

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

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SUPPLEMENT

The eco-genetic model describes ecological and genetic processes affecting individual female North Sea plaice as a function of exploitation. Model variables are summarized in Table S1. Model parameters, their values, and their sources are summarized in Table S2.

Energy allocation

According to eq. (1), an individual's somatic growth rate dw/dt is given by the energy-acquisition rate $aw^{3/4}$ diminished by the maintenance rate bw and, for adults, the reproductive-investment rate cw (Fonds et al. 1992, West et al. 1997, 2001). Thus, reproduction is prioritized over growth. Furthermore, if the acquired energy cannot even cover the maintenance costs, the individual neither grows nor reproduces and instead experiences starvation mortality (see below).

Growth

From eq. (1), we obtain the annual growth increment by expressing the somatic weight w_{t+1} at age $t+1$ as a function of the somatic weight w_t at age t at the start of the growing season, taking into account that adult females do not feed during their spawning period of 6 weeks (or 0.125 years),

$$w_{t+1}^{1/4} = \frac{a}{b} - \left(\frac{a}{b} - w_t^{1/4} \right) e^{-b/4} \quad \text{if juvenile,} \quad (\text{S1a})$$

$$w_{t+1}^{1/4} = \frac{a}{b+c} - \left(\frac{a}{b+c} - w_t^{1/4} \right) e^{-0.875(b+c)/4} \quad \text{if adult.} \quad (\text{S1b})$$

The annual reproductive investment γ_{t+1} at age $t+1$, measured in terms of a somatic-tissue weight equivalent, consists of gonadic and behavioral investment and is given by the integration of the reproductive-investment rate cw between ages t and $t+1$,

$$\begin{aligned} \gamma_{t+1} &= \int_t^{t+1} c w(t') dt' = \\ & \frac{c}{b+c} \left[w_t - w_{t+1} + \frac{4a}{3(b+c)} \right] (w_t^{3/4} - w_{t+1}^{3/4}) + \frac{2a^2}{(b+c)^2} (w_t^{1/2} - w_{t+1}^{1/2}) + \frac{4a^3}{(b+c)^3} (w_t^{1/4} - w_{t+1}^{1/4}) \\ & + \frac{4a^4}{(b+c)^4} \ln \frac{a - (b+c)w_t^{1/4}}{a - (b+c)w_{t+1}^{1/4}}. \end{aligned} \quad (S2)$$

The length-weight relationship applies immediately after reproduction (Rijnsdorp 1990),

$$l_t = \sqrt[3]{w_t / k}. \quad (S3)$$

The phenotypic weight-specific energy-acquisition rate a decreases with population biomass relative to the genetically determined weight-specific energy-acquisition rate a_g because of intraspecific competition for food. For North Sea plaice, such density dependence is only important on the nursery grounds for fish smaller than 25 cm (Bolle et al. 2004, Rijnsdorp and van Beek 1991): therefore the energy acquisition of these fish depends on their total biomass B ,

$$a = \begin{cases} a_g / [1 + (\delta_1 B)^{\delta_2}] & \text{if } l \leq 25 \text{ cm} \\ a_g & \text{otherwise.} \end{cases} \quad (S4)$$

Maturation

The PMRN is determined by an intercept u and a slope s defining the PMRN midpoints $l_{p50}(t)$ at age t according to eq. (2). For any given age and size, the probability of maturing is given by eq. (3).

Reproduction

The number of 1-year-old recruits is given by

$$N_r = \frac{r_1}{1 + r_2 w_{\text{egg}} / \sum_{i=1}^n \gamma_i}, \quad (S5)$$

where n is the total number of individuals and γ_i is the reproductive investment of individual i .

The reproductive success v_i of individual i is given by its individual fecundity relative to the population fecundity. Assuming a constant egg weight, fecundity is proportional to reproductive investment γ , and therefore,

$$v_i = \gamma_i / \sum_{j=1}^n \gamma_j. \quad (S6)$$

Natural mortality

Fish are exposed to both natural and fishing mortality. The instantaneous rate M of natural mortality is given by the sum of three mortality rates describing foraging mortality m_f (implying a growth-survival trade-off), reproduction mortality m_r (implying a reproduction-survival trade-off), and starvation mortality m_s (implying a maintenance-survival trade-off),

$$M = m_f + m_r + m_s. \quad (S7)$$

Data and theory suggest that in marine systems the rate of foraging mortality due to predation scales with body size (Peterson and Wroblewski 1984, Brown et al. 2004, Savage et al. 2004). Higher weight-specific energy-acquisition rates a_g require higher foraging rates, and thus higher risks of exposure to predation,

$$m_f = \nu e^{\alpha a_g} w^\eta, \quad (S8)$$

where no foraging ($a_g = 0$) results in the baseline predation-mortality rate νw^η .

