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Interim Report

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Assessing evolutionary consequences of size-selective recreational fishing on multiple life-history traits, with an application to northern pike (*Esox lucius*)

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1 Title

2 **Assessing evolutionary consequences of size-selective recreational fishing on multiple**
3 **life-history traits, with an application to northern pike (*Esox lucius*)**

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15

1 Abstract

2 Despite mounting recognition of the importance of fishing-induced evolution, methods for
3 quantifying selection pressures on multiple adaptive traits affected by size-selective harvest-
4 ing are still scarce. We study selection differentials on three life-history traits – reproductive
5 investment, size at maturation, and growth capacity – under size-selective exploitation of
6 northern pike (*Esox lucius* L.) with recreational-fishing gear. An age-structured population
7 model is presented that accounts for the eco-evolutionary feedback arising from density-
8 dependent and frequency-dependent selection. By introducing minimum-length limits, maxi-
9 mum-length limits, and combinations of such limits (resulting in harvestable-slot length lim-
10 its) into the model, we examine the potential of simple management tools for mitigating selec-
11 tion pressures induced by recreational fishing. With regard to annual reproductive investment,
12 we find that size-selective fishing mortality exerts relatively small positive selection differen-
13 tials. By contrast, selection differentials on size at maturation are large and consistently nega-
14 tive. Selection differentials on growth capacity are often large and positive, but become nega-
15 tive when a certain range of minimum-length limits are applied. In general, the strength of se-
16 lection is reduced by implementing more stringent management policies, but each life-history
17 trait responds differently to the introduction of specific harvest regulations. Based on a simple
18 genetic inheritance model, we examine mid- and long-term evolutionary changes of the three
19 life-history traits and their impacts on the size spectrum and yield of pike. In general, fishing-
20 induced evolution reduces sizes and yields, but details depend on a variety of factors such as
21 the specific regulation in place. We find no regulation that is successful in reducing to zero all
22 selection pressures on life-history traits induced by recreational fishing. Accordingly, we must
23 expect that inducing some degree of evolution through recreational fishing is inevitable.

24

1 Introduction

2 Recently, questions regarding fishing-induced evolution have been attracting substantial at-
3 tention in the literature (for reviews, see Dieckmann and Heino 2007; Hutchings and Fraser
4 2007; Jørgensen et al. 2007; Kuparinen and Merilä 2007; Heino and Dieckmann 2008; Ander-
5 sen and Brander 2009; Dunlop et al. 2009a). As fisheries may impose remarkably high, and
6 often size-selective, mortalities on fish populations, they have the potential to cause evolu-
7 tionary changes in the life history, morphology, physiology, and behaviour of fish (Uusi-
8 Heikkilä et al. 2008). Empirical evidence suggesting strong selection pressures and rapid evo-
9 lutionary changes in life-history traits due to fishing is accumulating (e.g., Jørgensen et al.
10 2007; Darimont et al. 2009; Dieckmann et al. 2009; Dunlop et al. 2009a; Sharpe and Hendry
11 2009). Key future research questions are to quantify the strength of selection caused by spe-
12 cific fisheries on specific traits, the speed of the corresponding evolutionary changes, and the
13 repercussions of these changes for fish populations and the ecological services they provide to
14 society (Jørgensen et al. 2007; Dunlop et al. 2009a).

15 If current fishing practices cause substantial selection pressures on fish stocks, fisher-
16 ies managers may want to identify effective ways to mitigate the strength of these pressures
17 (Arlinghaus et al. 2009; Okamoto et al. 2009). In theoretical studies, different management
18 policies have been examined by varying fishing selectivity between mature and immature fish
19 (e.g., Heino 1998; Ernande et al. 2004), age classes (e.g., Law and Grey 1989; Grey 1993),
20 size classes (e.g., Dunlop et al. 2009b), or by assuming representative shapes of size-selective
21 exploitation (e.g., Jørgensen et al. 2009), in addition to changing harvest rates (e.g., Thériault
22 et al. 2008; Enberg et al. 2009) and introducing marine reserves (e.g., Baskett et al. 2005;
23 Dunlop et al. 2009c). However, more systematic investigations are required on a set of other
24 management policies that have traditionally been used in, or are easily applicable to, fisheries.

