

Reconstructing the effects of fishing on life-history evolution in North Sea plaice *Pleuronectes platessa*

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ABSTRACT: Growing evidence suggests that fishing may induce rapid contemporary evolution in certain life-history traits. This study analyzes fisheries-induced changes in life-history traits describing growth, maturation, and reproduction, using an individual-based eco-genetic model that captures both the population dynamics and changes in genetic trait values. The model was successfully calibrated to match the observed life-history traits of female North Sea plaice *Pleuronectes platessa* around the years 1900 and 2000. On this basis, we report the following findings. First, the model indicates changes in 3 evolving life-history traits: the intercept of the maturation reaction norm decreases by 27%, the weight-specific reproductive-investment rate increases by 10%, and the weight-specific energy-acquisition rate increases by 1%. Together, these changes reduce the weight at maturation by 46% and the asymptotic body weight by 28% relative to the intensification of fishing around 1900. Second, while the maturation reaction norm and reproductive-investment rate change monotonically over time, the energy-acquisition rate follows a more complex course: after an initial increase during the first 50 yr, it remains constant for about 30 yr and then starts to decline. Third, our analysis indicates that North Sea plaice has not yet attained a new evolutionary equilibrium: it must be expected to evolve further towards earlier maturation, increased reproductive investment, and lower adult body size. Fourth, when fishing continues in our model 100 yr into the future, the pace of evolution slows down for the maturation reaction norm and the rate of energy acquisition, whereas no such slowing down is expected for the rate of reproductive investment.

KEY WORDS: Fisheries-induced evolution · Eco-genetic model · Individual-based model · Density-dependent growth · Energy allocation · Energy acquisition · Reproductive investment · Maturation reaction norm

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INTRODUCTION

Fisheries-induced life-history evolution

The exploitation of fish stocks is increasingly recognized as a driving force in the evolution of life-history traits, such as those affecting growth, maturation, and reproduction (Law & Grey 1989, Rijnsdorp 1993a, Stokes et al. 1993, Heino 1998, Hutchings 2005, Dieckmann et al. 2009, Heino et al. 2015). Fish-

eries typically increase mortality rates and select against larger body sizes, rendering a fish's current reproduction more important than its future reproduction (Heino & Kaitala 1999). As a consequence, exploited fish stocks are expected to mature earlier and invest more into reproduction (Law 2000). Growth rates may increase or decrease depending on the direction and strength of the corresponding direct selection pressures and of those resulting from stock-specific life-history trade-offs (Sinclair et al.

2002, Dunlop et al. 2009b, Enberg et al. 2009, 2012). In agreement with these theoretical expectations, several empirical studies have indicated fisheries-induced evolution towards earlier maturation, increased reproductive investment, and changes in growth rate (Conover & Munch 2002, Olsen et al. 2004, Jørgensen et al. 2007, Kuparinen & Merilä 2007)

Growth, maturation, and reproduction are intricately linked in the energy-allocation schedules of individuals. Hence, changes in life-history traits will be a combined effect of genetic responses and phenotypic plasticity that is difficult to disentangle (Rijnsdorp 1993a, Marshall & Browman 2007, Wright et al. 2014). Since life-history changes due to size-selective fishing may cause a reduction of sustainable yield (Law & Grey 1989, Heino & Godø 2002), it is important to understand the eco-evolutionary mechanisms underlying these changes in order to develop science-based management strategies that take into account the possible consequences of the evolutionary effects of fishing (Jørgensen et al. 2007, Kuparinen & Hutchings 2012, Laugen et al. 2014).

Models are a powerful tool to study the dynamics of complex systems and to provide guidance for management. Recently, individual-based eco-genetic models have been developed to study fisheries-induced evolution (Dunlop et al. 2009b). These models capture essential ecological processes (such as growth, maturation, reproduction, and mortality) alongside essential genetic processes (such as mating, inheritance, and expression). As such, they provide a quantitative basis for studying the evolution of life-history traits, their correlation structure, and the effects of different exploitation strategies (Dunlop et al. 2007, 2009b, Thériault et al. 2008, Enberg et al. 2009, Jørgensen et al. 2009, Okamoto et al. 2009). Furthermore, they provide guidance to managers on the potential consequences of fisheries-induced evolution for the sustainable management of fisheries resources and help identify options for mitigating adverse effects (Dunlop et al. 2009a, Jørgensen et al. 2009, Heino et al. 2013, Laugen et al. 2014, Mollet et al. 2015).

North Sea plaice and its exploitation history

Changes in the life-history traits and exploitation patterns of North Sea plaice *Pleuronectes platessa* are well documented. Between the early 1900s and the mid-1980s, size at maturation decreased by 10 to 16% and 35% in females and males, respectively;

likewise, age at maturation decreased by 30 to 35% and 50 to 60% in females and males, respectively (Rijnsdorp 1989). Since these changes coincided with a downward shift in the probabilistic maturation reaction norm (PMRN; Heino et al. 2002a, Dieckmann & Heino 2007, Heino & Dieckmann 2008), part of this change has been attributed to fisheries-induced evolution (Grift et al. 2003, 2007, van Walraven et al. 2010). Over the same period, size-specific fecundity increased in females up to 40 cm, but not in larger females, complicating the interpretation of these observations (Rijnsdorp et al. 2005). Changes in growth rates were mainly observed for juvenile fish, most likely due to an increase in the productivity of the environment during and after the 1960s and 1970s (Rijnsdorp & van Leeuwen 1996). The growth rates of larger-sized plaice have not changed substantially (Bolle et al. 2004), but the asymptotic length (L_{∞}) of the Von Bertalanffy growth equation has declined since the early 1900s (van Walraven et al. 2010). Density-dependent reductions in growth rate appear to be restricted to the juvenile phase, when plaice are concentrated in shallow coastal nursery areas (Rijnsdorp & van Leeuwen 1996, Teal et al. 2008).

North Sea plaice has been exploited through trawl fisheries for centuries (Bennema & Rijnsdorp 2015), but fishing mortality did not increase to substantial levels before the last decade of the 19th century, when steam trawlers were introduced (Engelhard 2008, Kerby et al. 2012). The fishing mortality rate (F) increased from about 0.3 yr^{-1} in the first half of the 1890s to 0.7 yr^{-1} around 1910. Fishing was severely reduced during World Wars I and II, but increased to peak levels of 0.9 yr^{-1} in the 1930s and 0.8 yr^{-1} in the 1980s and 1990s (Rijnsdorp & Millner 1996). Since 2000, F has gradually decreased to the management target of 0.3 yr^{-1} (ICES 2014). Fishing mortality averaged about 0.5 yr^{-1} during the 20th century, well above the rate of natural mortality (M) of 0.1 yr^{-1} (Beverton 1964). Because plaice is a sexually dimorphic species, the selection differential imposed by fishing differs between the sexes (Rijnsdorp 1993b).

