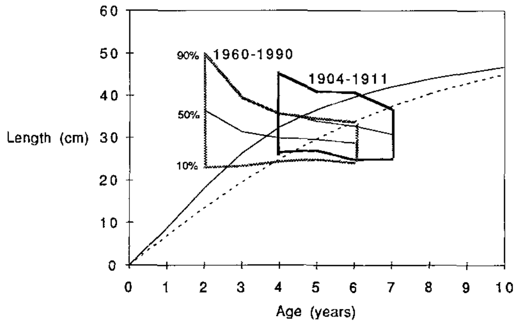

Fig. 4. Maturation envelopes that encompass the individual juvenile – adult transition points of female plaice for period I (1904–1911) and period III (1960–1990) and associated average growth curves (*dashed line*, period I; *full line*, period III). The envelopes were constructed from the estimated length at which 10% and 90% of the females reached maturity at various age groups. Within the envelopes the relationship between L_{mat}, at which 50% of the females reached maturity, is plotted against age

Reproductive investment

Data on the fecundity of plaice were available for the three periods (Reibisch 1899; Franz 1910a, b; Simpson 1951; Horwood et al. 1986) and have been reviewed by Rijnsdorp (1991). Since 1900, no obvious increase in size-specific fecundity has been observed except for the smaller size classes (<40 cm; Fig. 5). However, the fecundity samples of period I originated from the southeastern North Sea, where L_{mat} was around 40 cm (Rijnsdorp 1989). Hence, the size classes that showed an increase in fecundity comprised mainly recruit spawners, which may have had a lower fecundity than repeat spawners (Hislop 1988).

The main change in fecundity observed during this century was a 30–60% decrease in period II (Fig. 6). The reduction in the number of eggs in period II, however, did not coincide with a proportional decrease in ovary weight, suggesting that egg size must have increased. The reduction in fecundity and the inferred increase in egg size coincided with a substantial reduction in somatic growth. Calculation of the relationship between the surplus production, defined as the sum of the somatic growth and reproductive investment expressed in units of weight, from the back-calculated somatic growth and observed ovary weights, showed that surplus production in period II was 20–32% lower than in period III, whereas the reproductive investment was only 13% lower (Fig. 7).

Phenotypic plasticity

Maturation

Sexual maturation is a developmental process which can be characterized for each individual fish by a transition point in the length-age space. These individual juvenile-adult transition points are not fixed but may be influenced by environmental conditions (Stearns and Crandall 1984; Stearns and Koella 1986; Chambers and Leggett 1987, 1992). The family of individual transition points can be represented by a maturation envelope encompassing all size-age combinations at first maturation of individuals of a single genotype raised under different environmental conditions (MacKenzie et al. 1983; Policansky 1982, 1983). For a natural population, comprising a variety of genotypes raised under different environmental conditions, a maturation envelope be constructed from the maturity – length relationships at each age (Chambers Leggett 1987, 1992; Rijnsdorp 1993) as shown in Fig. 4.

From these maturation envelopes it is inferred that the probability of maturation increases with growth rate: a small fish at a particular age will have a lower probability than a large fish of that age. However, comparison of two fish that have reached a similar size at different ages shows that the faster-growing fish has a lower probability of maturation than the slower-growing fish. These contrasting results imply that maturation is influenced by the length reached at spawning as well as the growth history in previous years.

A further analysis of the effects of growth history during the juvenile phase on the maturation process was