1 For example, some authors have suggested that saving large fish by applying maximum-
2 length limits will mitigate fishing-induced evolution (Conover and Munch 2002; Law 2007),
3 but so far only a few studies (Baskett et al. 2005; William and Schertzer 2005) have explored
4 the benefits of applying maximum-length limits relative to other management tools.

5 Another important issue is to evaluate the influences of fishing-induced evolution of
6 life-history traits on fisheries metrics. For example, large changes in life-history traits could
7 cause small changes in yield, because of the confounding effects of density dependence, phe-
8 notypic plasticity, or other ecological processes. By contrast, even small life-history changes
9 may have a critical impacts (Kinnison et al. 2009), for example, on stock recovery or stock
10 stability (Enberg et al. 2009). Because of these uncertainties, the importance of fishing-
11 induced evolution for long-term population dynamics and fisheries yields remains controver-
12 sial (Andersen and Brander 2009; Kinnison et al. 2009).

13 Models are expected to play an important role in tackling the aforementioned issues,
14 because systematic manipulation of management policies and evaluation of the resultant out-
15 comes is usually not feasible in wild fish stocks. Crucial demographic effects on individual
16 life histories, such as density-dependent growth (Lorenzen and Enberg 2002) and fecundity
17 (Craig and Kipling 1983), need to be incorporated into demographic models. Model-based
18 studies should also consider sufficiently encompassing sets of life-history traits, at least in-
19 cluding traits describing evolutionary changes in growth, maturation, and reproduction. To
20 date, only few studies have tackled this challenge using so-called eco-genetic models (Théri-
21 ault et al. 2008; Dunlop et al. 2009b, c; Enberg et al. 2009; Okamoto et al. 2009). However,
22 because these models are individual-based, their numerical implementation is computationally
23 more costly than that of age-structured population models, which makes their utilization by
24 fisheries managers more demanding (Arlinghaus et al. 2009).

1 Fishing-induced evolution caused by recreational fisheries has not yet attracted much
2 attention in the literature. However, exploitation rates of fish stocks by recreational fisheries
3 can be substantial, and most recreational fisheries are also selective for morphological and
4 behavioural traits (Arlinghaus et al. 2002; Lewin et al. 2006; Uusi-Heikkilä et al. 2008). Thus,
5 in addition to ecological changes, rapid evolutionary changes are expected to occur in re-
6 sponse to the recreational exploitation of fish stocks (Arlinghaus et al. 2009; Philipp et al.
7 2009; Redpath et al. 2009), inter alia because stocks exploited by anglers often comprise
8 small, isolated freshwater fish populations (Heino and Godø 2002; Lewin et al. 2006). Our
9 previous study using an age-structured fish population model with angler exploitation and
10 multi-dimensional density dependence (Arlinghaus et al. 2009) is among the few (see also
11 Theriault et al. 2008; Saura et al. 2010) that explicitly dealt with recreational fisheries in the
12 context of fishing-induced evolution.

13 The objectives of the present study were (1) to quantify the selection strengths caused
14 by recreational fishing on three different life-history traits, (2) to evaluate the effectiveness of
15 different management policies to mitigate such selection, and (3) to examine possible evolu-
16 tionary consequences of evolution induced by recreational fishing in terms of important stock
17 variables such as average size at age and yield. Our model is based on northern pike, *Esox*
18 *lucius* L., which is a common target of recreational fisheries (Paukert et al. 2001; Arlinghaus
19 et al. 2008). To address our objectives, we extended our previous model, which considered
20 only a single life-history trait (reproductive investment; Arlinghaus et al. 2009), to incorporate
21 three life-history traits: growth capacity, size at maturation, and reproductive investment. In
22 addition to minimum-length limits, which are the most commonly used harvest regulations in
23 pike (Paukert et al. 2001), we considered maximum-length limits and harvestable-slot length
24 limits, with the latter being designed to protect immature and large fish simultaneously (Ar-
25 linghaus et al. 2010). We deliberately constrained our study to such relatively simple harvest

1 regulations, as these offer the greatest potential to be easily applied in the practices of recrea-
2 tional-fisheries management.