Objectives of this study

Here, we present an eco-genetic model for female North Sea plaice to describe the effects of one century of fishing on co-evolving biological traits intimately linked to the energy allocation between growth and reproduction. By matching model pre-

dictions with empirical observations of weight at age, onset of maturation, and reproductive investment for 2 periods (historic, around 1900 and present, around 2000), we explore how these traits will continue to evolve if fishing mortality remains at the historic level. We focus on females only and ignore sexual dimorphism, because a mechanistic eco-evolutionary explanation of the sexual dimorphism in flatfish is so far lacking.

MATERIALS AND METHODS

Empirical data

Phenotypic trait values were obtained from the literature for the historic period (around 1900) and present period (around 2000). Historic data have been derived from the literature and analyzed by Rijnsdorp & Millner (1996) and van Walraven et al. (2010). For the present period, biological sampling data collected between 1960 and the present were obtained from the IMARES database and were used to estimate (1) length and weight at age, (2) probabilistic maturation reaction norms (PMRNs), and (3) ovary weights. Female reproductive investment was then estimated from ovary weights and migration costs and expressed in terms of an equivalent somatic weight, to determine a ratio relative to total body weight (Mollet et al. 2010).

Model description

We developed an individual-based eco-genetic model (Dunlop et al. 2009b) with annual time increments. Each year, a cohort of super-individuals is born (Scheffer et al. 1995), characterized by their age and size, as well as by 3 genetic traits. Individuals inherit the mean genetic trait value of their parents, with variation. The model allows us to quantify changes in population abundance together with changes in the population's composition with regard to age, size, genetic traits, and emerging phenotypic traits. This is achieved by following through time the individual-based processes of growth, maturation, mating, reproduction, inheritance, expression, and mortality, taking into account life-history trade-offs between growth and mortality and between reproduction and mortality (Fig. 1). The model comprises 23 parameters and 3 evolving genetic traits: the weight-specific energy-acquisition rate (a), the intercept (u) of the PMRN, and the weight-specific reproductive-investment rate (c) (see Table S1 in the Supplement at www.int-res.com/articles/suppl/m542_p195_supp.pdf). The other parameters are fixed (Table S2 in the Supplement). Fishing starts in 1895 with a constant mortality rate of $F = 0.5 \text{ yr}^{-1}$ and continues until the end of the study period in 2100. The model is calibrated to data on weights at age and PMRN midpoints available for the first decade of the 20th century, and to data on weights at age, PMRN midpoints, and reproductive investments collected be-

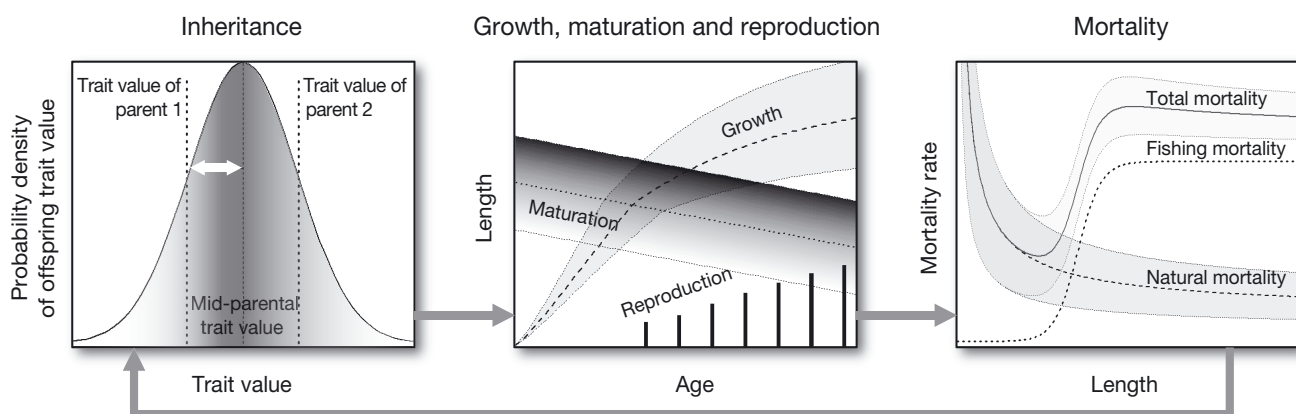


Fig. 1. Annual cycle of North Sea plaice *Pleuronectes platessa* life-history processes in the individual-based eco-genetic model. Depending on evolving traits describing energy acquisition, maturation reaction norm, and reproductive investment, individuals grow, mature, reproduce, and die. Size-dependent mortalities arise from fishing and trade-offs between growth and survival, reproduction and survival, and maintenance and survival. Mature individuals reproduce once per year and pass on their genetic traits to their offspring. The inherited traits are phenotypically expressed and, in turn, determine the offspring's growth, maturation, reproduction, and mortality. The arrow in the left panel indicates the standard deviation of genetic variation. The envelopes in the middle panel illustrate the probabilistic maturation reaction norm and the effects of trait variation on growth. The envelopes in the right panel illustrate the effects of trait variation on natural mortality

tween 2000 and 2010. The salient aspects of the model are presented below. Details are given in the Supplement, including parameter values and their sources.

Somatic growth and reproductive investment follow the energy-allocation model by West et al. (2001),

$$\frac{dw}{dt} = aw^{3/4} - bw - \begin{cases} 0 & \text{if } t < t_{\text{mat}} \\ cw & \text{if } t \geq t_{\text{mat}}, \end{cases} \quad (1)$$

where w is an individual fish's somatic weight, t is its age, and t_{mat} is its age at maturation. We assume an allometric energy-acquisition rate ($aw^{3/4}$) as suggested by theory (West et al. 1997) and empiric data (Fonds et al. 1992). After becoming mature, fish invest into reproduction at the rate cw , resulting in a total annual reproductive investment at age t of $\gamma_t = \int_{t-1}^t cw(t') dt'$. The rates of maintenance investment (bw) and reproductive investment (cw), respectively, are proportional to body weight and cause the growth curve to level off at the asymptotic weight $w_{\infty} = [a/(b+c)]^4$, where b is the weight-specific maintenance-investment rate. The weight-specific energy-acquisition rate, a , decreases with increasing population biomass. Since density-dependent growth in North Sea plaice occurs only in the nursery areas where juvenile plaice are concentrated (Rijnsdorp & van Leeuwen 1996, Bolle et al. 2004), this density dependence in growth is applied only to fish smaller than 25 cm.