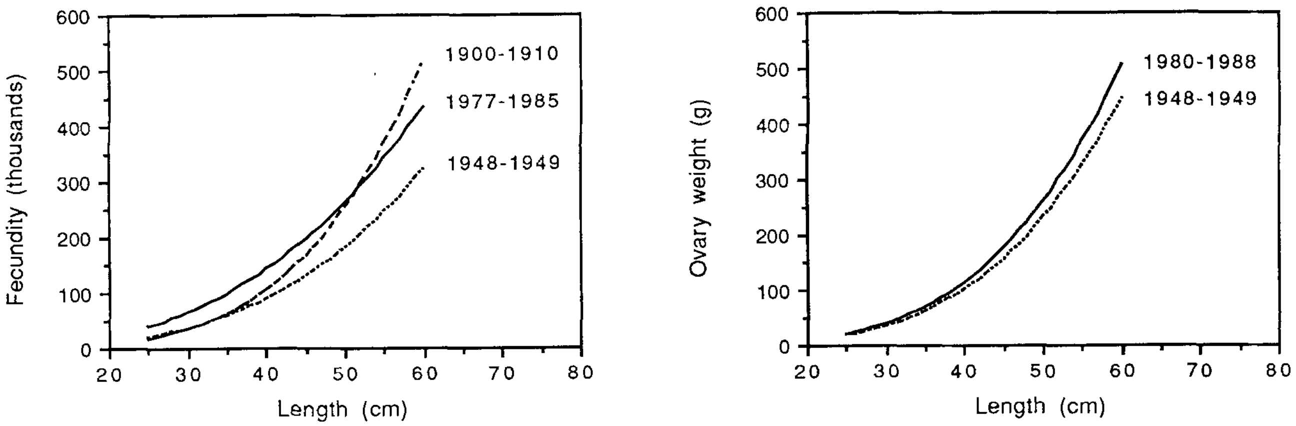

Fig. 5. Fitted regressions of fecundity *(left panel)* and ovary weight *(right panel)* against length of female plaice in three periods: I, 1900–1910; II, 1948–1949; III, 1977–1985. For period I no ovary weight data were available

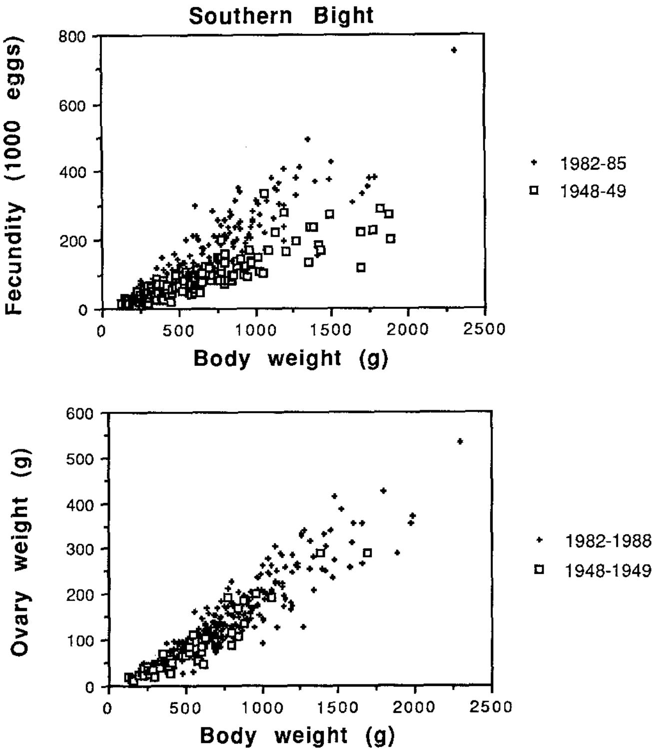

Fig. 6. Scatter plot of fecundity *(above)* and ovary weight *(below)* against body weight for period II (1948–1949) and period III (1982–1985)

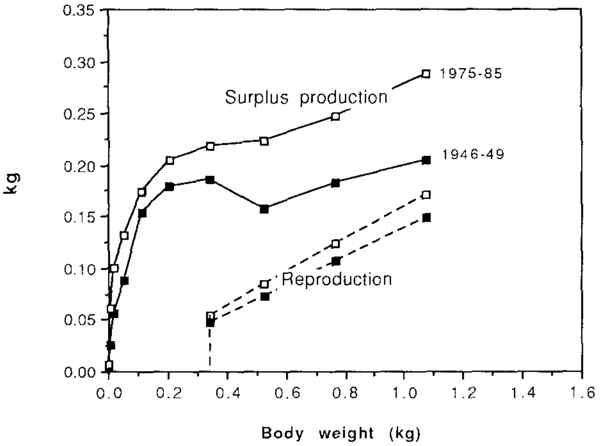

Fig. 7. Annual surplus production (somatic growth plus reproductive investment in kg) and reproductive investment (kg) in relation with body weight (kg) in period II (1946–1949) and period III (1975–1985). The substantial increase in surplus production between the periods does not coincide with a proportional increase in reproductive investment

