



Fisheries-induced evolution in growth, maturation and reproductive investment of the sexually dimorphic North Sea plaice (*Pleuronectes platessa* L.)

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ABSTRACT

Changes in the onset of sexual maturation, reproductive investment and growth of North Sea plaice are studied between three periods: 1900s, 1980s and 2000s. Probabilistic maturation reaction norms of both males and females, describing the probability of becoming mature conditional on age and size, shifted towards smaller sizes and younger ages, indicating a fisheries-induced evolutionary change. A higher rate of change was observed during the past 20 years, which may be related to higher temperature conditions. Reproductive investment was estimated from the decrease in lipid, protein, dry weight content and condition factor of the whole body between pre- and post-spawning adults. Reproductive investment expressed as the energy loss over the spawning period increased with body size from 19% at 20 cm to 30% at 40 cm in males and from 35% at 30 cm to 48% at 50 cm in females. No change in reproductive investment could be detected between the 1980s and the 2000s. Von Bertalanffy (VB) growth parameters showed a decrease in L_{∞} , the asymptotic size and an increase in K , the velocity to reach L_{∞} , in both males and females. The changes in VB growth are consistent with an increase in energy acquisition and reproductive investment. The observed changes in maturation, reproductive investment and growth are consistent with fisheries-induced evolution, but the changes in reproductive investment and growth need further investigation to disentangle the role of phenotypic plasticity.

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1. Introduction

Since fishing mortality is often several times higher than natural mortality and size-selective due to minimum mesh size or minimum landing size regulations, evolutionary changes in the life history traits, such as a decrease in the size and/or age of first maturity, an increase in reproductive investment and a change in growth rate, may be expected (Heino, 1998; Law, 2000; Ernande et al., 2004). Depending on the specific selection pattern, growth rate may evolve towards slower growth, e.g. to remain smaller than the size at first capture as long as possible, or towards faster growth, to reach the size of maturity and start reproducing as quick as possible and thereby 'outpace' cumulative (fishing) mortality by higher reproductive fitness (Dunlop et al., 2009).

Evidence for fisheries-induced evolution (FIE) has been reported in a number of different species (see reviews in Jørgensen et al., 2007; Kuparinen and Merila, 2007). The main problem in the study of FIE is to disentangle genetic changes from the phenotypic plasticity in traits values (Rijnsdorp, 1993a; Law, 2000; Heino et al., 2002a). Most studies

of FIE have focused on changes in sexual maturation, applying the probabilistic maturation reaction norm (PMRN) method of Heino et al. (2002a). This method studies the probability to become mature as a function of the size and age. Assuming that all environmental variability affects maturation indirectly via variation in growth, a downward shift of the reaction norm in the size – age plane provides support for FIE. Most of the studies reported a downward shift in the reaction norm supporting the hypothesis of FIE (reviews in Dieckmann and Heino, 2007; Jørgensen et al., 2007).

Studies of FIE in reproductive investment in natural populations are scarce since the estimation of reproductive investment is complicated. Fecundity provides the most direct estimate, but is restricted to females of species in which the fecundity is determined at the start of the spawning season (determinate spawners). Alternatively, reproductive investment is often estimated by the gonad weight. However, it is difficult to get an accurate estimate since the gonad weight changes substantially in the weeks before the spawning season due to the continuous growth of the ripening oocytes (Rijnsdorp, 1991; Kennedy et al., 2007). More importantly, gonad weight might not be a reliable estimator of reproductive investment because energy continues to be re-allocated from the soma to ripening oocytes during spawning, and because reproductive investment also includes behavioural cost of activities related to spawning (Rijnsdorp,

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1990; Kjesbu et al., 1991; Tyler and Sumpter, 1996). Gonad weight consequently underestimates the total reproductive investment. In capital spawning fish, where the energy reserves for reproduction are stored in the body, reproductive investment can therefore be estimated more reliably from the energy loss over the spawning period (Rijnsdorp and Ibelings, 1989; Rijnsdorp et al., 2005). But also if an accurate estimate of reproductive investment can be made, it will remain difficult to disentangle the effect of environmental conditions such as food or temperature from a potential genetic effect on changes in reproductive investment (Rijnsdorp et al., 2005; Kjesbu and Withames, 2007). A few studies, which attempted to disentangle phenotypic plasticity in reproductive investment, have provided support for a FIE increase in reproductive investment (Yoneda and Wright, 2004; Wright, 2005; Edeline et al., 2007; Thomas et al., 2009).

Fisheries may select for a change in growth rate by a direct selection on intrinsic growth rates (Ricker, 1981; Sinclair et al., 2002a, b), or indirectly by selection on maturation or reproductive investment, which may typically result in a decrease in growth rate of adults as fish mature earlier and invest more into reproduction under size-selective fishing (Law, 2000; Dunlop et al., 2009). Evidence for a FIE change in intrinsic growth rate is reported for a number of natural populations (Edeline et al., 2007; Biro and Post, 2008; Swain et al., 2007), although the interpretation remains controversial (Heino et al., 2008; Dutil et al., 2008).

In this paper we analyse FIE in North Sea plaice. This flatfish species has already been exploited intensively since the mid 19th century (Rijnsdorp and Millner, 1996) and has been studied intensively since the birth of fisheries science in the late 19th century (Wimpenny, 1953; Rijnsdorp, 1993a). FIE in maturation of plaice is suggested by the downward shift in the reaction norm of female cohorts since 1960 (Grift et al., 2003, 2007), but the evidence for a FIE increase in female reproductive investment is equivocal (Rijnsdorp et al., 2005), while the observed changes in growth have been interpreted in relation to changes in the environment (Rijnsdorp and Van Leeuwen, 1996; Bolle et al., 2004). These earlier studies are extended to include males and include data collected in the first decade of the 1900s. Specific objectives are to estimate changes in (i) PMRNs, (ii) reproductive investment and (iii) Von Bertalanffy (VB) growth parameters in males and females between three time periods: I – 1900s (female maturation and male and female growth), II – 1980s and III – 2000s. Results are discussed against the background of differences in environmental condition (temperature, eutrophication, population density) between the time periods.

2. Methods

2.1. Maturation

2.1.1. Data selection

Maturity data for period I were taken from Wallace (1914), where length distributions of immature and mature females were tabulated by age group as recorded from samples taken on the commercial fishing grounds during the spawning season (January–March). For period II and III, we used samples of the commercial landings from the south-eastern North Sea collected between December and February and providing information on the fish length (cm), body weight (g), age (assuming the 1st of January as birthday), sex and maturity stage. Maturity stage was determined by macroscopic inspection of the gonads (Rijnsdorp, 1989). Market samples cannot be used to study the maturation in males because most males mature already below the minimum landing size of 27 cm. Therefore, results of a dedicated maturity survey (Rijnsdorp, 1989) carried out in 1985 and 1986 (period II), and samples collected during the discard monitoring programme on board of commercial fishing vessels and research vessel surveys between September and November in the south-eastern North Sea in 2007 and 2008 (period III) were used. Maturity

data of males as reported by Wallace (1914) could not be used because these were collected on the spawning grounds where mature males are known to predominate (Rijnsdorp, 1989). Sampling levels are shown in Table 1.