3 **Materials and Methods**

4 We use an age-structured population model parameterized for northern pike (hereafter simply
5 called pike) by integrating information available from various literature sources (Table 1). We
6 extend the model by Arlinghaus et al. (2009) to the simultaneous consideration of three im-
7 portant aspects of life history, i.e., reproduction, growth, and maturation. To promote general-
8 ity and reduce the number of parameters, we remove some of the density-dependent processes
9 considered by Arlinghaus et al. (2009) that were found to exert only small effects on estimates
10 of the selection strength on reproductive investment caused by recreational fishing. For a spe-
11 cific level of fishing mortality, we calculate selection differentials on all three life-history
12 traits, assuming that the population is at demographic equilibrium. Furthermore, we go be-
13 yond the original type of analysis conducted by Arlinghaus et al. (2009) by using our esti-
14 mates of the strength of selection to model the resultant evolutionary dynamics (Hilborn and
15 Minte-Vera 2008). Assuming a fixed heritability ($h^2 = 0.2$), we thus predict evolutionary
16 changes in the three life-history traits caused by 100 years of fishing. In addition, we identify
17 the evolutionary endpoints at which selection pressures on all three traits vanish.

18 Below, we explain the key ingredients of our model. For more details, please see Ar-
19 linghaus et al. (2009).

20 **Population dynamics**

21 Using a Leslie population-projection matrix $\mathbf{K}(\mathbf{X}, \mathbf{E})$ that depends on life-history trait values
22 \mathbf{X} and environmental variables \mathbf{E} , together with vectors $\mathbf{N} = (N_1, N_2, \dots, N_{a_{\max}})^T$ that describe

1 age-specific population densities (Caswell 2001), the population dynamics of a monomorphic
 2 fish population are given by

3 (1a) $\mathbf{N}(t+1) = \mathbf{KN}(t)$,

4 with

5 (1b)

6
$$\mathbf{K}(\mathbf{X}, \mathbf{E}) = \begin{pmatrix} f_1(\mathbf{X}, \mathbf{E})y(\mathbf{X}, \mathbf{E}) & f_2(\mathbf{X}, \mathbf{E})y(\mathbf{X}, \mathbf{E}) & \cdots & f_{a_{\max}-1}(\mathbf{X}, \mathbf{E})y(\mathbf{X}, \mathbf{E}) & f_{a_{\max}}(\mathbf{X}, \mathbf{E})y(\mathbf{X}, \mathbf{E}) \\ s_1(\mathbf{X}, \mathbf{E}) & 0 & \cdots & 0 & 0 \\ 0 & s_2(\mathbf{X}, \mathbf{E}) & \cdots & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & \cdots & s_{a_{\max}-1}(\mathbf{X}, \mathbf{E}) & 0 \end{pmatrix}$$

7 .