Maturation is defined by a maturation reaction norm (Stearns & Koella 1986), which is assumed to be linear with intercept u and slope s ,

$$I_{p50}(t) = u + st. \quad (2)$$

Maturation is a probabilistic process, and I_{p50} defines the reaction-norm midpoints, i.e. the body lengths at which the probability of maturing reaches 50%. Using a PMRN (Heino et al. 2002a, Dieckmann & Heino 2007, Heino & Dieckmann 2008), we assume that for any given combination of age and size, the probability of maturing is given by

$$p_{\text{mat}}(l, t) = \frac{1}{1 + \exp[-(l(t) - I_{p50}(t)) / \phi]} \quad (3)$$

where l is body length and ϕ is a scaling parameter determining the width, d , of the PMRN, i.e. the difference in body length over which maturation probability rises from 25 to 75%, according to $d = 2\phi \log(0.75)$.

The instantaneous rate of natural mortality (M) is size-dependent and consists of (1) a predation mortality rate (m_p) that decreases with size and increases with foraging activity (describing the growth-survival trade-off), (2) a reproduction mortality rate (m_r)

that depends on the relative energy loss due to reproduction (describing the reproduction-survival trade-off), and (3) a starvation mortality rate (m_s) that applies when the maintenance costs (i.e. bw) cannot be met (describing the maintenance-survival trade-off).

The processes of maturation, mating, reproduction, inheritance, expression, and mortality are all modeled stochastically.

The fishing mortality rate that an individual experiences (F_l) is a function of its body size, l . Mesh-size selection is described by a logistic relationship, defined by the mesh size (ψ), the mesh-selection factor (λ), and the mesh-selection sharpness (ϕ) (Sparre & Venema 1998),

$$F_l = \frac{F_{\text{max}}}{1 + \exp[-\phi(l - \lambda\psi)]}, \quad (4)$$

where F_{max} is the maximum fishing mortality rate, which applies to the size groups that are fully recruited to the fishery. The realized fishing mortality rate F_{pop} experienced by the population as a whole is estimated from the annual decline in the number of fish of age 2 yr and older, correcting for the number of fish that died from natural causes. To keep F_{pop} at a target level F despite changes in the population's size distribution, the maximum fishing mortality rate F_{max} is adjusted each year (see Eq. S12 in the Supplement).

Model calibration

Parameterization was carried out in 3 steps. In the first step, parameters for which independent estimates are available were either taken from the literature or directly estimated from empirical data on age, size, and maturity from Dutch market samples and scientific surveys (Table S2 in the Supplement).

In the second step, the coefficients of genetic variation were fixed at 10% (see below) and the remaining parameters were fitted (Table S2), separately for the historic period (around 1900) and the present period (around 2000), so as to minimize the sum (Δ) of squared relative deviations at ages $t = 1, \dots, 10$ of model-predicted (subscript M) from empirically observed (subscript E) population-averaged body weights \bar{w}_t , PMRN midpoints $\bar{I}_{p50,t}$ and relative reproductive investments $\bar{r}_t = \gamma_t / w_t$,

$$\Delta = \frac{1}{10} \sum_{t=1}^{10} \left(\frac{\bar{w}_{t,M} - \bar{w}_{t,E}}{\bar{w}_{t,E}} \right)^2 + \frac{1}{6} \sum_{t=1}^6 \left(\frac{\bar{I}_{p50,t,M} - \bar{I}_{p50,t,E}}{\bar{I}_{p50,t,E}} \right)^2 + \frac{1}{5} \sum_{t=6}^{10} \left(\frac{\bar{r}_{t,M} - \bar{r}_{t,E}}{\bar{r}_{t,E}} \right)^2. \quad (5)$$

As empirical observations on reproductive investments are unavailable for the historic period, the third term above was omitted when calculating Δ for that period. Model-predicted values were obtained assuming that the population was at evolutionary equilibrium. Parameter combinations minimizing Δ were determined using a grid search (Table S2). The average natural mortality rate at age 6 yr was set to $M = 0.1 \text{ yr}^{-1}$ in accordance with the ICES stock assessment (ICES 2011). The density dependence of energy-acquisition rates (Eq. S4 in the Supplement) was assumed to be absent (negligible) in the heavily exploited (and thus, low-density) present population state. For both the historic period and the present period, F_{\max} was included in the estimated parameters (yielding $F_{\max,H} = 0.27 \text{ yr}^{-1}$ and $F_{\max,P} = 0.37 \text{ yr}^{-1}$, respectively).

In the third step, the coefficients of genetic variation for the 3 evolving traits (Eqs. S13 & S14) were fitted so as to optimize the match of the model-predicted to the empirically observed evolutionary transient between the historic period (subscript H) and the present period (subscript P) while assuming a constant fishing mortality of $F = 0.5 \text{ yr}^{-1}$. To identify the model that best describes this transition from the historic state to the present state within 100 yr of fisheries-induced evolution, we minimized the sum Δ_{evo} of 3 deviations,

$$\Delta_{\text{evo}} = \Delta_{H,t_H} + \Delta_{t_P-t_H} + 2\Delta_{P,t_P}, \quad (6)$$

where Δ_{H,t_H} and Δ_{P,t_P} are time averages of Δ according to Eq. (5) for the historic and present empirical observations over 10 yr periods starting at t_H and t_P , respectively, with t_H and t_P chosen so as to minimize

Δ_{H,t_H} and Δ_{P,t_P} , respectively, and $\Delta_{t_P-t_H} = \{[(t_P - t_H) - 100 \text{ yr}] / (100 \text{ yr})\}^2$ is the squared relative deviation from 100 yr of the temporal distance $t_P - t_H$ between those 2 periods. The factor 2 in the third term strengthens the estimated model's match with empirical observations for the present period, which is important for extrapolating model results into the future. Coefficients of genetic variation minimizing Δ_{evo} were determined using a grid search (Table S2).