2.1.2. Probabilistic maturation reaction norms (PMRNs)

The changes in maturation were analysed by comparing the probabilistic reaction norm (PMRN) estimated for the three time periods. PMRNs were estimated according to the method of Heino et al. (2002a) and Barot et al. (2004), which describes the probability to become mature as a function of size and age. The method assumes that environmental variability is reflected in differences in somatic growth, so that any change in an environmental factor that has its effect on maturation through changes in growth can be disentangled (Dieckmann and Heino, 2007). However, changes in the PMRN can not completely control for phenotypic plasticity in maturation, as it does not disentangle genetic effects from environmental factors affecting maturation other than through size and age (Dieckmann and Heino, 2007; Kraak, 2007; Marshall and Browman, 2007). Nevertheless, by incorporating other variables as a third or higher dimension, the role of other environmental variables can be tested, potentially strengthening the interpretation of FIE (Grift et al., 2007; Mollet et al., 2007; Vainikka et al., 2009).

The estimation is based on individual data to yield a PMRN estimate on the population level. Since the aim is to compare three periods, fish from the different periods are treated as distinct populations. For each period, the probability of being mature $m(a,l)$ was estimated from individual data by logistic regression by

$$\text{logit}(m) = \beta_0 + \beta_a a + \beta_l l + \beta_{al} a \times l + \varepsilon \quad (1)$$

where m is the proportion of mature fish per age and length class, a is age in decimal years, l is length (cm), the β 's are the regression parameters and ε is a normally distributed error term. As the data was aggregated by age and 1 cm length classes, the regression was weighted by the number of observations. As first time spawners in plaice can not be distinguished from repeat spawners, the probability of becoming mature p was calculated from the probability of being mature at a certain age a and length l , conditional on the probability of being immature in the previous year by taking account of the length increment (Δl) grown in the course of this year of age group a (Barot et al., 2004):

$$p(a,l) = \frac{m(a,l) - m(a-1, l - \Delta l)}{1 - m(a-1, l - \Delta l)} \quad (2)$$

This approach relies on the simplifying assumption that the growth rate and mortality rate at a certain size and age are the same for immature and mature individuals. Although this may not be true in reality, Barot et al. (2004) confirmed that the method is robust to the relaxation of this assumption. L_{p50} is used to denote the length

Table 1

Number of observations (N) and percentages of matures (mat) that were used in the maturation analysis per sex, period and age.

			Age 1	Age 2	Age 3	Age 4	Age 5	Age 6
♀	1900s	N	0	263	1199	1831	1125	378
		mat	n.a.	2%	9%	17%	38%	75%
	1980s	N	0	3	555	605	628	439
		mat	n.a.	1%	8%	45%	93%	n.a.
	2000s	N	8	44	410	764	915	644
		mat	0%	25%	82%	97%	100%	100%
♂	1980s	N	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
		mat	1%	50%	74%	95%	100%	100%
	2000s	N	44	155	76	14	11	1
		mat	0%	78%	92%	100%	100%	100%

For males in the 1980s only the ogives per age and size class were available.

at a given age at which the probability of becoming mature is 50%. Estimation of length increments was based on the Von Bertalanffy fit to the mean length at age (see Section 2.3.2).

2.1.3. Randomization tests

We used a randomization approach to test for statistical differences of *Lp50s* at age between the three periods. For this purpose the data from all three periods were merged and the three periods were permuted randomly to generate a new randomly created data set. From such a randomly created data set the PMRNs and differences between *Lp50s* at age were calculated for each period and this process was repeated 10^5 times. To indicate how likely the observed differences between sex and period might have arisen randomly, the *p*-value of the test was calculated as the proportion of sampled permutations for which the difference in *Lp50s* at age was greater than or equal to the observed differences.

2.2. Reproductive investment

2.2.1. Data selection

Energy content was determined by chemical analysis of the body constituents (%dry weight, %lipid, %ash, %protein). A total of 28 grouped samples of pre-spawning fish ($n = 193$ individual fish), collected between 5 and 20 December 2007, and 26 grouped samples of post-spawning fish ($n = 113$ individual fish), collected between 11 and 29 February 2008, were analysed. Samples were collected by commercial vessel and RV Tridens in the south-eastern North Sea. Maturity stages were classified according to Rijnsdorp (1989). Pre-spawning fish comprised ripening (stage 2) or early spawning (stage 3 or 4) males ($n = 98$) and ripening (stage 2) females ($n = 95$). The post-spawning fish comprised of spent (stage 6 or 7) males ($n = 58$) and females ($n = 55$). In order to study the relationships of reproductive investment with body size, between 3 and 19 fish were pooled in 3–4 size groups representing the full size range. Fish were selected to minimize the size variation within a group. The standard deviation of the groups ranged from 0.41 cm to 3.69 cm.

2.2.2. Sample processing

Fish were stored on ice immediately after being caught, except for the February samples of RV Tridens, which were frozen in sealed polythene. At the laboratory, samples were sorted by sex, maturity stage and length. The frozen samples were thawed slowly at 4 °C before processing. Food, sand or shell particles were removed from the gut to prevent bias in body energy content. The grouped samples were then minced in a commercial meat grinder, thoroughly mixed and a subsample of 300 g was stored in sealed polythene bags for later analysis at –20 °C.

The fraction of dry weight was determined by weighing the samples before and after freeze drying, and by drying samples in an oven for 3 h at 105 °C. The ash content was obtained by heating the samples in a muffle furnace at 550 °C for 22 h. Lipid content was determined using the method of Bligh and Dyer (1959). As the amount of carbohydrates in fish is generally very small (<0.14%; Craig, 1977; Dawson and Grimm, 1980) it was assumed zero. The fraction of protein was not measured but estimated as the difference between the dry weight and the sum of the ash and lipid content.

2.2.3. Estimation of the reproductive investment

Reproductive investment *R* was estimated from the decrease in energy content of the whole body from pre-spawning E_1 to post-spawning E_2 fish,

$$R = E_1 - E_2 \quad (3)$$

The energy density (E , kJ/cm³) can be estimated as

$$E = \delta \varphi \alpha \quad (4)$$

where δ is the dry weight percentage, φ is the energy density per gram dry weight, and α is Fulton's condition factor $\alpha = w/l^3$. The energy density per gram dry weight (φ) is estimated from the %lipid and %protein per gram dry weight and the energy values 39.5 kJ/g for lipids and 23.6 kJ/g for protein. The Fulton's condition factor was estimated for the pre-spawning and post-spawning stages from Dutch market samples from December and January–February, respectively.

The size-dependence of the reproductive investment was studied by estimating the size-dependence of the parameters δ , φ , α and body constituents using a GLM:

$$Z = \beta_0 + \beta_l l + \beta_S S + \beta_P P + \beta_{Sl} S \times l + \beta_{Pl} P \times l + \beta_{PS} P \times S + \beta_{PSl} P \times S \times l + \varepsilon \quad (5)$$

where *Z* stands for the dependent variables (δ , φ , α , %lipid, %ash, %protein, %dry weight) and *l* is body length (cm) in the pooled samples or individual fish, *S* is sex and *P* is spawning stage (pre-spawning, post-spawning). Starting from this model with all interactions, we evaluated all other possible models consisting of combinations of these parameters and selected then the model with lowest AIC and significant parameter estimates ($p < 0.05$). For illustration of the selected model, the dependent variable was predicted as a function of body size for males and females in the pre-spawning and post-spawning stage. The selected model was therefore transformed in a simple linear regression with an intercept incorporating the effect of sex and spawning stage and a slope giving the size-dependence. If the size variable was not selected to explain variation in the dependent variable, the slope is 0 and the expectation is given by the intercept.