8 Here, $N_a(t)$ and $N_a(t+1)$ represent the density of fish at age a years in years t and $t+1$, re-
 9 spectively. The survival probability of individuals from age a to age $a+1$ is denoted by s_a ,
 10 f_a is the fecundity (measured by the number of hatched eggs) at age a , and y is the first-
 11 year survival from hatched eggs to the age of 1 year. We consider a maximum age of
 12 $a_{\max} = 12$ years and assume that individuals at $a = a_{\max}$ die immediately after spawning
 13 ($s_{a_{\max}} = 0$). In the present study, a thus varies between 1 and a_{\max} . The annual survival prob-
 14 ability s_a is given by

15 (2) $s_a = (1 - m_a)(1 - k_a)$,

16 where $0 < m_a < 1$ and k_a are annual probabilities of natural mortality and angling mortality,
 17 respectively. Age-specific fecundities f_a and survival probabilities s_a , as well as the first-
 18 year survival probabilities y , are functions of the life-history trait values \mathbf{X} and the envi-
 19 ronmental variables \mathbf{E} . The latter dependence represents density-dependent environmental
 20 feedback.

1 Growth and maturation

2 There are a multitude of models for describing the growth and maturation of fish. For our
3 evolutionary considerations, it is important to choose models that account for the trade-off be-
4 tween energy allocation to somatic growth and energy investment in reproduction (Dunlop et
5 al. 2009a). Also, to ensure wide applicability of the methods used for the present study, mod-
6 els with as few parameters as possible are preferred. Accordingly, we describe the growth tra-
7 jectory of fish based on the biphasic somatic growth model by Lester et al. (2004), which is a
8 special case of the model by Quince et al. (2008),

$$9 \quad (3a) \quad L_{a+1} = \frac{3}{3 + g_a}(L_a + h),$$

$$10 \quad (3b) \quad L_1 = h(1 - t_1),$$

11 where g_a is the annual reproductive investment and $t_1 < 1$ is the age intercept of the pre-
12 maturation growth curve. The annual reproductive investment g_a is represented as

13 $g_a = \omega GSI$, with the gonado-somatic index GSI (the ratio of gonad weight to somatic
14 weight) being weighted by a factor $\omega > 1$ that captures the higher caloric density of gonad tis-
15 sue relative to somatic tissue. We define maturation as the start of energy allocation to repro-
16 duction, with first spawning occurring in the following year. In accordance with the original
17 formulation by Lester et al. (2004), we assume a constant investment $g_a = g$ for all mature
18 individuals, as opposed to $g_a = 0$ for all immature individuals. Consequently, the annual
19 length increment equals h for juveniles ($g_a = 0$) and becomes smaller than h after matura-
20 tion.

21 Following Dunlop et al. (2009a), the probability of becoming mature at age a is de-
22 scribed as a function of the length L_a at age a ,

1 (4a)
$$P_{m,a} = \frac{1}{1 + \exp(-(L_a - L_{p50})/d)}$$

2 (4b)
$$d = \frac{\nu L_{p50}}{\text{logit}(p_u) - \text{logit}(p_l)},$$

3 where L_{p50} is the length at 50% maturation probability at age a and d determines the steep-
 4 ness of the change in maturation probability around L_{p50} . The probabilities p_u and p_l define
 5 the upper and lower bounds of the probabilistic maturation envelope around L_{p50} (for example,
 6 75% and 25%, respectively), and ν determines the width of this envelope in units of L_{p50}
 7 (Fig. 1a).

8 Density dependence

9 To obtain more realistic predictions, three mechanisms of density-dependent feedbacks on fit-
 10 ness are incorporated in the model (Arlinghaus et al. 2009). First, somatic growth rates are as-
 11 sumed to decrease as biomass density D increases. Specifically, the annual juvenile growth
 12 increment is defined as

13 (5)
$$h = \frac{h_{\max}}{1 + \gamma(D/D_u)^\delta},$$

14 where h_{\max} , called growth capacity, is the maximum juvenile growth increment realized for
 15 $D = 0$, and D_u is a unit-standardizing constant.

16 Second, also the fecundity f_a at age a is assumed to decrease as biomass density D
 17 increases,

18 (6)
$$f_a = \psi \frac{G_a}{2W_E} \exp(-\rho D),$$

19 where ψ is the hatching probability, W_E is the egg weight, and G_a is the gonad weight of in-
 20 dividuals at age a ($GSI = G_a/W_a$). Parameters determining density-dependent relationships

1 above are determined based on studies on pike in Lake Windermere, UK (Craig and Kipling
 2 1983; Kipling 1983a, 1983b; see Table 1 and Arlinghaus et al. 2009 for details).