RESULTS

Dynamics of population abundance

The largest change in population abundance occurs during the first 10 yr of exploitation, after which it reaches a dynamical equilibrium, implying a stable population abundance (Fig. 2, Table 1). The population abundance is reduced to about 50% of the unexploited abundance. The total biomass across all size classes is reduced much more, to about 10% of the unexploited total biomass, whereas the biomass of fish smaller than 25 cm is reduced to just 50% of the corresponding unexploited biomass. The percentage of adults in the population drops from 29 to 3% after 10 yr of exploitation, and from then on gradually increases again, to about 6% after 200 yr of exploitation, as plaice evolves to mature at a smaller size (Table 1). To maintain the population fishing mortality rate at $F = 0.5 \text{ yr}^{-1}$, F_{\max} had to be raised from 0.5 yr^{-1} to about 0.67 yr^{-1} to compensate for the population's changing size distribution (Fig. 2).

Fig. 2. Model-predicted changes in main population characteristics of North Sea plaice *Pleuronectes platessa* resulting from fishing starting in 1895 with a target fishing mortality rate of $F = 0.50 \text{ yr}^{-1}$. Changes in population abundance (thick gray continuous curve), population biomass (thick black continuous curve), and proportion of adults (thick black dotted curve) are shown relative to their values in the unexploited population (left vertical axis), while the realized population fishing mortality rate (F_{pop} ; thin black continuous curve) and the maximum fishing mortality rate (F_{\max} ; thin gray continuous curve) are shown on an absolute scale (right vertical axis). The gray vertical bars indicate the unexploited, historic, present, and future periods (see Fig. 4, Table 1)

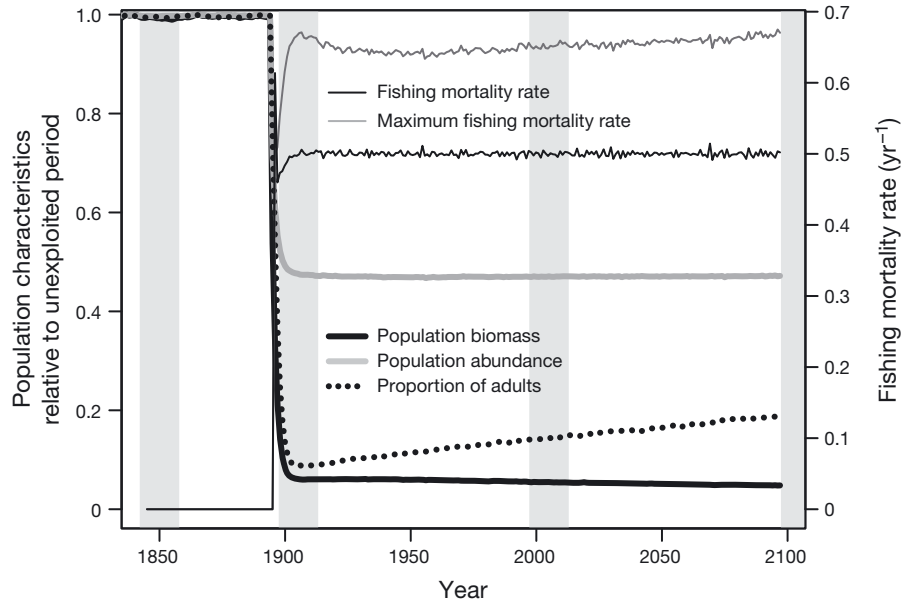


Table 1. Changing population characteristics in the eco-genetic model of female North Sea plaice *Pleuronectes platessa* during 4 consecutive periods: initial period before the start of exploitation in 1895, historic period after 10 yr of exploitation, present period after 110 yr of exploitation, and future period after 210 yr of exploitation. All values are averaged over the adult population and the indicated 10 yr periods

Description	Symbol	Unexploited (before 1895)	Historic (after 10 yr, 1900–1910)	Present (after 110 yr, 2000–2010)	Future (after 210 yr, 2100–2110)	Units
Evolving traits						
Weight-specific energy-acquisition rate	a	5.76	5.75	5.81	5.78	$\text{g}^{1/4} \text{yr}^{-1}$
Weight-specific reproductive-investment rate	c	0.61	0.61	0.67	0.73	yr^{-1}
PMRN intercept	u	53.1	50.9	38.7	32.1	cm
Emergent traits						
Population abundance	N	53552	25646	25217	25278	–
Fraction of adults	–	0.29	0.03	0.04	0.06	–
Maximum body weight (extrapolated)	w_{∞}	2584	2105	1823	1522	g
Age at maturation	t_{mat}	5.9	4.1	3.8	3.6	yr
Length at maturation	l_{mat}	47.9	37.8	34.0	30.9	cm
Weight at maturation	w_{mat}	1099	542	394	295	g
Annual weight increment relative to body weight	$\Delta w/w$	0.43	0.62	0.64	0.64	–
Annual reproductive investment relative to body weight	γ/w	0.163	0.189	0.215	0.236	–
Juvenile mortality rate		0.089	0.137	0.133	0.123	yr^{-1}

Evolution of genetic traits

The 3 evolving genetic traits cannot be directly measured empirically. Our model, however, provides insights into the dynamics of these genetic traits (Fig. 3a–c), as well as the phenotypic traits that emerge from the genetic traits and can be measured (Fig. 3d–i). Some of these emerging phenotypic traits were used in the calibration of those model parameters for which no independent estimates were available (Table S2). Our model calibration not only resulted in a good match between the model-predicted and empirically observed values for the historic and present period, but also between model predictions and the trends in lengths at age observed between 1950 and 2000 (Fig. 3g), in PMRN midpoints observed between 1960 and 2000 (Fig. 3h), and in reproductive investments observed between 1980 and 2000 (Fig. 3i).

The calibrated model shows that fishing results in changes in the evolving traits for energy acquisition, maturation, and reproductive investment (Fig. 3a–c). The shown trait values are averaged over all adult individuals. The weight-specific energy-acquisition rate (a) decreases during the first years of exploitation from the pre-exploitation level of $5.76 \text{ g}^{1/4} \text{ yr}^{-1}$ to $5.72 \text{ g}^{1/4} \text{ yr}^{-1}$, increases to $5.88 \text{ g}^{1/4} \text{ yr}^{-1}$ after 50 yr of exploitation, remains constant for about 3 decades, and then gradually declines towards the pre-

exploitation value in 2100 (Fig. 3a). The PMRN intercept u decreases gradually from 53 to 32 cm after 200 yr of exploitation (Fig. 3b). The weight-specific reproductive-investment rate c gradually increases from 0.61 yr^{-1} to 0.73 yr^{-1} after 200 yr of exploitation (Fig. 3c). Since the values of the evolving traits continue to change up to 2100, it can be concluded that the population at that time has not yet reached an evolutionary equilibrium.