For the period II, estimates of reproductive investment were available from pooled samples of the commercial fisheries (Rijnsdorp and Ibelings, 1989). Because the sizes of the fish in the pooled samples were not available, the reproductive investment between the period II and period III was compared for the average size of adult fish in the market samples in period II (males: 31.6 cm; females: 41.2 cm).

2.3. Growth

2.3.1. Data selection

For period I, the mean length at age reported by Herwig (1908) was used for the ages 1–4. For the older age groups, mean length at age were reported by Masterman (1911) and Wallace (1914). Averages were weighted by the number of observations per area and 0.5 was added to the age to account for sampling throughout the year.

For period II and III, the survey data of ages ≤ 6 and commercial data of ages ≥ 6 were merged because the commercial data is biased towards larger sizes due to the minimal mesh and landing size regulations. To account for the length stratification of the sampling, observations were weighted by their relative frequency in the population.

2.3.2. Analysis

To analyze the changes in growth over time, Von Bertalanffy (VB) growth curves were fitted for each period separately:

$$l_t = L_\infty - (L_\infty - L_0)e^{-Kt} \quad (6)$$

where l_t is length at age *t*, L_∞ is the asymptotic length, *K* the velocity to reach this asymptotic length and L_0 the length at $t = 0$. For the interpretation of changes in growth, the function was fitted to all age groups and forced to go through the origin ($L_0 = 0$). Since for the maturation estimation only ages 1–6 are relevant, the function was fitted to the survey data of only these ages and the annual length increments Δl used in the PMRN estimation (see Section 2.1.2.) were derived directly from this fit.

3. Results

3.1. Maturation

The PMRN shifted over the three periods to a smaller size and younger age in both male and female plaice (Fig. 1). The change in female PMRN over the last 20 years was about as important as the change in the 80 years before. The L_{p50} of 4 year old females decreased from 41.6 cm in the 1900s, to 33.3 cm in the 1980s and 22.9 cm in the 2000s. The negative slope of the female reaction norm reflects that the probability of becoming mature at a given length increases with the age of the fish. The male PMRN, which was well below the female PMRN, decreased from 1980s to 2000s: the L_{p50} of 2 year olds decreased from 19.5 cm to 16.0 cm.

The randomization tests indicate that the observed differences are mostly significant at the age where most of the plaice become mature (Table 2). The differences between the female L_{p50} s of the 1900s and the 1980s were significant for all ages ($p < 0.01$), while the differences between the 1980s and the 2000s were only significant for the maturation relevant ages 3 and 4, i.e. the ages at which the population growth trajectory hits the PMRN midpoints (Fig. 1). For the males, differences in the L_{p50} s between the 1980s and the 2000s were only significant for age 2 when most males mature. The large difference in male PMRNs at age 3 is not significant and can be considered an artefact due to the very low number of males maturing at this age.

3.2. Reproductive investment

Parameter estimates of the linear regressions of the energy density and body constituents with body size are given in Table 3 and the corresponding regressions (Eq. (5)) are plotted in Figs. 2 and 3. The energy density (kJ/cm^3) of pre-spawning plaice showed a significant positive relationship with body size. In post-spawning plaice, no relation with fish size was observed. Pre-spawning females had a

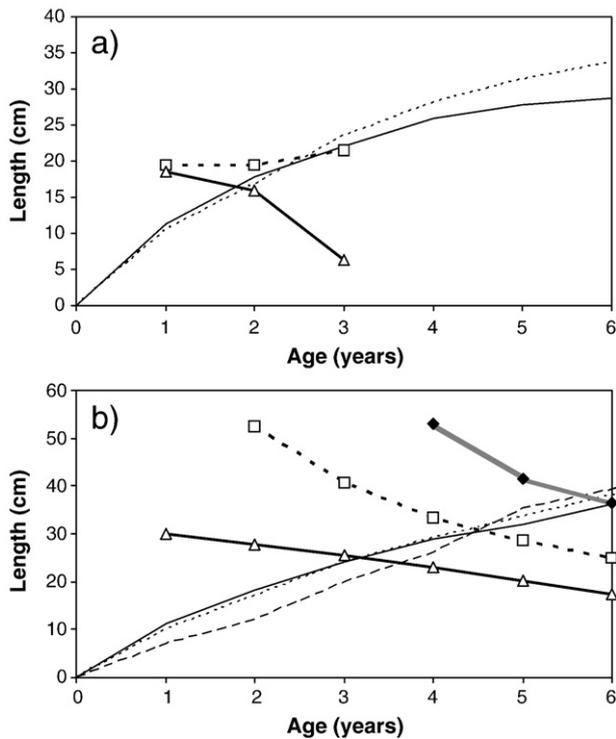


Fig. 1. Probabilistic maturation reaction norms (PMRNs, thick lines) for (a) males and (b) females showing the length (cm) at which the probability of becoming mature is 50% (L_{p50}) in relation to age (years) for three study periods: period I (◆), period II (□) and period III (△) and the average growth curves (thin lines): period I (dashed), period II (dotted) and period III (solid).

Table 2

Significance of the differences (cm) in the probabilistic reaction norm midpoints L_{p50} s by age between the periods for females and for males based on 10^5 permutations.

		Age 1	Age 2	Age 3	Age 4	Age 5	Age 6
♀	I – 1900s	n.a.	n.a.	12.4**	8.3**	7.9**	8.4*
	II – 1980s			$p = 0.003$	$p = 0.003$	$p = 0.007$	$p = 0.017$
	III – 2000s	n.a.	24.7	15.1**	10.4**	8.3	7.7
♂	II – 1980s	0.9	3.5*	15.2	n.a.	n.a.	n.a.
	III – 2000s	$p = 0.335$	$p = 0.048$	$p = 0.596$			

For some ages the L_{p50} s could not be obtained (n.a.). Level of significance: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

slightly higher energy density than males, whereas in the post-spawning stage, they had a lower energy density (Fig. 2a). The decrease in the energy density between the pre- and post-spawning stage reflects the reproductive investment. Reproductive investment increases with body size in both sexes. Females lose more energy than males, also relative to their larger body size (Fig. 2b).

Comparison of the reproductive investment in period II and period III, estimated for the mean size of adult plaice in the commercial samples in period II, revealed similar results: period II: 27% and 44% (Rijnsdorp and Ibelings, 1989); period III: 26% and 43% in males and females, respectively.

The difference in reproductive investment between males and females is reflected in the body constituents – size relationships (Fig. 3). Lipid content increased with size. Pre-spawning males had a higher lipid content than pre-spawning females, but in the post-spawning stage no difference was apparent (Fig. 3a). Relative protein

Table 3

Relationships with body length l (cm) of the energy density (kJ/cm^3), lipids (% dry weight), protein (% dry weight), ash (% dry weight), dry weight (%), and condition factor from the selected models from Eq. (5) with the proportion of deviance explained (r^2) and the p -value.