3 Third, based on an empirical relationship reported by Minns et al. (1996), the survival
 4 probability y of hatched eggs during the first year depends on the density of hatched eggs,
 5 with overcompensation,

$$6 \quad (7) \quad \log_e y = \lambda + \frac{\kappa B^\mu}{B^\mu + B_{1/2}^\mu},$$

7 where λ is the logarithmic maximum survival probability, $\lambda + \kappa$ is the logarithmic minimum
 8 survival probability, and $B_{1/2}$ and μ are parameters determining the shape of this overcom-
 9 pensating density-regulation relationship. A Ricker stock-recruitment relationship seems to be
 10 appropriate for cannibalistic pike (Edeline et al. 2008).

11 Trade-offs and natural mortality

12 The growth model by Lester et al. (2004) implies a trade-off between somatic growth and re-
 13 productive investment (Fig. 1b). In addition, we assume a trade-off between somatic growth
 14 and natural mortality. For individual fish, an increase in growth capacity typically necessitates
 15 foraging in the face of predation risk and/or decreasing energy allocation to maintenance,
 16 which are both likely to diminish survival (Stamps 2007). Incorporating such a trade-off is
 17 crucial in models with evolving growth, because fish with infinitely fast growth could other-
 18 wise evolve, which clearly is unrealistic. As the simplest representation (Dunlop et al. 2009a),
 19 we assume that the annual survival probability declines linearly as growth capacity h_{\max} in-
 20 creases. The annual natural mortality probability m_a is thus defined as

$$21 \quad (8) \quad m_a = \begin{cases} \tau h_{\max} & \text{if } h_{\max} \leq 1/\tau \\ 1 & \text{if } h_{\max} > 1/\tau \end{cases},$$

1 where τ determines the maximum growth capacity $1/\tau$ beyond which survival is zero. The
 2 value of τ is determined so that realised values of h_{\max} in our hypothetical, non-exploited
 3 population are within the range of values reported for pike populations in the field (Fig. 1c).

4 Fishing mortality

5 We consider three types of harvest regulations, which are widely used in recreational fisher-
 6 ies: minimum-length limits (MinL-Ls), maximum-length limits (MaxL-Ls), and a combina-
 7 tion of these (harvestable-slot length limits, HSL-Ls). The annual fishing mortality k_a repre-
 8 sents the proportion of fish removed from the population by recreational fishing, and is calcu-
 9 lated as

$$10 \quad (9) \quad k_a = \begin{cases} V_a [1 - \exp(-F)] & \text{if } L_{\min} \leq L_a \leq L_{\max} \\ V_a [1 - \exp(-\phi F)] & \text{otherwise} \end{cases},$$

11 where F is the instantaneous fishing mortality, $\phi < 1$ is the hooking mortality probability af-
 12 ter catch-and-release, and V_a (Fig. 1d) measures the portion of fish of age a that is vulnerable
 13 to angling (with other fish at age a being invulnerable to angling, e.g., due to size-dependent
 14 gape limitation to hooking or due to the choice of safe habitats; Post et al. 2003). Note that in
 15 Arlinghaus et al. (2009) F was represented as the product of a catchability coefficient and an
 16 angling-effort density, but this representation was simplified in the present model. Note also
 17 that we further simplified the model of Arlinghaus et al. (2009) by removing angling-effort
 18 responses to changes in the density of vulnerable fish, as well as dynamically determined ille-
 19 gal harvest, because these processes had little effect on estimates of the selection differentials
 20 for reproductive investment (Arlinghaus et al. 2009).