Evolution of emerging phenotypic traits

Among the emerging phenotypic traits, the annual weight increment relative to body weight quickly increases from 43 to 64 % during the first 20 yr of exploitation, and thereafter stays constant (Fig. 3d). The weight at maturation falls from about 1100 g to less than 600 g after 10 yr of exploitation, and to less than 300 g after 200 yr of exploitation (Fig. 3e). The annual reproductive investment relative to body weight jumps from about 16 to 19% after 10 yr of exploitation, and then gradually increases to 24 % after 200 yr of exploitation (Fig. 3f).

The changes in lengths at age predicted by the model differ between age classes (Fig. 3g). The length at age 1 yr increases slightly after the start of fishing, coinciding with the strong decline in population abundance, which relaxes density-dependent com-

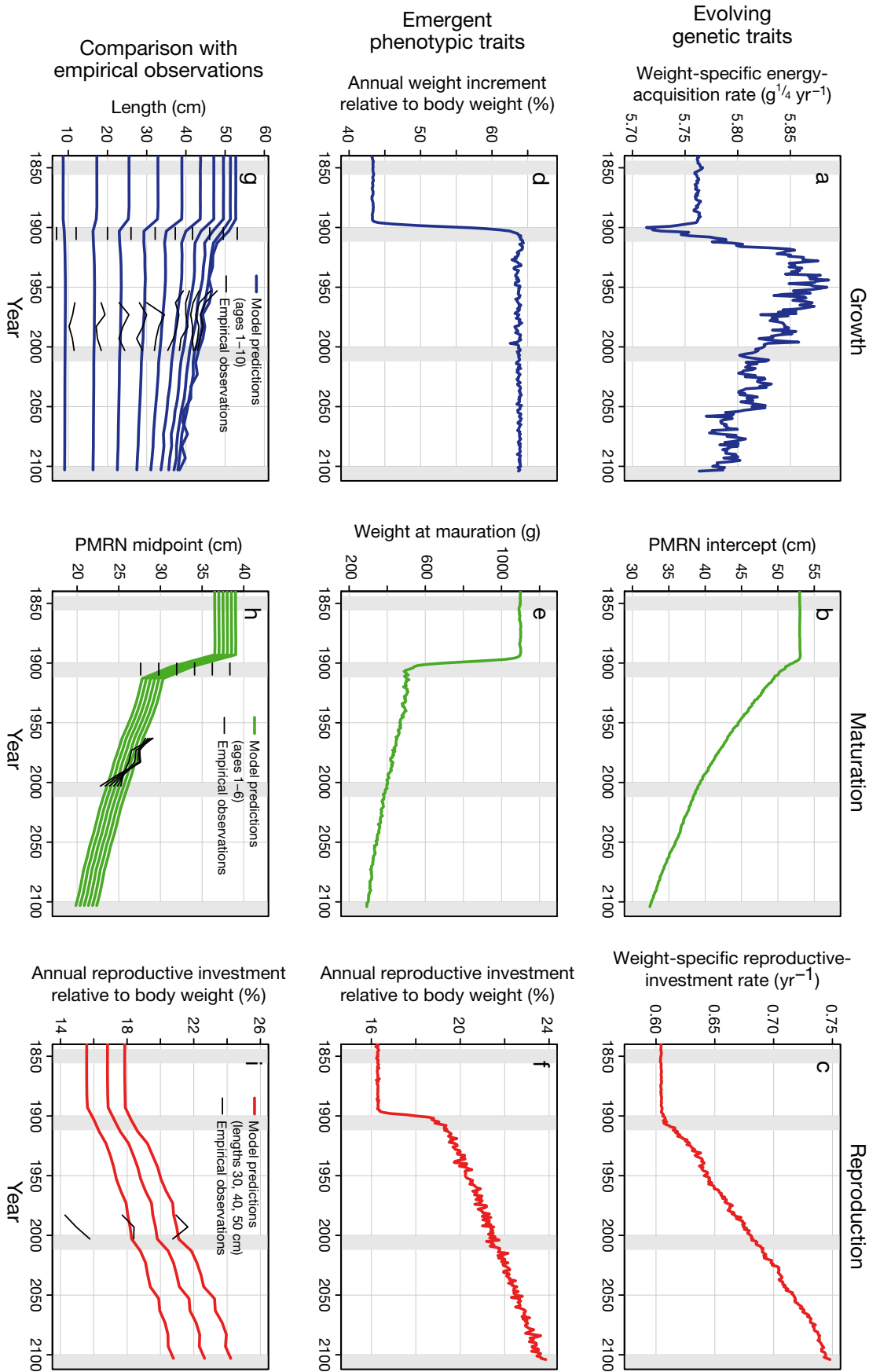


Fig. 3. Model-predicted changes in evolving genetic traits and emergent phenotypic traits of North Sea plaice *Pleuronectes platessa* resulting from fishing starting in 1895 with a target fishing mortality rate of $F = 0.5 \text{ yr}^{-1}$. The top row shows the evolving genetic traits (a) weight-specific energy-acquisition rate a , (b) probabilistic maturation reaction norm (PMRN) intercept u , and (c) weight-specific reproductive-investment rate c . The middle row shows emergent phenotypic traits: (d) annual weight increment relative to body weight, (e) weight at maturation, and (f) annual reproductive investment relative to body weight. The bottom row compares model-predicted emergent phenotypic traits (thick curves) with the corresponding empirically observed emergent phenotypic traits (thin curves): (g) lengths at age for ages 1–10, (h) PMRN midpoints for ages 1–6, and (i) annual reproductive investments relative to body weight for lengths around 30 cm (25–35 cm), 40 cm (35–45 cm), and 50 cm (above 45 cm). The gray vertical bars indicate the unexploited, historic, present, and future periods (see Fig. 4, Table 1)