Table 2. Coefficients of the GLM multiple regression model of the logit maturity probability as a function of the ultimate length (L) and the relative growth rate in the last completed year (G_{-1}), 2 years (G_{-2}) and 3 years (G_{-3}) prior to sampling: logit $Y = \alpha + \beta L + \gamma(G_{-1}) + \delta(G_{-2}) + \varphi(G_{-3})$ (from Rijnsdorp 1993)

	Coefficient	SE
α	−8.244	0.9924
β	0.2698	0.03038
γ	−0.2406	0.07066
δ	0.0374	0.6438
φ	0.1141	0.05535

Table 3. Coefficients of the linear regression $Y = \alpha + \beta X$ where Y= length at first maturity (L_{mat}, cm) at sampling age 4 and 5 and X= the length attained at age 4(L_4, cm) of cohorts of female plaice in the southern North Sea born between 1956 and 1985

	Sampling age 4		Sampling age 5	
	Coefficient	SE	Coefficient	SE
$L_{\mathrm{mat}} = \alpha + \beta L_4$				
α	46.51	3.80	40.67	3.09
β	−0.461	0.112	−0.306	0.091
r	0.636		0.558	
n	27		27	
P	<0.05		<0.05	

made by Rijnsdorp (1993). A study of the probability of maturity of individual females in relation to back-calculated individual growth curves suggested a 3-year maturation time. Maturation probability was significantly related to the ultimate size reached as well as to the relative growth rate 1 and 3 years prior to sampling (Table 2). Relatively fast growth 1 year prior to sampling (G_{-1}) was associated with a lower maturation probability, whereas relatively fast growth 3 years prior to sampling (G_{-3}) was associated with a higher probability of maturation. An effect of growth on maturation was further suggested by the negative correlation between the L_{mat} and the length attained at age 4 (L_4) of cohorts born between 1956 and 1985 (Table 3).

Reproduction

Phenotypic plasticity in reproductive investment in response to growth is indicated by various experimental studies in both plaice (Horwood et al. 1989; Rijnsdorp 1990) and other teleost species (Scott 1962; Bagenal 1969; Wootton 1973, 1977; Hislop et al. 1978; Waiwood 1982; Townshend and Wootton 1984; Springate et al. 1985; Knox et al. 1988; Bromage et al. 1990; Kjesbu et al. 1992). However, a descriptive study relating the relative width of the last annulus of the otolith with the size-specific fecundity or ovary weight did not reveal such an effect (Rijnsdorp 1990). A similar results has been obtained for sole (Millner et al. 1991). Also, the analysis of the inter-year variability in somatic growth and size-specific fecundity did not reveal a clear relationship (Rijnsdorp 1990, 1991). The relative constancy of the size-specific reproductive investment is further corroborated by the comparison of the ovary weights between 1948–1949 and 1980–1985 when the levels of surplus production, i.e. the energy in excess of maintenance requirements that is available for somatic growth and reproduction, were substantially different (Fig. 7).

Since the experimental studies did not address the problem of energy allocation between reproduction and somatic growth in individual fish, and generally manipulated food rations only during part of the annual cycle, the discrepancy between the descriptive and experimental studies may be due to variations in the temporal pattern of food availability (Rijnsdorp 1991; Kjesbu et al. 1992). It is, therefore, concluded that even under large variations in the conditions for growth the size-specific reproductive investment of female plaice is constant.

The reduced fecundity and the inferred larger egg weight in period II coincided with reduced somatic growth in the larger females (Fig. 1). The simultaneous change in fecundity and somatic growth on one hand and the peak in spawning stock biomass due to the reduction in fishing during the 1939–1945 war (Baerends 1947; Margetts and Holt 1947; Jenssen 1947; Beverton and Holt 1957; Simpson 1959; Rijnsdorp and van Leeuwen 1992) on the other hand, suggests that a trade-off between egg numbers and egg size may occur at a high level of spawning stock biomass.

Correcting the observed change in length at first maturity for phenotypic plasticity in response to changes in growth

With the quantitative relationships describing the effects of juvenile growth on the probability of maturation we may evaluate their contribution to the observed change in L_{mat} between period I and period III.