Sex (S)	Spawning stage (P)	Intercept	SE	Slope	SE	n
Energy density = $\beta_0 + \beta_{il} + \beta_{sS} + \beta_{pP} + \beta_{sS} \times l + \beta_{pP} \times l + \beta_{psP} \times S$ ($r^2 = 0.837$; $p < 0.001$)						
♀	1	3.322	0.290	0.065	0.009	12
♀	2	3.404	0.103	0.000	–	9
♂	1	3.872	0.429	0.036	0.015	12
♂	2	3.696	0.101	0.000	–	9
%lipid = $\beta_0 + \beta_{il} + \beta_{sS} + \beta_{pP} + \beta_{psP} \times S$ ($r^2 = 0.824$; $p < 0.001$)						
♀	1	8.140	1.680	0.314	0.047	12
♂	1	11.176	1.451	0.314	0.047	12
♀ + ♂	2	0.815	1.527	0.314	0.047	18
%ash = $\beta_0 + \beta_{il} + \beta_{pP} + \beta_{psP} \times l$ ($r^2 = 0.764$; $p < 0.001$)						
♀ + ♂	1	17.543	0.984	–0.181	0.032	24
♀ + ♂	2	16.844	0.385	0.000	–	18
%protein = $\beta_0 + \beta_{il} + \beta_{sS} + \beta_{pP}$ ($r^2 = 0.667$; $p < 0.001$)						
♀	1	75.690	1.552	–0.171	0.044	12
♀	2	76.812	1.658	–0.171	0.044	9
♂	1	72.217	1.335	–0.171	0.044	12
♂	2	79.198	1.321	–0.171	0.044	9
%dry weight = $\beta_0 + \beta_{il} + \beta_{pP}$ ($r^2 = 0.521$; $p < 0.001$)						
♀ + ♂	1	20.899	0.803	0.056	0.025	24
♀ + ♂	2	18.363	0.822	0.056	0.025	18
Condition factor = $\beta_0 + \beta_{il} + \beta_{sS} + \beta_{pP} + \beta_{sS} \times l + \beta_{pP} \times l + \beta_{psP} \times S$ ($r^2 = 0.655$; $p < 0.001$)						
♀	1	0.858	0.035	0.005	0.001	394
♀	2	0.810	0.002	0.000	–	824
♂	1	0.942	0.006	0.000	–	111
♂	2	0.965	0.054	–0.004	0.002	154

To simplify the illustration of the size-dependence, the selected model was transformed for each combination of sex (S) and spawning stage (P = pre-spawning stage 1 and post-spawning stage 2) in a simple linear model consisting only of an intercept and the body size-effect (slope). If the size-effect was not selected in Eq. (5), the slope is consequently 0. n denotes the number of grouped samples, except for condition factor where it refers to the number of individual fish.

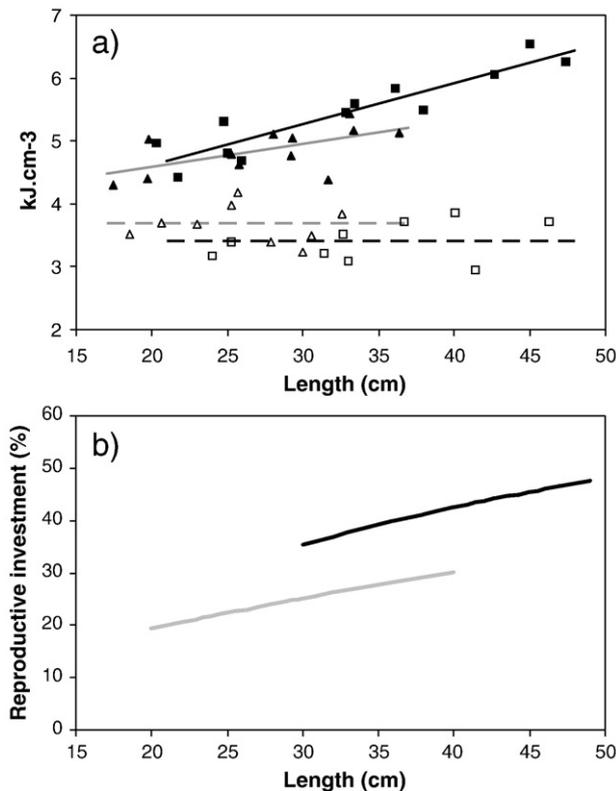


Fig. 2. The energy density (kJ/cm^3) – body size relationship in pre-spawning and post-spawning male and female plaice (a), and the corresponding reproductive investment expressed as the loss of energy density during the spawning period (b). In panel (a), symbols represent estimates of pre-spawning males (closed triangles), pre-spawning females (closed squares), post-spawning males (open triangles) and post-spawning females (open squares). Lines represent significant linear regressions for pre-spawning males (grey), pre-spawning females (black), post-spawning males (grey dashed grey) and post-spawning female (black dashed). In panel (b), the black line represents females and the grey line males.

content increased during the spawning season, in particular in males, and showed a negative relationship with body size (Fig. 3b). No difference in ash content occurred between the sexes. The ash content decreased with body size in pre-spawning fish, whereas in post-spawning fish, the ash content was higher and showed no relationship with fish size (Fig. 3c). The percentage dry weight did not differ between the sexes, but showed a positive relationship with body size and decreased over the spawning period (Fig. 3d). Fulton's condition factor differed between males and females. In males, pre-spawning condition was lower than in females and showed no relationship with body size. In post-spawning males, the condition was higher than in females and showed a slight decrease with body size. Pre-spawning condition factor in females increased with body size, whereas the post-spawning condition factor did not (Table 3).

3.3. Growth

The growth curves of both male and female plaice showed a gradual decrease in the L_∞ since the 1900s, whereas the slope of the curves in the origin or K , the velocity to reach L_∞ , increased between period I and period II (Fig. 4). For females, the estimated L_∞ decreased from 90 cm in period I to 53 cm in period II to 48 cm in period III, whereas K increased from 0.087 to 0.200 and 0.232 (Table 4). For the males, the L_∞ decreased from 51.3 to 41.2 cm and 32.6 cm, whereas K increased from 0.155 to 0.281 and 0.393 in period I, period II and period III, respectively.

4. Discussion

4.1. Maturation

Estimating PMRNs for males is difficult because almost all males are currently mature at age 2 (Table 1), making the estimation procedure rather sensitive for the incorrect classification of older males as immature. This may have influenced the estimated relation for the 1980s, in particular the lift in the L_{p50} at age 3, as these data were collected during the spawning period when some of the spent males are not easily distinguished from immature males (Rijnsdorp, 1989) and confident intervals incorporating these uncertainties would be rather large. The randomization test revealed that the difference in the male PMRNs is not significant at age 3. Because in period III samples were collected prior to the spawning period, the results for this period are less affected by the problem of misclassification and therefore more reliable although consisting of much less data. Sampling the male plaice population prior to the spawning season may be advisable to study the maturation process as it may also overcome the differences in spatial distribution of immature and mature fish during the spawning period (Rijnsdorp, 1989) as well as differences in catchability (Rijnsdorp, 1993b; Solmundsson et al., 2003). The difference in spatial distribution between immature and mature plaice during the spawning season rendered the data on males of Wallace (1914) unsuitable to estimate the PMRNs for period I. Nevertheless, the current maturation characteristics of males are quite different from the mean length or age at which Wallace (1914) estimated 50% to be mature: 30–37 cm and 5–6 years of age (Rijnsdorp, 1989). This suggests that also the male PMRN has shifted downwards substantially between period I and II.