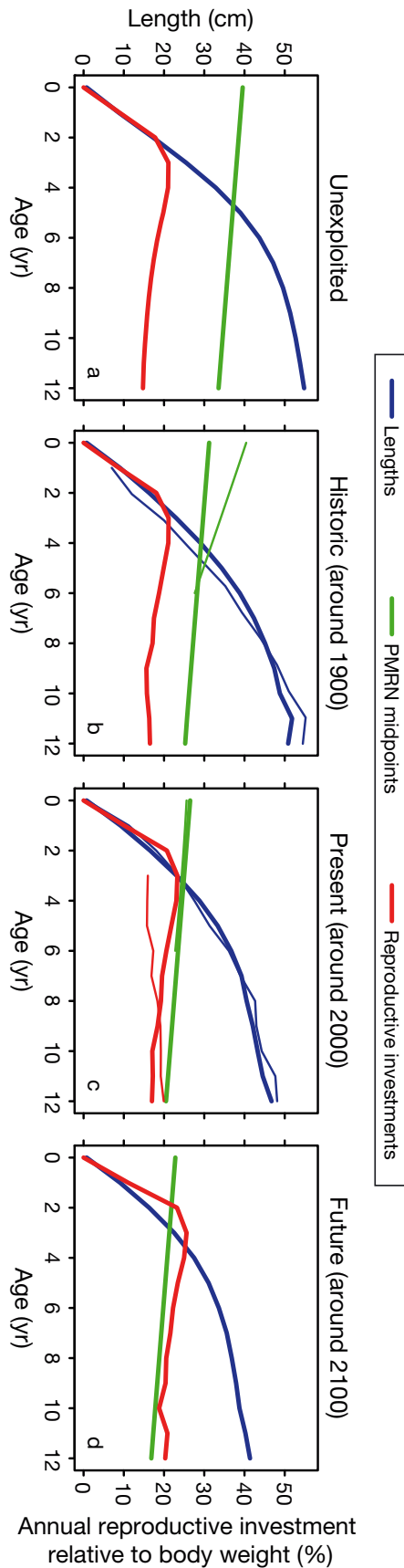


Fig. 4. Model-predicted changes in life histories of North Sea plaice *Pleuronectes platessa* resulting from fishing starting in 1895 with a target fishing mortality rate of $F = 0.5 \text{ yr}^{-1}$. Four periods are shown (see Table 1): (a) before the start of exploitation, (b) during the historic period around 1900, (c) during the present period around 2000, and (d) during the future period around 2100. Blue curves: lengths at age; green curves: midpoints of probabilistic maturation reaction norms (PMRNs; left vertical-axis); red curves: reproductive investments relative to body weight; thick curves: model predictions; thin curves: empirical observations

petition for resources. The lengths at age of older age classes show a slight decrease immediately after the start of fishing, but tend to increase again after a few years in correspondence with the evolutionary increase in the weight-specific energy-acquisition rate. The lengths at age of the oldest age classes show a continuous decline throughout the study period. After 200 yr of exploitation, all lengths at age are lower than before exploitation, except at age 1 yr (Fig. 3g).

The PMRN midpoints shift to lower levels. The model-predicted rate of this decrease is slightly lower than empirically observed (Fig. 3h). The relative reproductive investment increases after the start of exploitation and continues to do so during the entire exploitation period. This model-predicted increase matches the empirical observations (Fig. 3i), but absolute levels are overestimated.

During the first decade after the start of fishing, when population abundance exhibits a strong decline, a number of life-history traits show a relatively fast change. This change is likely due to the demographic effect of the selective removal of faster-growing genotypes. This applies to the weight-specific energy-acquisition rate (Fig. 3a), the weight at maturation (Fig. 3e), the relative reproductive investment (Fig. 3f), the lengths at age 2 yr and older (Fig. 3g), and the midpoints of the PMRN (Fig. 3h). Moreover, the increase in growth rate (Fig. 3d) and in the length at age 1 yr (Fig. 3g) during this period is due to the relaxation of density-dependent competition among plaice smaller than 25 cm.

Fig. 4 compares the model-predicted growth trajectory, PMRN midpoint curve, and reproductive-investment schedule for 4 time periods: for the unexploited stock, the historic period (after 10 yr of exploitation), the present period (after 100 yr of exploitation), and a future period (after 200 yr of exploitation). For the historic and present periods, the model predictions can be compared with empirical observations, showing a good match. Emergent phenotypic traits for these 4 time periods are given in Table 1. Age (length) at maturation decreases from 5.9 yr (47.9 cm) in the unexploited population to 3.8 yr (34.0 cm) in the present period and to 3.6 yr (30.9 cm) in 2100. Asymptotic body weight (length) decreases from 2.6 kg (64 cm) in the unexploited population to 1.8 kg (57 cm) in the present period and to 1.5 kg (53 cm) in 2100.

The current asymptotic body weight is 28% lower than at the start of fishing. Since this weight is determined as $w_{\infty} = [a/(b+c)]^4$, and because the increased weight-specific energy-acquisition rate (+1%), if act-

ing alone, would increase the asymptotic weight, the observed decrease in asymptotic weight is mainly a consequence of the increased weight-specific reproductive-investment rate (+10%; Table 1). The decreased PMRN intercept (-27%) explains the decrease in size at maturation (l_{mat} or w_{mat}) and the decrease in any subsequent size at age (Table 1, Figs. 3g & 4).

DISCUSSION

Main insights gained from eco-genetic model

To our knowledge, this is the first study of fisheries-induced evolution using an eco-genetic model that matches 3 key life-history traits (describing growth, maturation, and reproduction) to observations from 2 periods spanning a century of exploitation. It is this unique setting that allowed us to calibrate the model-predicted rate of evolution to the empirically observed rate. Similar studies in Northeast Arctic cod *Gadus morhua* and smallmouth bass *Micropterus dolomieu* did not have such detailed empirical data available for model calibration, and instead had to base model calibration on fitting size at age or the age or size at 50% maturity (Dunlop et al. 2007, 2009b, Enberg et al. 2012).

Our model allows us to study the simultaneous response of the different life-history traits to fishing, as it incorporates a mechanistic description of the energy-allocation processes, key life-history trade-offs, and the explicit inheritance of the evolving traits. Our model captures the empirically observed changes in life-history traits within and between the first decade of the 20th century and the time period 1960 to 2000. Our model predicts that lengths at age and age at maturation decrease, and reproductive investment increases after the start of exploitation. These results are in line with theoretical expectations (Law 2000), empirical evidence (Olsen et al. 2004, Jørgensen et al. 2007, Kuparinen & Merilä 2007, Devine et al. 2012, Audzijonyte et al. 2013a), and other model-based studies (Andersen et al. 2007, Dunlop et al. 2009b, Enberg et al. 2009).