The effect of the change in juvenile growth between period I and period III on the L_{mat} was estimated in two ways. Approach A followed the GLM analysis of Rijnsdorp (1993) in which the maturation probability (Y) of individual females was related to ultimate length (L) and back-calculated previous growth rates G_{-1}, G_{-2} and G_{-3}: $\mathrm{logit}\,Y = \alpha + \beta L + \gamma(G_{-1}) + \delta(G_{-2}) + \varphi(G_{-3})$. With the parameter estimates of the GLM model of Table 2 and the previous growth rates of Table 4, L_{mat} can be estimated when logit $Y=0$, thus $L_{\mathrm{mat}} = -\beta^{-1}(\alpha + \gamma(G_{-1}) + \delta(G_{-2}) + \varphi(G_{-3}))$. The calculation indicated that the increase in juvenile growth between period I and period III may have resulted in a decrease in L_{mat} of 0.18 cm and 0.67 cm at age 4 and age 5, respectively (Table 5). The approximate standard errors, which were estimated from the variance of the linear predictor at a value of the linear predictor of zero, showed that the predicted change in L_{mat} did not differ significantly from zero (Table 5).

A second estimate (approach B) was obtained from the regression between L_{mat} and the length attained at age 4 (Table 3). Between period I and period III, the L_4 increased by 7.4 cm (Table 4), leading to a change in L_{mat} of $-7.4 \times 0.461 = -3.4$ cm at age 4 (SE = 0.83) and $-7.4 \times 0.306 = -2.26$ cm at age 5 (SE = 0.67).

The observed change in L_{mat} can now be corrected for the predicted change from the increase in juvenile growth

Table 4. A, Length (cm) at age of female North Sea plaice in three time periods as reconstructed from otolith back-calculations and B, the relative annual growth rate in comparison with a standard growth rate at age i ($G_i = 10.8 - 0.18\ L_i$) and mean growth rate at age 1 of 8.3 cm

Age (i)	A Backcalculated length at age (L_i in cm)			B Relative growth rate		
	1930–1939	1946–1949	1975–1984	1930–1939	1946–1949	1975–1984
1	7.0	7.6	8.7	−1.30	−0.70	0.40
2	13.5	15.0	18.2	−3.04	−2.03	0.27
3	19.5	21.8	26.3	−2.37	−1.30	0.58
4	24.9	27.7	32.3	−1.89	−0.98	−0.07
5	29.6	32.5	36.6	−1.62	−1.01	−0.69

Table 5. Procedure to estimate the 'unexplained' change in L_{mat} between period I and period III from the observed change and the predicted change due to phenotypic plasticity in response to the increase in juvenile growth for age group 4 and 5

	Age 4		Age 5	
	Change in L_{mat}	SE	Change in L_{mat}	SE
Change in L_{mat} (cm):				
Observed	−5.83	0.70	−4.24	0.47
Approach A:				
A Predicted from juvenile growth rate	−0.18	1.45	−0.67	1.26
Unexplained = observed–A	−5.65	1.61	−3.57	1.35
Approach B:				
B Predicted from length at age 4	−3.41	0.83	−2.26	0.67
Unexplained = observed–B	−2.42	1.09	−1.98	0.82

The effect of juvenile growth on L_{mat} was estimated following two approaches. Approach A makes used the GLM model that relates the maturation probability with length attained and relative growth rates in three previous years. Approach B employs the linear regression of L_{mat} and L_4

following approaches A and B. The results showed that in all of the four cases a decrease in L_{mat} remained, suggesting that the increase in growth rate can only explain a part of the observed change in L_{mat}. The approximate standard errors of the corrected change in L_{mat} are rather wide, but the 95% confidence interval did not include zero in any of the four cases (Table 5).

Life-history evolution in reproductive parameters

Maturation

In the above section we have obtained indirect support for the hypothesis that fishing has caused genetical selection for earlier maturation: the observed change in L_{mat} cannot be fully explained by the phenotypic response to an increase in juvenile growth. In this section we will investigate whether the observed change in L_{mat} corresponds to the expected change due to genetical selection by the fisheries.

The selective effects of fishing were studied using a simulation model, which described the cost of reproduction in terms of decelerated somatic growth and reduced future reproduction (Rijnsdorp in press). The relative fitness of various combinations of length at first maturity and reproductive investment was estimated at the current pattern and level fishing mortality at age. Reproductive investment was modelled as a fixed proportion of the body energy reserves. Fitness was calculated as the lifetime reproductive output. The fitness profiles indicated that the current exploitation select for genotypes coding for reduced L_{mat} or an increased reproductive investment (Fig. 8).