Depletion of stored energy due to reproduction may lower survival probability (Hutchings and Myers 1994). Reproduction mortality is therefore assumed to increase with the weight-specific reproductive investment γ/w ,

$$m_r = m_0 e^{\chi(\gamma/w)}, \quad (S9)$$

where no reproduction ($\gamma = 0$) results in the baseline reproduction-mortality rate m_0 , describing the mortality due to diseases and parasites.

If individuals do not acquire sufficient energy to cover their maintenance costs, i.e., if

$aw^{3/4} - bw \leq 0$, they starve at an instantaneous mortality rate proportional to their rate of energy loss per unit of somatic weight,

$$m_s = \max(0, -\rho(aw^{3/4} - bw)/w). \quad (S10)$$

Fishing mortality

The population fishing mortality F_{pop} depends on its size distribution in relation to the size-dependent exploitation pattern. We estimate F_{pop} from the annual decline in the number of fish of age 2 years

and older (age 2+) between the beginnings of years y and $y + 1$, accounting for the proportion $p_{F,y}$ of fish that die due to fishing mortality relative to total mortality (i.e., the sum of fishing mortality and natural mortality) during year y ,

$$F_{\text{pop},y} = p_{F,y} \ln(N_{2+,y} / N_{3+,y+1}) / \text{yr}. \quad (\text{S11})$$

To keep the population fishing mortality $F_{\text{pop},y}$ in our model equal or close to a given target mortality rate F , the maximum fishing mortality rate $F_{\text{max},y}$ is annually adjusted according to

$$F_{\text{max},y} = F_{\text{max},y-1} F / F_{\text{pop},y-1}. \quad (\text{S12})$$

Inheritance and expression

The genetic values of the three evolving traits a , u , and c are inherited from parent to offspring. Parents for each offspring are selected with a von Neumann rejection algorithm (Von Neumann 1951) based on the reproductive success of potential parents (eq. S6). The genetic trait values $x_{g,o}$ of the offspring are then sampled from a normal distribution N with a mean given by the mid-parental value (i.e., the average of the two parental genetic trait values $x_{g,1}$ and $x_{g,2}$) and a recombination-segregation variance given by a constant coefficient of variation, C ,

$$x_{g,o} \sim N((x_{g,1} + x_{g,2}) / 2, (C\mu_g(x))^2), \quad (\text{S13})$$

where $\mu_g(x)$ is the population's current mean genetic value of trait x .

These genetic trait values $x_{g,o}$ are translated into phenotypic trait values x_o by sampling the latter from a normal distribution with a mean given by $x_{g,o}$ and an environmental variance given by a constant narrow-sense heritability h^2 (Roff 1991),

$$x_o \sim N(x_{g,o}, \frac{1-h^2}{h^2} (C\mu_g(x))^2). \quad (\text{S14})$$

TABLES IN SUPPLEMENT

Table S1. Model variables of the eco-genetic model of female North Sea plaice. The table includes evolving genetic traits and emergent phenotypic traits. The latter are changing with the evolving genetic traits and the environment.

	Symbol	Description	Unit
Individual traits	t	Age	yr
	w	Somatic weight	g
	l	Body length	cm
	a, a_g	Weight-specific (phenotypic, genetic) energy-acquisition rate (evolving)	$\text{g}^{1/4} \text{yr}^{-1}$
	c	Weight-specific reproductive-investment rate (evolving)	yr^{-1}
	u	PMRN intercept (evolving)	cm
Emergent traits	$p_{\text{mat}}(l, t)$	Probability of maturation	-
	$l_{p50}(t)$	Age-specific PMRN midpoint	cm
	d	Interquartile PMRN width	cm
	γ	Reproductive investment	g
	v	Reproductive success	-
	m_p	Foraging-mortality rate	yr^{-1}
	m_r	Reproduction-mortality rate	yr^{-1}
	m_s	Starvation-mortality rate	yr^{-1}
	M	Natural-mortality rate	yr^{-1}
	F	Fishing-mortality rate	yr^{-1}
	B	Total biomass of individuals smaller than 25 cm	g
	N_r	Number of recruits	-

Table S2. Non-evolving parameters of the eco-genetic model of female North Sea plaice. As indicated under “Reference”, parameter values were (i) taken from the literature, (ii) directly estimated from empirical data on age, size, and maturity from Dutch market samples and scientific surveys, or (iii) estimated through model calibration.