To gain insights into how traits that are intimately linked in an individual's dynamic energy budget simultaneously evolve under the influence of fishing, we kept both environmental conditions and exploitation characteristics constant throughout the study period. The model-predicted changes in lengths at age, PMRN midpoints, and reproductive investments show the consequences of fisheries-induced evolu-

tion after population dynamics reach equilibrium within about 10 yr. Changes in maturation and reproductive investment follow a monotonic trend, whereas energy acquisition changed from increasing to decreasing. The latter change in direction takes place while population abundance is stable and demographic effects can therefore be ruled out. This suggests that the model-predicted change in the direction of selection on energy acquisition, after about 50 yr of exploitation, is due to the size at maturation decreasing relative to the size at which fish recruit to the fishery. During the first decades of exploitation, reproduction occurs at sizes above the size at recruitment to the fishery. The predicted increase in energy acquisition during this period can therefore be attributed to the energy demands of increased reproductive investment and earlier maturation (Dunlop et al. 2009b). As the size at maturation decreases, reproduction more often occurs at sizes below the size at recruitment to the fishery. By reducing the energy-acquisition rate during this period, fish increase the number of seasons in which they can reproduce before recruiting to the fishery.

Model assumptions and rate of fisheries-induced evolution

The model-predicted evolutionary response is influenced by the fishing mortality rate and the selectivity pattern of the fishery. The assumed start of fishing in 1895 and the sigmoid exploitation pattern at a fishing mortality rate of $F = 0.5 \text{ yr}^{-1}$ is a crude simplification of the actual history of exploitation. Plaice has been fished commercially in a bottom-trawl fishery in coastal waters since at least the 15th century (van Neer et al. 2002, Bolle et al. 2004, Bennema & Rijnsdorp 2015). Given the available technology and the resultant restriction to coastal fishing grounds, fishing mortality will have been rather low and targeted at the intermediate size classes (van Neer et al. 2002, Bolle et al. 2004). After the expansion of the fishing fleets at the end of the 19th century (Kerby et al. 2012), substantial changes occurred in fishing pressure, mesh size, and fishing gear (Rijnsdorp & Millner 1996, Kerby et al. 2012, Fock 2014). Fishing mortality varied between 0.2 yr^{-1} and 0.9 yr^{-1} , except for the 2 war periods when fishing was substantially reduced (Rijnsdorp & Millner 1996). With regard to the exploitation pattern, the available data suggest that in the 1930s fishing mortality peaked at intermediate age classes and decreased for older fish. This dome-shaped exploitation pattern became less

apparent after World War II (Rijnsdorp & Millner 1996). Hence, during the first half of the century, the fishery may have exploited a size range that included juvenile size classes, with peak mortality on intermediate size classes.

Since our interest here has been to describe the broad pattern of fisheries-induced evolution in North Sea plaice between the start and the end of the 20th century, ignoring variations of fishing mortality that occurred within this period is an acceptable simplification. A misspecification of the average fishing mortality rate is unlikely to affect the modelled rate of evolution, because the evolutionary rate was calibrated by adjusting the coefficients C of genetic variation of the 3 evolving traits a , u , and c . The model with $C_a = 23\%$, $C_u = 15\%$, and $C_c = 23\%$ gave the best fit to the empirically observed phenotypic trait values around 1900 and 2000. If we had assumed a lower average fishing mortality rate, this calibration would have estimated higher coefficients of genetic variation to match the observed phenotypic trait values for the historic and present periods.

In contrast, deviations from the assumed flat-topped exploitation pattern have implications for the estimated rate of evolution. Model-based studies have shown that a dome-shaped exploitation pattern results in reduced selection for earlier maturation and higher reproductive investment. It is even possible that fishing may select for an increase in growth rate, a delay in maturation, and a reduction in reproductive investment, to allow fish to grow as fast as possible through the vulnerable size window (Taborsky et al. 2003, 2012, Gårdmark & Dieckmann 2006, Hutchings 2009, Jørgensen et al. 2009, Mollet et al. 2015). Hence, the assumed flat-topped exploitation pattern may overestimate the rate of evolution for the time period during which the stock was exploited with a dome-shaped pattern. This could imply that the model-predicted evolutionary changes in maturation and reproductive investment might be overestimated for the first part of the 20th century and underestimated for the second part of the 20th century.

The estimated rate of evolution may also be affected by trends in temperature and food conditions, if these influenced the phenotypic trait values for the historic and present periods used to calibrate the model. The present period is relatively warm, whereas the historic period was relatively cool (MacKenzie & Schiedek 2007, van Aken 2010). The change in ambient temperature actually experienced by the fish, however, may be smaller, because North Sea plaice has moved to deeper and cooler waters since the

1990s (van Keeken et al. 2007, Dulvy et al. 2008, Engelhard et al. 2011). A recent analysis has indeed confirmed that North Sea plaice is able to maintain the maximum ambient temperature it experiences during summer by moving to deeper waters, despite a substantial increase in water temperature (van Hal et al. 2016).

Food availability has likely increased due to a variety of reasons: (1) a reduction in North Sea plaice biomass due to fishing, (2) an increase in secondary production following the increase in nutrients in the 1960s, particularly in coastal waters (Beukema & Cadée 1986, Colijn et al. 2002, Philippart et al. 2007), and possibly (3) a shift in the benthic ecosystem from large long-lived species to small short-lived species favored as prey by North Sea plaice (Rijnsdorp & Vingerhoed 2001).

The higher temperatures and improved food conditions experienced by North Sea plaice in the present period may have resulted in a higher growth rate of juveniles (Rijnsdorp & van Leeuwen 1996, Teal et al. 2008). For adult plaice, the effects are less clear, although a decrease in population biomass in combination with a possible increase in temperature may also have positively affected adult lengths at age in the present period. During their feeding period, a part of the older age classes inhabit stratified waters with rather constant temperature conditions that are well within their thermal preference range, whereas others inhabit shallower waters with temperatures that may exceed their thermal preference range (Fretitas et al. 2010, Teal et al. 2012). An increase in temperature may thus have a positive effect on the growth of the part of the population that inhabits the stratified waters and may negatively affect the growth of the older fish inhabiting the shallower waters. Evidence for a density-dependent reduction of adult growth is mixed. Beverton (1964) showed that the mean weight at age of adult North Sea plaice was reduced during World War II, when fishing pressure was low and density-dependent competition was consequently strong. Also, Rijnsdorp & van Leeuwen (1992) concluded that adult growth is affected by density dependence, based on an analysis of growth increments in otolith samples. However, the apparent reduction in growth at high population density could also have been due to the survival of slower-growing fish that would have been selectively removed by the fishery if fishing had continued during World War II (Bolle et al. 2004). The unprecedented increase in North Sea plaice biomass in the 2000s (ICES 2014) may provide, in the near future, new information to assess the role of density-dependent growth in adult

plaice. This may also shed light on the surprising similarity in the growth patterns of otoliths collected from archaeological excavation sites and of otoliths collected before the increase in juvenile growth in the 1960s and 1970s. The similarity could be due to the combined effect of an increase in growth due to the relaxation of density dependence in adult growth and a reduction in growth due to fisheries-induced evolution throughout the 20th century (Bolle et al. 2004).