The selection differential, which represents the difference between the quantitative trait of the parents and that of the stock from which they were selected, was estimated from the fitness profiles and the observed variance in L_{mat} (μ 35, $\sigma = 2.5$ cm). Figure 9 illustrates the calculation. When there is no selection, the population before and after selection will be composed of females that mature according to the distribution shown. However, when selection occurs, the composition of the population after selection will have changed. The effect of selection is indicated by the fitness profile, which reflects the relative proportion of each L_{mat} in the population after selection. The selection differential (s) can now be estimated as the difference between the average L_{mat} (population before selection) and the average L_{mat} weighted over the fitness profile (population after selection). The calculation estimated S at 0.27 cm per generation. The associated generation time was estimated at 7.7 years, corresponding to 8.8 generations over the interval of 68 years between period I (midpoint 1907) and period III (midpoint 1975; Rijnsdorp in press).

The quantitative relationship between the selection differential (S) and the change in a quantitative trait per generation (R) is given by the expression $R = h^2 S$, where h^2 is the heritability coefficient (Falconer 1989). With the estimates of S from the simulation and R from the corrected change in L_{mat} per generation, the corresponding h^2 was estimated (Table 6). Approaches A and B yielded substantially different estimates of h^2 due to the difference in the estimated contribution of the increase in growth to the phenotypic plasticity in L_{mat}. Three of the heritability estimates were higher than unity, which is in theory the maximum possible value. The heritability estimate for age 5 from approach B, although <1, is still high compared to the average value $h^2 = 0.24$ for life history traits of teleosts (Roff 1991; Polikansky in press a).

The high values of h^2 may be due to a number of factors, which will be discussed below. The most important one is the low precision of the estimated change in L_{mat} after correction for environmental effects (Table 5). The 95% confidence limits around the corrected L_{mat} included values which yield heritability estimates that are closer to the average value of $h^2 = 0.24$ derived from breeding experiments. This can be shown by calculating the h^2 corresponding to the lower 95% confidence limit of the corrected L_{mat}. These h^2 values range between 0.37 and 1.02 for approach A and between 0.10 and 0.14 for approach B.

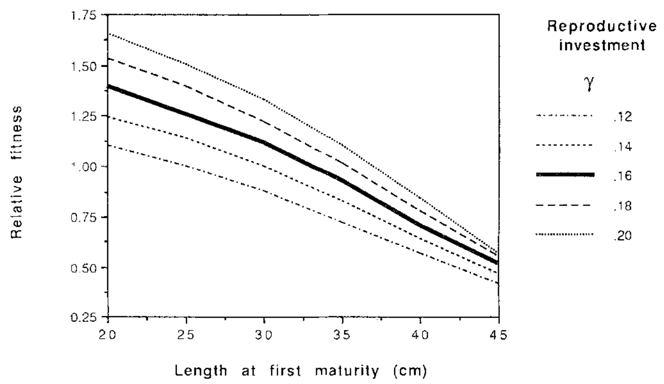

Fig. 8. Fitness profiles for the length at first maturity (L_{mat}) for different levels of reproductive investment (γ) expressed as the ratio of gonad weight to the total body weight. The fitness is expressed relative to the current reproductive strategy: $L_{\mathrm{mat}} = 33$ cm, $\gamma = 0.16$ (from Rijnsdorp in press)

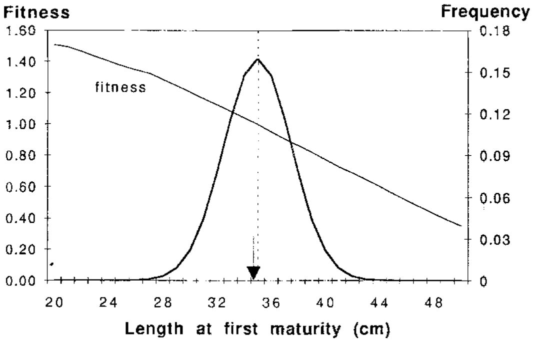

Fig. 9. Normal distribution of the length at first maturity in female plaice ($\mu = 35$ cm, $\sigma = 2.5$ cm) and the relationship between the fitness (lifetime reproductive investment) and L_{mat}. The *arrow* indicates the average length at first maturity, weighted over the fitness profile, representing the L_{mat} after selection. The selection differential $S = 0.27$ was estimated from the difference between the L_{mat} before (*dashed line*: $L_{\mathrm{mat}} = 35$ cm) and after selection (*arrow*: $L'_{\mathrm{mat}} = 34.73$ cm) (from Rijnsdorp in press)