As the PMRN disentangles the phenotypic plasticity in maturation caused by variability in growth from an evolutionary genetic effect (Heino et al., 2002a,b), the observed shift in the PMRNs of male and female plaice is indicative for FIE. The decrease in the female PMRN since period II suggests that the decline in the PMRN as observed by Grift et al. (2003) is still continuing (Fig. 5). It is possible, however, that the PMRN may be influenced by other factors that have not been taken into consideration (Kraak, 2007; Marshall and Browman, 2007; Mollet et al., 2007). It has been suggested that the PMRN may shift downward due to increasing temperatures (Grift et al., 2003; Kraak, 2007). The relative large shift over the recent two decades coincided with an increase in sea water temperature on the coastal nursery ground (van Aken, 2008). The average surface temperature during the season when the maturation process occurs (2nd and 3rd quarter, Rijnsdorp, 1989) increased from 13.6 °C in period I, to 14.3 °C (period II) to 15.5 °C (period III). Kraak (2007) showed that the L_{p50} of 4 year old females decreased by 1.0–1.4 cm for an increase in temperature of 1 °C. Hence, the increase in temperature of 1.2 °C between period II and III may explain only a small part (1.2–1.7 cm) of the observed decrease in the L_{p50} of 10.4 cm at age 4 (Table 2). The same conclusion can be drawn about the observed decrease in L_{p50} between period I and II. These results support the conclusion that the observed shifts in the maturation reaction norm are most likely due to FIE and corroborate the conclusions of earlier studies (Rijnsdorp, 1993a; Grift et al., 2003, 2007; Kraak, 2007).

Our results imply that the market sampling database becomes less suitable to monitor the changes in maturation of plaice as an increasing proportion of plaice matures at lengths below the minimum landing size of 27 cm. The problem can be solved for females when discards will be included in the monitoring program. For male plaice, however, this may not be sufficient as the maturation already occurs around the minimum size in the catch (~17 cm). Therefore, a maturation sampling program, for instance during the ongoing flatfish surveys in September and October, is needed to monitor further changes in maturation characteristics.

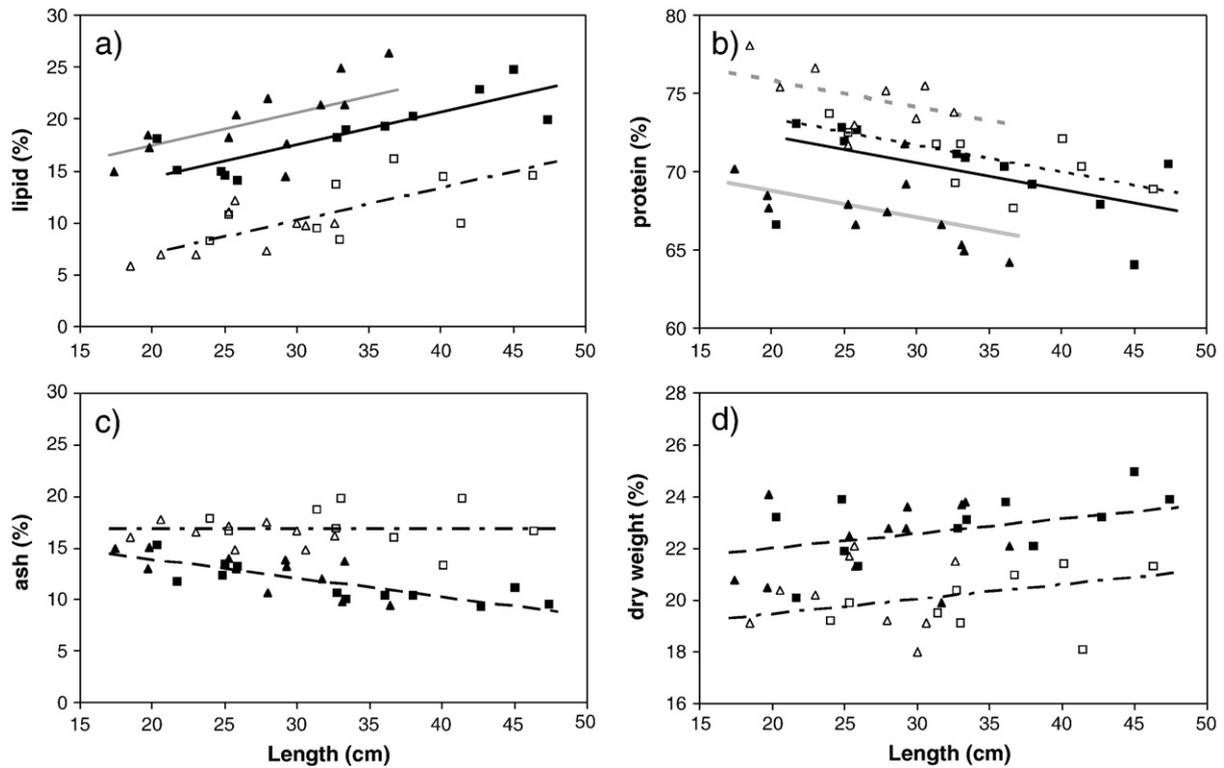


Fig. 3. Relationships of (a) lipid (%dry); (b) protein (%dry); (c) ash (%dry); (d) dry weight (%wet weight) with body size (cm) in male and female plaice. Symbols represent estimates of pre-spawning males (closed triangles), pre-spawning females (closed squares), post-spawning males (open triangles), post-spawning females (open squares). Lines represent significant linear regressions for pre-spawning males (grey), post-spawning males (grey dashed grey), pre-spawning females (black), post-spawning female (black dashed), pre-spawning males and females (long-dashed lines) and post-spawning males and females (dot-dashed).

4.2. Reproductive investment

Our study showed that the reproductive investment increased with body size in both males and females. These estimates include both spawning products and activity costs. The increase in reproductive investment with fish size correlates with a longer spawning duration of older fish (Rijnsdorp, 1989; Bromley, 2000), and may reflect the change in the trade-off between current and future reproduction.

Adult male and female plaice, differ in the percentage of lipids and protein. Pre-spawning males have a higher lipid content and lower protein content than females, whereas post-spawning males have a higher protein content than females. This reflects the differences in the chemical demands imposed by the spawning activities of male and female fish. Females require substantial amounts of both protein and lipids to produce eggs, while males will require relatively more lipids for spawning behaviour (Dawson and Grimm, 1980; Rijnsdorp and Ibelings, 1989).

Although the best solution currently available, the approach of estimating reproductive investment from the decrease in the energy density during the spawning period is still crude as it relies on a number of simplifying assumptions: First, it is assumed that during

Table 4

Von Bertalanffy parameters estimates of male and female plaice for three periods assuming that the size at $l(t=0) = 0$.

	Period I (1900s)			Period II (1980s)			Period III (2000s)		
	K	L_{∞}	KL_{∞}	K	L_{∞}	KL_{∞}	K	L_{∞}	KL_{∞}
♀	0.087	90.1	7.8	0.2	53.1	10.6	0.232	48.1	11.2
♂	0.155	51.3	8.0	0.281	41.2	11.6	0.393	32.6	12.8

K is a proxy for reproductive investment whereas the product KL_{∞} is a proxy of the rate of energy acquisition (see Discussion).