	Symbol	Description	Equation	Reference	Value	Unit
Energy allocation and growth	b	Weight-specific maintenance rate	1	Mollet et al. (2010)	0.6	yr ⁻¹
	k	Parameter of length-weight relationship	S3	Rijnsdorp (1990)	0.01	g cm ⁻³
	δ_1, δ_2	Parameters describing density-dependent energy acquisition	S4	Calibration ^a	$9.6 \times 10^{-7}, 10.82$	g ⁻¹ , -
Maturat-ion	ϕ	Parameter scaling PMRN width	3	Grift et al. (2003)	0.11	cm
	s	PMRN slope	2	Direct estimation	-0.5	cm yr ⁻¹
Repro-duction	w_{egg}	Egg weight	S5	Direct estimation	4.2×10^{-3}	g
	r_1, r_2	Parameters of stock-recruitment relationship	S5	ICES (2011)	$8 \times 10^3, 1 \times 10^6$	-, -
Natural mortality	M	Total natural-mortality rate for average-sized fish at age 6 years	S7	Beverton (1964), ICES (2011)	0.1	yr ⁻¹
	v	Parameter scaling predation-mortality rate	S8	Calibration ^a	1.25×10^{-4}	g ^{1/4} yr ⁻¹
	ω	Parameter scaling the strength of growth-survival trade-off	S8	Calibration ^a	1.28	g ^{-1/4} yr
	η	Parameter describing weight dependence of predation-mortality rate	S8	Peterson and Wroblewski (1984), Brown et al. (2004)	-0.25	-
	m_0	Parameter scaling reproduction-mortality rate	S9	Calibration ^a	0.009	yr ⁻¹
	χ	Parameter scaling the strength of reproduction-survival trade-off	S9	Calibration ^a	9.4	-
	ρ	Parameter scaling starvation-mortality rate	S10	Schultz and Conover (1999)	5.0	g ⁻¹
Fishing mortality	φ	Mesh-selection sharpness	4	van Beek et al. (1983)	0.594	cm ⁻¹
	λ	Mesh-selection factor	4	van Beek et al. (1983)	2.2	-
	ψ	Mesh size	4	van Beek et al. (1983)	8.0	cm
Inheritance and expression	C	Coefficient of genetic variation for evolving traits a , c , and u	S13	Calibration ^b	23%, 23%, 15%	-
	h^2	Heritability	S14	Roff (1991)	24%	-

^a The following search grid was applied: $F_{\text{max}} = 0, 0.1, \dots, 0.5 \text{ yr}^{-1}$; $\omega = 1, 1.01, \dots, 1.5 \text{ g}^{-1/4} \text{ yr}$; and $\chi = 5, 5.2, \dots, 15$. For each parameter combination on this grid, v and m_0 were determined assuming that the natural-mortality rate M equals 0.1 yr^{-1} (ICES 2011) and that the reproduction-mortality rate m_r and the foraging-mortality rate m_f equally contribute to M for a female with average traits at age 6 years. To estimate δ_1 and δ_2 , a search grid was applied for the reduction of energy acquisition due to density dependence in the historic situation: $a/a_g = 0.5, 0.51, \dots, 1$. Assuming that there was no such reduction in the present situation, the parameters δ_1 and δ_2 were then determined from the two corresponding instances of eq. (S4).

^b The following search grid was applied: $C_a, C_u, C_c = 0, 0.01, \dots, 0.5$.

Table S3. Empirically observed trait values used for calibrating the eco-genetic model of female North Sea plaice.

Age, t	Historic period (1900-1910)		Present period (2000-2010)		
	Body weight, \bar{w}_t (g)	PMRN midpoint, $\bar{l}_{p50,t}$ (cm)	Body weight, \bar{w}_t	PMRN midpoint, $\bar{l}_{p50,t}$ (cm)	Relative reproductive investment, \bar{r}_t
1	3.4	31.8	13.3	25.3	-
2	17.3	31.3	54.0	24.8	-
3	80.0	30.8	119.5	24.4	0.160
4	175.8	30.3	194.0	23.9	0.158
5	332.6	29.8	290.2	23.4	0.158
6	518.5	29.3	434.2	22.8	0.173
7	724.86	-	556.0	-	0.169
8	977.5	-	733.3	-	0.184
9	-	-	753.8	-	0.191
10	-	-	770.3	-	0.192

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