Table 6. Summary of the selective effects of fishing (from Rijnsdorp in press) and the estimated change in L_{mat} after correction for the phenotypic plasticity in response to juvenile growth from Table 5

	Age 4	Age 5
Selective effects of fishing (from Rijnsdorp in press):		
Time span (years)	68	
Generation time (years)	7.7	
Number of generations	8.8	
S=predicted selection differential	−0.27	
Change in L_{mat} after correcting for phenotypic plasticity		
Approach A:		
Unexplained change in L_{mat} (cm)	−5.65	−3.57
R=unexplained change in L_{mat} per generation	−0.64	−0.41
h^2=heritability ($h^2 = R.S^{-1}$)	2.38	1.50
Approach B:		
Unexplained change in L_{mat} (cm)	−2.42	−1.98
R=unexplained change in L_{mat} per generation	−0.28	−0.22
h^2=heritability ($h^2 = R.S^{-1}$)	1.02	0.83

It cannot be ruled out that between period I and period III other environmental factors may have changed that contributed to the observed change in L_{mat}. Temperature might be such a factor, as monthly temperature records showed that the average summer temperature at a coastal station on the nursery grounds increased by approximately 1° C between period I and period III (van der Hoeven 1982; Rijnsdorp and van Leeuwen 1992). A possible influence of temperature on the onset of sexual maturity is suggested by the increase in L_{mat} with latitude, which might be related to latitudinal differences in temperature. A temperature effect was further suggested by the negative correlation between the L_{mat} of 4-year-old females and the water temperature on the nursery grounds during the summer of the year prior to spawning. If L_{mat} decreases at higher water temperatures, we can expect temperature to have contributed to the observed decrease in L_{mat}. From the slope of the negative relationship between L_{mat} and temperature the contribution can tentatively be calculated as −0.7 cm (Rijnsdorp 1993). However, this estimate is uncertain because the ambient temperature conditions and the critical time period during which the process of maturation may be affected are not known. Further, the correlations of L_{mat} and temperature were insignificant for the other quarters as well as for 5-year-old females.

The discrepancy between the expected and observed change in L_{mat} may be due to inaccuracies in the estimated selection differential. The simulation did not take account of the observed changes in growth and likely variations in the level of exploitation. The slower growth of juveniles in the first part of this century implies that the generation time, defined as the age at which 50% of the life-time reproductive output is realized, must have been longer, reducing the speed of genetical selection. However, the estimated generation time will decrease if the level of exploitation has been underestimated. This might indeed be the case because the pattern and level of fishing mortality prior to 1950 are still uncertain. Bannister (1978) derived an average instanteneous fishing mortality coefficient in the 1930s of F=0.3, whereas Beverton and Holt (1957) and Gulland (1968) derived a value of F=0.7. Therefore, the level of 0.5 used in the present study cannot be very precise. Preliminary results of a reanalysis of the 1930 data corroborated the high level of fishing mortality of F=0.7. A higher level of exploitation in the early part of the century would imply a stronger selection for reduction in L_{mat} and in the generation time.

Finally, if heterosomal genes contribute to the genetical coding of maturation, the selection on maturation in females will be affected by the selection on maturation of males. Rijnsdorp (in press) showed that the selection differential of L_{mat} of males was substantially higher than that of females, S=1.89 and S=0.27, respectively. This implies that the estimated selection differential of females may have been underestimated.

It is obvious that the above analysis must be considered speculative because of the many uncertainties. Therefore, a conclusive interpretation of the observed changes in L_{mat} is not possible. The results can nevertheless be regarded as support for the hypothesis that fishing has caused genetical selection in L_{mat} because of the qualitative agreement between the direction of the observed and predicted change in L_{mat}, and because the 95% confidence interval of the unexplained change in L_{mat} encompassed values that corresponded with the predicted selection differential and likely coefficient of heritability.