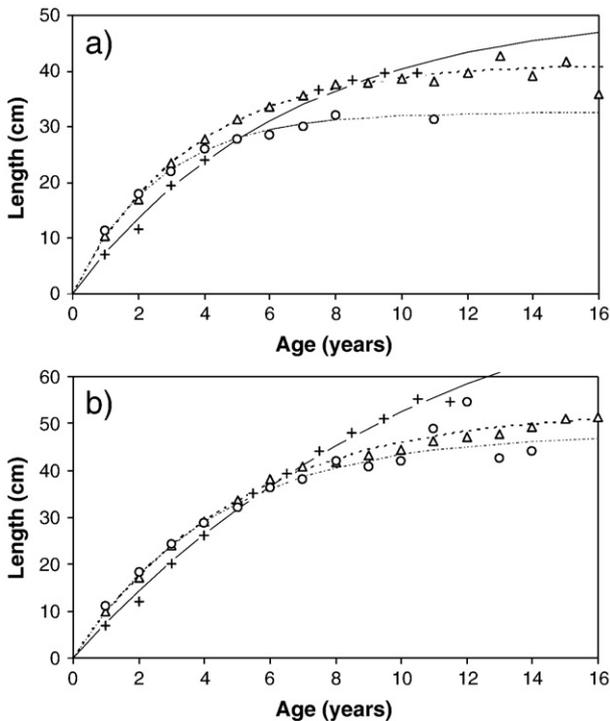


Fig. 4. Von Bertalanffy growth curves (smooth lines) fitted through the observed mean length at age for period I (+), period II (Δ) and period III (o) for males (a) and females (b), assuming that the size at $l(t=0) = 0$.

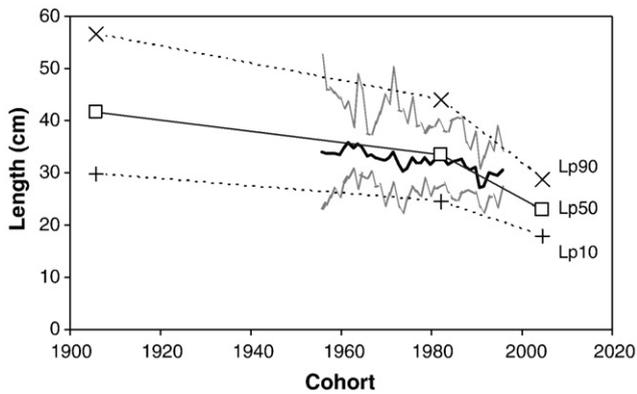


Fig. 5. PMRN midpoints (cm) at which the probability of 4-year old females to become mature is 10% (+ L_{p10}), 50% (\square L_{p50}) and 90% (\times L_{p90}) in period I (1900s), period II (1980s) and period III (2000s) as compared to the results of individual cohort (L_{p50} – black line; L_{p10} and L_{p90} – grey lines) from Grift et al. (2003).

the spawning period fish do neither feed or grow in body length. Tagging experiments have shown that body growth stops during the spawning period in winter (Dawson and Grimm, 1980; Rijnsdorp, 1990). Second, it is well established that plaice that are in spawning condition hardly feed. Less than 10% of the spawning males and about 2% of the spawning females were recorded with food remains in their guts in the middle of the spawning period (Rijnsdorp, 1989). Third, the assumption that the fish sampled in February had just ceased spawning, may not be true since the February samples may comprise fish from the eastern English Channel spawning ground that spawned a few weeks earlier than in our study area (Harding et al., 1978). As plaice from this spawning ground migrate through the southern North Sea on their return migration to the northern feeding grounds (Metcalf and Arnold, 1997; Hunter et al., 2003), it is likely that the spent females caught in the southern North Sea and that were already feeding in January (Rijnsdorp, 1989) originated from this spawning ground. Although fish with food remains in their gut were excluded from our samples we cannot exclude the possibility that some of the fish in our sample may have resumed feeding.

No change in reproductive investment between period II and period III could be detected. Because sampling in the 1980s did not take account of the effect of body size on reproductive investment and the sizes of the sampled fish in period II were not available, the results should be interpreted with caution. Nevertheless, the results are in agreement with a recent study which was unable to detect a change in female gonad weights since 1980 (Rijnsdorp et al., 2005). The lack of support for a change in reproductive investment contrasts the change in the VB growth parameters that suggest an increase in reproductive investment (see below). Further evidence for an increase in reproductive investment in North Sea plaice stems from the increase in potential fecundity between the late 1940s and the 1977–1984 of females up to about 40 cm (Rijnsdorp, 1991; Rijnsdorp et al., 2005). That the evidence for FIE in reproductive investment is sparse (Yoneda and Wright, 2004; Edeline et al., 2007) is partly due to the few studies that have addressed this issue (Jørgensen et al., 2007), but may also be due to the difficulty in disentangling a genetic change from the phenotypic plasticity (Rijnsdorp et al., 2005; Kjesbu and Witthames, 2007).

4.3. Growth

Age reading errors may have affected the accuracy of the growth estimated for the three periods. For period I and II, whole otoliths were analysed, whereas in period III, otolith sections were analysed. The first method may be relatively more prone to the underestimation of the age of older fish, because growth increments become smaller with age. Masterman (1911) discussed that this underestimation occurred

in male otoliths with more than seven rings. The estimated L_{∞} of the period I and II may therefore be overestimated. The estimated L_{∞} of 90 cm for period I was high compared with the maximum size observed in the catch for females of 73 cm, but the L_{∞} of 51 cm in males was close to the maximum size of 49 cm observed in the catch (Masterman, 1911; Wallace, 1914). Nevertheless, it is unlikely that age reading errors can fully explain the large change in L_{∞} observed and we conclude that K has increased and L_{∞} has decreased in both male and females plaice.

In order to interpret the observed changes in the VB growth parameters K and L_{∞} , we explore how a change in reproductive investment, or a change in the rate of energy acquisition may affect the asymptotic size L_{∞} and the growth velocity K . The VB growth model assumes that somatic growth is the result of the rate of energy acquisition and the rate of energy expenditure (Von Bertalanffy and Pirozynski, 1952). Since the VB growth model does not include maturation, a change in the onset of maturation will not affect the VB growth parameters. Integration of the energy allocation model shows that VB parameter K is related to the energy expenditure, L_{∞} is related to the ratio of energy acquisition over energy expenditure and the product KL_{∞} is related to energy acquisition (Charnov et al., 2001; West et al., 2001; Lester et al., 2004). Assuming that energy expenditure will be mainly determined by reproductive investment, the observed change in K in males and females may suggest that reproductive investment has increased throughout the 20th century. Further, the increase in the rate of energy acquisition (KL_{∞}) was insufficient to balance the increase in energy expenditure (K) resulting in a decrease in L_{∞} .

The changes in energy acquisition and energy expenditure may be due to changes in environmental conditions as well evolutionary changes. Earlier studies have shown that density-dependent reductions in growth are restricted to the juvenile phase when plaice are concentrated in restricted coastal nursery grounds. Juvenile growth increased in the 1960s and 1970s coinciding with an increase in eutrophication and bottom trawling, which may have improved the food availability (Rijnsdorp and Van Leeuwen, 1996). Since the mid 1980s, annual growth increments of plaice and sole have decreased, which was interpreted as a decrease in the available food (Rijnsdorp et al., 2004; Philippart et al., 2007). This decrease contrasts with the increase in the indicator of energy acquisition rate KL_{∞} between the 1980s (period II) and the 2000s (period III) observed in this study. This suggests that part of the increase in energy acquisition KL_{∞} may not be related to the phenotypic plastic response to the environment and may be due to a fisheries-induced evolutionary response to cope with the increasing reproductive investment. A comparison of size specific fecundity revealed an increase since the 1940s, consistent with the change expected from FIE (Rijnsdorp, 1991; Rijnsdorp et al., 2005).