Our model calibration used the PMRN midpoints estimated for the historic period around 1900 and the present period around 2000 (van Walraven et al. 2010). The PMRN estimation accounts for the phenotypically plastic effects of growth changes on maturation. A shift in a stock's PMRN is thus indicative of evolutionary changes (Heino et al. 2002b), but may also be affected by changes in other environmental conditions directly affecting maturation, such as temperature (Kuparinen et al. 2011). By including temperature as an additional explanatory variable, it was shown that while an increase in temperature contributed to the empirically observed decrease in PMRN midpoints, this contribution was too small to explain the decreasing trend (Grift et al. 2003, Kraak 2007). The empirically observed trend in PMRN midpoints is therefore consistent with our model predictions, although the empirically estimated rate of evolutionary change might be overestimated by not accounting for direct temperature effects on maturation.

The increase in temperature during the 20th century could also have increased the metabolic rates of North Sea plaice. It can therefore not be ruled out that part of the empirically observed increases in metabolic rates might have been due to climate change. Accordingly, our model might overestimate trends in metabolic rates by not accounting for temperature effects. However, the observed trends exceed the changes that would be expected based on metabolic theory: a 1°C change in average water temperatures (van Aken 2010) would be expected to result in a metabolic change of not more than 10% (van der Veer et al. 2001). Furthermore, since the temperature effect equally applies to the weight-specific maintenance-investment rate and other metabolic rates, it is likely that the temperature effects on observable sizes and reproductive investments are partly balanced. Assuming a constant weight-specific maintenance rate in our model is therefore not expected to significantly affect the conclusions.

There is some controversy in the literature on the rate of fisheries-induced evolution. Andersen & Brander (2009) argued that the rate reported in

experimental studies and analyses of population time series was 5 times higher than the rate predicted by their generic evolutionary model. Audzijonyte et al. (2013a) reviewed rates estimated in experimental, empirical, and model-based studies and concluded that rates of phenotypic change observed in wild fish are about 4 times higher than the evolutionary rates reported in model-based studies. Rates of evolution estimated by models of evolutionary dynamics were not significantly different among 10 out of 13 model-based studies. This suggests that the discrepancy between the model-based and the empirical results may be due to a lack of quantitative understanding of the processes that affect selection pressures and the phenotypic expression of genotypes.

For simplicity, we have focused on the fisheries-induced evolution of females. Because North Sea plaice is a sexually dimorphic species in which males mature at a smaller size and a younger age, and subsequently grow to a smaller maximum body size than females, the selection pressure imposed by fishing will differ between the sexes (Rijnsdorp 1993b). Empirical data suggest that males may show a stronger selection response than females (Rijnsdorp 1989, van Walraven et al. 2010). In terms of assessing both sexes together, the model-based results we have reported here must therefore be considered conservative. Also, if the fisheries-induced evolutionary dynamics of the sexes are not independent, female evolution might be accelerated by the faster male evolution.

Because of the sources of uncertainty reported above—concerning (1) the influence of environmental effects on phenotypic traits (phenotypic plasticity), (2) the exploitation pattern of the fishery, (3) model parameters (in particular the heritabilities and coefficients of genetic variation of the evolving traits), and (4) the mechanisms incorporated in the model (life-history trade-offs, no sex structure)—the model-predicted rates of evolution should be considered as indicative only. In contrast, the directions of the model-predicted evolutionary changes will be robust and are in agreement with the results of other studies, both model-based and empirical (Andersen et al. 2007, Jørgensen et al. 2007, Kuparinen & Merilä 2007, Audzijonyte et al. 2013a).

Implications for productivity

Fisheries-induced evolution may have repercussions for long-term yield (Law & Grey 1989, Law 2000). As fish mature earlier and stay smaller, the yield resulting for a given fishing mortality rate will

decrease (as long as the population's abundance and age structure stay the same). Also, the fishing mortality rate at maximum sustainable yield (F_{MSY}) is expected to change under exploitation due to these evolutionary effects (Mollet 2010, Heino et al. 2013). Furthermore, fisheries-induced evolution may influence recruitment to the population, and hence its recovery potential—this may happen, for instance, through density-dependent feedbacks changing as a result of life-history evolution (Hutchings 2005, Enberg et al. 2010, Kuparinen et al. 2014).

Fisheries-induced evolution will typically change the size structures of exploited populations towards smaller sizes. Because many trawl fisheries catch a mixture of species, the imposed selective effects will not normally be limited to the target species, but may apply to bycatch species as well. Changes in size structures will have repercussions for food-web processes, which tend to be dominated by size-based interactions (Andersen & Beyer 2006). The implications of such changes were explored in a marine ecosystem model showing that a slow (less than 0.1% yr⁻¹) decrease in the average lengths of 5 fished species could affect species interactions, biomasses, and yields: even small decreases in fish sizes are amplified by positive feedbacks in the ecosystem and can lead to major changes in natural mortality (Audzijonyte et al. 2013b).

Conclusions

The eco-genetic model devised and calibrated for female North Sea plaice has allowed us to study the simultaneous evolution of 3 life-history traits in response to selective fishing throughout the 20th century. Despite the assumption of constant fisheries selection, our model shows that the resultant evolutionary responses are not necessarily monotonic in time: whereas reproductive investment and the PMRN continually changed in one direction, the weight-specific rate of energy acquisition first increased during the initial decades of intensified fishing and then decreased again during the second half of the 20th century. Although the empirically observed phenotypic trait values were no doubt influenced by phenotypic plasticity in response to changes in environmental conditions during the 20th century, our study demonstrates that these empirically observed phenotypic trait values are consistent with the model-predicted evolutionary changes in energy acquisition, PMRN intercept, and reproductive investment that are expected from the selective effects of fishing

during the 20th century. Indeed, our model suggests that North Sea plaice has not yet reached an evolutionary equilibrium and is expected to evolve further towards earlier maturation, increased reproductive investment, and lower adult body size.

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