Reproduction

The simulation showed that the current level of exploitation imposed a strong selection for an increase in reproductive investment (Fig. 8). Contrary to this expectation, no evidence was obtained that reproductive investment has changed since 1900. One possible explanation for the lack of change in reproductive investment may be that morphology imposes a constraint on the maximum reproductive investment (Roff 1992). Jones (1974) showed that the number of eggs per gram body weight varies substantially between flatfish species with a coefficient of variation CV=97% (range 142–4193 eggs.g^{-1}), while the volume of eggs per gram body weight is much less variable, CV = 20% (range 534–922 mm^3). Secondly, the simulation model included a cost of reproduction in terms of a reduction in growth and future reproduction but not in an increase in mortality rate. Although the latter is very difficult to measure, it is generally assumed in life history theory (Roff 1991, 1992; Reznick 1992; Stearns 1992). In plaice, a mortality cost is not unlikely since spawning causes a substantial reduction of the body condition of both males and females, which may make the fish more vulnerable to diseases and predation.

Discussion

This study focused on the genetical effects of exploitation on size at maturity and reproductive investment. However, exploitation may lead to genetical effects on other characteristics such as growth rate (Nelson and Soulé 1987; Law and Rowell in press; Stokes et al. in press), sex change (Charnov 1981) and genetic diversity (Smith et al. 1991). In plaice, the increase in growth rate since 1900 is unlikely to be related to genetical selection, because of the relatively short period over which the increase in growth occurred (20 years) and because recent experiments on the maximum growth of plaice showed similar values to experiments carried out at the beginning of this century (Rijnsdorp and van Leeuwen 1992).

The possibility of genetical changes in life-history parameters such as the size and age at first maturity and reproductive investment is well accepted, because exploitation is selective and life history characters are heritable (Nelson and Soulé 1987; Stokes et al. in press; Polikansky in press a). Conclusive evidence for life-history evolution in exploited natural populations, however, is hard to obtain, although there are some suggestive examples (reviews in Nelson and Soulé 1987; Stokes et al. 1993). This paper provides a suggestive example of life-history evolution in the decrease in the size at maturity since 1900. Other examples are provided by Handford et al. (1977) and Ricker (1981). Handford et al. (1977) showed that growth rate as well as size at maturity decreased, but age at maturity increased, in *Coregonus clupeaformis* in response to a gillnet fishery for more than 30 years. Ricker (1981) showed that size at maturity decreased in pink salmon *(Oncorhynchus gorbuscha)* and chinook salmon *(O. tshawytscha)* and estimated that the observed change corresponded with heritabilities of about 0.25.

Conclusive evidence that exploitation may cause life-history evolution stems from experimental work (Reznick et al. 1990). Although fisheries can be considered a large-scale experiment on life history evolution, the experimental conditions are not well known. Hence, it is not realistic to expect that such field studies will yield conclusive evidence. In our case a multitude of uncertainties with regard to the level of historic mortality rates, the genetics of maturation and the phenotypic plasticity in maturation in response to temperature and growth remained. Nevertheless, a more refined analysis of the expected selective effects of exploitation and of the contribution of environmentally induced changes in L_{mat} are possible in future when more detailed studies on these aspects become available. Further, simulation of the selective effects of the current exploitation suggested that selection for a decrease in L_{mat} still continues, so more clearcut effects may be expected in future when longer time series will be available. Longer time series will have the additional advantage that the power of the statistical tests increases with the number of observations.

The evidence presented in this paper and others underscores the necessity of considering the implications of possible genetic effects of exploitation in fisheries management (Policansky in press b). Law and Grey (1989) explored the potential effects of genetical changes in L_{mat} on the yield of Arcto-Norwegian cod. For plaice, a continuation of the exploitation at the current level may further reduce L_{mat} (Fig. 8), which may lead to a decrease in the equilibrium yield to the fishery of about 5% (Rijnsdorp 1992). Although the decrease in yield seems rather small, it nevertheless emphasizes that negative long-term effects of exploitation may occur, which should be incorporated in fisheries management considerations. Simulation studies seem powerful tools to explore the sensitivity of the yield for different patterns of exploitation, which may guide fisheries managers to formulate short-term management advice within genetically safe long-term limits.

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