In order to address the changes in growth in more detail, a careful study of changes in growth rate of cohorts in relation to changes in size-selective harvesting, temperature and food availability employing the available otolith collections may help to test the hypothesis of FIE (Sinclair et al., 2002a,b). Swain et al. (2007) adopted this approach and concluded that the mean size at age 4 in Gulf of St Lawrence cod decreased due to FIE, although their conclusion was challenged (Heino et al., 2008; Dutil et al., 2008).

4.4. Conclusion

Our analysis provided support for FIE changes in maturation in males and females over the past century. The higher rate of change observed in the recent two decades might be due to synergistic effects with increasing temperature. The evidence for a FIE increase in reproductive investment is inconclusive. An increase in reproductive investment is suggested by the changes in the VB growth parameters, but the evidence for FIE from the direct measurement of reproductive

investment is inconclusive as no change in the size-conditional reproductive energy loss could be detected between period II and period III. Literature data suggests that reproductive investment increased between period I and period II in females up to 40 cm, but not in larger sized females. The observed changes in maturation, reproductive investment and growth are consistent with FIE, but the changes in reproductive investment and growth need further investigation to disentangle the role of phenotypic plasticity.

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References

- Barot, S., Heino, M., O'Brien, L., Dieckmann, U., 2004. Estimating reaction norms for age and size at maturation when age at first reproduction is unknown. *Evolutionary Ecology Research* 6, 659–678.
- Biro, P.A., Post, J.R., 2008. Rapid depletion of genotypes with fast growth and bold personality traits from harvested fish populations. *Proceedings of the National Academy of Sciences of the United States of America* 105, 2919–2922.
- Bligh, E.G., Dyer, W.J., 1959. A rapid method of total lipid extraction and purification. *Canadian Journal of Biochemistry and Physiology* 37, 911–917.
- Bolle, L.J., Rijnsdorp, A.D., Van Neer, W., Millner, R.S., van Leeuwen, P.I., Ervynck, A., Ayers, R., Ongena, E., 2004. Growth changes in plaice, cod, haddock and saithe in the North Sea: a comparison of (post-)medieval and present-day growth rates based on otolith measurements. *Journal of Sea Research* 51, 313–328.
- Bromley, P.J., 2000. Growth, sexual maturation and spawning in central North Sea plaice (*Pleuronectes platessa* L.), and the generation of maturity ogives from commercial catch data. *Journal of Sea Research* 44, 27–43.
- Charnov, E.L., Turner, T.F., Winemiller, K.O., 2001. Reproductive constraints and the evolution of life histories with indeterminate growth. *Proceedings of the National Academy of Science of the United States of America* 98, 9460–9464.
- Craig, J.F., 1977. Body-composition of adult perch, *Perca fluviatilis* in Windermere, with reference to seasonal changes and reproduction. *Journal of Animal Ecology* 64, 617–632.
- Dawson, A.S., Grimm, A.S., 1980. Quantitative seasonal changes in the protein, lipid and energy content of the carcass, ovaries and liver of adult female plaice, *Pleuronectes platessa* L. *Journal of Fish Biology* 16, 493–504.
- Dieckmann, U., Heino, M., 2007. Probabilistic maturation reaction norms: their history, strengths, and limitations. *Marine Ecology Progress Series* 335, 253–269.
- Dunlop, E.S., Heino, M., Dieckmann, U., 2009. Eco-genetic modelling of contemporary life-history evolution. *Ecological Applications* 19, 1815–1834.
- Dutil, J.D., Jabouin, C., Larocque, R., Desrosiers, G., Blier, P.U., 2008. Atlantic cod (*Gadus morhua*) from cold and warm environments differ in their maximum growth capacity at low temperatures. *Canadian Journal of Fisheries and Aquatic Sciences* 65, 2579–2591.
- Edeline, E., Carlson, S.M., Stige, L.C., Winfield, I.J., Fletcher, J.M., James, J.B., Haugen, T.O., Vøllestad, L.A., Stenseth, N.C., 2007. Trait changes in a harvested population are driven by a dynamic tug-of-war between natural and harvest selection. *Proceedings of the National Academy of Sciences of the United States of America* 104, 15799–15804.
- Ernande, B., Dieckmann, U., Heino, M., 2004. Adaptive changes in harvested populations, plasticity and evolution of age and size at maturation. *Proceedings of the Royal Society B-Biological Sciences* 271, 415–423.
- Grift, R.E., Rijnsdorp, A.D., Barot, S., Heino, M., Dieckmann, U., 2003. Fisheries-induced trends in reaction norms for maturation in North Sea plaice. *Marine Ecology Progress Series* 257, 247–257.
- Grift, R.E., Heino, M., Rijnsdorp, A.D., Kraak, S.B.M., Dieckmann, U., 2007. Three-dimensional maturation reaction norms for North Sea plaice. *Marine Ecology Progress Series* 334, 213–224.
- Harding, D., Nichols, J.H., Tungate, D.S., 1978. The spawning of the plaice (*Pleuronectes platessa* L.) in the southern North Sea and English Channel. *Rapports et Procès-Verbaux des Réunions Conseil International pour l'Exploration de la Mer* 172, 102–113.
- Heino, M., 1998. Management of evolving fish stocks. *Canadian Journal of Fisheries and Aquatic Sciences* 55, 1971–1982.
- Heino, M., Dieckmann, U., Gødo, O.R., 2002a. Estimating reaction norms for age and size at maturation with reconstructed immature size distributions, a new technique illustrated by application to Northeast Arctic cod. *ICES Journal of Marine Science* 59, 562–575.
- Heino, M., Dieckmann, U., Gødo, O.R., 2002b. Measuring probabilistic reaction norms for age and size at maturation. *Evolution* 56, 669–678.
- Heino, M., Baulier, L., Boukal, D.S., Dunlop, E.S., Eliassen, S., Enberg, K., Jørgensen, C., Varpe, O., 2008. Evolution of growth in Gulf of St Lawrence cod? *Proceedings of the Royal Society B-Biological Sciences* 275, 1111–1112.
- Herwig, W., 1908. Bericht über die Untersuchungen der Biologischen Anstalt auf Helgoland. *Deutsche Wissenschaftlichen Kommission für der Internationalen Meeresforschung IV/V*, pp. 1–187. Jahresbericht.
- Hunter, E., Metcalfe, J.D., Reynolds, J.D., 2003. Migration route and spawning area fidelity by North Sea plaice. *Proceedings of the Royal Society of London Series B-Biological Sciences* 270, 2097–2103.
- Jørgensen, C., Enberg, K., Dunlop, E.S., Arlinghaus, R., Boukal, D.S., Brander, K., Ernande, B., Gårdmark, A., Johnston, F., Matsumura, S., Pardoe, H., Raab, K., Silva, A., Vainikka, A., Dieckmann, U., Heino, M., Rijnsdorp, A.D., 2007. Managing evolving fish stocks. *Science* 318, 1247–1248.
- Kennedy, J., Witthames, P.R., Nash, R.D.M., 2007. The concept of fecundity regulation in plaice (*Pleuronectes platessa*) tested on three Irish Sea spawning populations. *Canadian Journal of Fisheries and Aquatic Sciences* 64, 587–601.
- Kjesbu, O.S., Witthames, P.R., 2007. Evolutionary pressure on reproductive strategies in flatfish and groundfish: relevant concepts and methodological advancements. *Journal of Sea Research* 58, 23–34.
- Kjesbu, O.S., Klungsoyr, J., Kryvi, H., Witthames, P.R., Walker, M.G., 1991. Fecundity, atresia, and egg size of captive Atlantic cod (*Gadus morhua*) in relation to proximate body composition. *Canadian Journal of Fisheries and Aquatic Sciences* 48, 2333–2343.
- Kraak, S.B.M., 2007. Does the probabilistic maturation reaction norm approach disentangle phenotypic plasticity from genetic change? *Marine Ecology Progress Series* 335, 295–300.
- Kuparinen, A., Merila, J., 2007. Detecting and managing fisheries-induced evolution. *Trends in Ecology and Evolution* 22, 652–659.
- Law, R., 2000. Fishing, selection, and phenotypic evolution. *ICES Journal of Marine Science* 57, 659–668.
- Lester, N.P., Shuter, B.J., Abrams, P.A., 2004. Interpreting the von Bertalanffy model of somatic growth in fishes: the cost of reproduction. *Proceedings of the Royal Society of London Series B-Biological Sciences* 271, 1625–1631.
- Marshall, C.T., Browman, H.I., 2007. Disentangling the causes of maturation trends in exploited fish populations. *Marine Ecology Progress Series* 335, 249–251.
- Masterman, A.T., 1911. Report on the Research Work of the Board of Agriculture and Fisheries in relation to the Plaice Fisheries of the North Sea. Volume IV. Biological statistics. Age and Sex. 1905–1906. His Majesty's Stationery Office, London. 61 pp.
- Metcalfe, J.D., Arnold, G.P., 1997. Tracking fish with electronic tags. *Nature* 387, 665–666.
- Mollet, F.M., Kraak, S.B.M., Rijnsdorp, A.D., 2007. Fisheries-induced evolutionary changes in maturation reaction norms in North Sea sole *Solea solea*. *Marine Ecology Progress Series* 351, 189–199.
- Philippart, C.J.M., Beukema, J.J., Cadee, G.C., Dekker, R., Goedhart, P.W., van Iperen, J.M., Leopold, M.F., Herman, P.M.J., 2007. Impacts of nutrient reduction on coastal communities. *Ecosystems* 10, 95–118.
- Ricker, W., 1981. Changes in the average size and average age of Pacific salmon. *Canadian Journal of Fisheries and Aquatic Sciences* 38, 1636–1656.
- Rijnsdorp, A.D., 1989. Maturation of male and female North Sea plaice (*Pleuronectes platessa* L.). *Journal du Conseil international pour l'Exploration de la Mer* 46, 35–51.
- Rijnsdorp, A.D., 1990. The mechanism of energy allocation over reproduction and somatic growth in female North Sea plaice, *Pleuronectes platessa* L. *Netherlands Journal of Sea Research* 25, 279–290.
- Rijnsdorp, A.D., 1991. Changes in fecundity of female North Sea plaice (*Pleuronectes platessa* L.) between three periods since 1900. *ICES Journal of Marine Science* 48, 253–280.
- Rijnsdorp, A.D., 1993a. 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. *Oecologia* 96, 391–401.
- Rijnsdorp, A.D., 1993b. Selection differentials in male and female North Sea plaice and changes in maturation and fecundity. In: Stokes, T.K., McGlade, J.M., Law, R. (Eds.), *The exploitation of evolving resources*. Springer-Verlag, Berlin, pp. 19–36.
- Rijnsdorp, A.D., Ibelings, B., 1989. Sexual dimorphism in the energetics of reproduction and growth of North Sea plaice, *Pleuronectes platessa* L. *Journal of Fish Biology* 35, 401–415.
- Rijnsdorp, A.D., Millner, R.S., 1996. Trends in population dynamics and exploitation of North Sea plaice (*Pleuronectes platessa* L.) since the late 1800s. *ICES Journal of Marine Science* 53, 1170–1184.
- Rijnsdorp, A.D., Van Leeuwen, P.I., 1996. Changes in growth of North Sea plaice since 1950 in relation to density, eutrophication, beam trawl effort, and temperature. *ICES Journal of Marine Science* 53, 1199–1213.
- Rijnsdorp, A.D., Van Keeken, O.A., Bolle, L.J., 2004. Changes in productivity of the southeastern North Sea as reflected in the growth of plaice and sole. *ICES CM2004/K:13*.
- Rijnsdorp, A.D., Grift, R.E., Kraak, S.B.M., 2005. Fisheries-induced adaptive change in reproductive investment in North Sea plaice (*Pleuronectes platessa*)? *Canadian Journal of Fisheries and Aquatic Sciences* 62, 833–843.
- Sinclair, A.F., Swain, D.P., Hanson, J.M., 2002a. Disentangling the effects of size-selective mortality, density, and temperature on length-at-age. *Canadian Journal of Fisheries and Aquatic Sciences* 59, 372–382.
- Sinclair, A.F., Swain, D.P., Hanson, J.M., 2002b. Measuring changes in the direction and magnitude of size-selective mortality in a commercial fish population. *Canadian Journal of Fisheries and Aquatic Sciences* 59, 361–371.
- Solmundsson, J., Karlsson, H., Pálsson, J., 2003. Sexual differences in spawning behaviour and catchability of plaice (*Pleuronectes platessa*) west of Iceland. *Fisheries Research* 61, 57–71.

- Swain, D.P., Sinclair, A.F., Hanson, J.M., 2007. Evolutionary response to size-selective mortality in an exploited fish population. *Proceedings of the Royal Society B-Biological Sciences* 274, 1015–1022.
- Thomas, G., Quoss, H., Hartmann, J., Eckmann, R., 2009. Human-induced changes in the reproductive traits of Lake Constance common whitefish (*Coregonus lavaretus*). *Journal of Evolutionary Biology* 22, 88–96.
- Tyler, C.R., Sumpter, J.P., 1996. Oocyte growth and development in teleosts. *Reviews in Fish Biology and Fisheries* 6, 287–318.
- Vainikka, A., Gårdmark, A., Bland, B., Hjelm, J., 2009. Two- and three-dimensional maturation reaction norms for the eastern Baltic cod, *Gadus morhua*. *ICES Journal of Marine Science* 66, 248–257. doi:10.1093/icesjms/fsn199.
- van Aken, H.M., 2008. Variability of the water temperature in the western Wadden Sea on tidal to centennial time scales. *Journal of Sea Research* 60, 227–234.
- Von Bertalanffy, L., Pirozynski, W.J., 1952. Tissue respiration, growth, and basal metabolism. *Biological Bulletin* 105, 240–256.
- Wallace, W., 1914. Report on the age, growth, and sexual maturity of the plaice in certain parts of the North Sea. *Fishery Investigations Series II—Sea Fisheries* 2, 1–79.
- West, G.B., Brown, J.H., Enquist, B.J., 2001. A general model for ontogenetic growth. *Nature* 413, 628–631.
- Wright, P.J., 2005. Temporal and spatial variation in reproductive investment of haddock in the North Sea. *ICES C.M.* 2005/Q:07.
- Wimpenny, R.S. 1953. *The plaice*. Vol. Arnold, London. 144 p.
- Yoneda, M., Wright, P.J., 2004. Temporal and spatial variation in reproductive investment of Atlantic cod *Gadus morhua* in the northern North Sea and Scottish west coast. *Marine Ecology Progress Series* 276, 237–248.