1 Selection differentials

2 Selection differentials measure the change of a population's mean trait value before and after
3 selection (Falconer and Mackay 1996). Selection differentials for the three life-history traits
4 considered in this study are calculated after the population reaches demographic equilibrium.
5 We assume that the population's phenotypic variation is normally distributed around the
6 population mean, with a coefficient of variation given by CV_p . The selection differential S
7 on a trait X is calculated as

$$8 \quad (10) \quad S = \frac{\int X \lambda(X) p(X) dX}{\int \lambda(X) p(X) dX} - \frac{\int X p(X) dX}{\int p(X) dX},$$

9 where $p(X)$ and $\lambda(X)$ are the probability density and fitness of trait values X , respectively
10 (Arlinghaus et al. 2009). Thus, the second term represents the mean trait value before selec-
11 tion, and the first term represents the mean trait value after selection. The fitness of a rare
12 variant phenotype with a set of values \mathbf{X} for the three life-history traits, in the resident popu-
13 lation of individuals whose trait values are identical to the population means, is calculated as
14 the dominant eigenvalue of the corresponding Leslie matrix $\mathbf{K}(\mathbf{X}, \mathbf{E})$ (Arlinghaus et al. 2009).
15 Selection differentials per generation are calculated using the dominant eigenvalue of the ma-
16 trix $\mathbf{K}^{T(\mathbf{X}, \mathbf{E})}(\mathbf{X}, \mathbf{E})$, where $T(\mathbf{X}, \mathbf{E})$ is the population's average generation time (Arlinghaus et
17 al. 2009).

18 Since the selection differential is not dimensionless, it must be standardized for com-
19 paring the selection strengths among traits or populations. In the present study, the mean-and-
20 variance-standardized selection differential (Arlinghaus et al. 2009), which has been referred
21 to in the literature as the mean-standardized selection gradient (Hereford et al. 2004), is calcu-
22 lated as

$$23 \quad (11) \quad S_{\text{std}} = \bar{X} \frac{S}{\sigma_X^2},$$

1 where \bar{X} is the population mean and σ_x^2 the population variance of the considered trait. The
2 mean-and-variance-standardized selection differential S_{std} represents the increase in relative
3 fitness for a proportional change in the considered trait (Hereford et al. 2004). It is viewed as
4 a suitable dimensionless measure of selection strength, because it approximates the mean-
5 standardized slope of the trait's fitness landscape at the population mean \bar{X} (Phillips and Ar-
6 nold 1989) and is largely independent of the population variance σ_x^2 .

7 Outline of analysis

8 Our numerical investigations were based on parameter values representative for pike (Table
9 1). The initial population densities for the considered age classes were taken from long-term
10 data of the Windermere pike population (Kipling and Frost 1970). Angling intensity was var-
11 ied by modifying the instantaneous fishing mortality F . For a range of combinations of an-
12 gling intensity and harvest regulation, the analysis proceeded in two steps:

13 1. Estimation of selection differentials for the three life-history traits:

14 • We focused on the type and strength of selection that a pristine pike population ex-
15periences at the commencement of harvesting. The default set of population means of
16 the three life-history traits was determined assuming that the present population is at
17 evolutionary equilibrium in the absence of harvesting. Annual selection differentials
18 S for the three traits were then calculated for the default resident population.

19 2. Estimation of evolutionary changes in the three life-history traits:

20 • Using the annual selection differential S and heritability h^2 for each trait, its selec-
21tion response was obtained as $R = h^2 S$ (Falconer and Mackay 1996). The trait's popu-
22lation mean for the next year was then obtained by adding the selection response to the
23 current population mean.

- 1 • This procedure was repeated for 100 years. The rate of evolution, in the unit Darwin,
2 was calculated as $r = |\ln z_2 - \ln z_1| / (t_2 - t_1)$, where z_1 and z_2 are the trait's population
3 means at the beginning (t_1) and end (t_2) of the considered period and the duration
4 $t_2 - t_1$ was measured in millions of years.
- 5 • Possible evolutionary endpoints, where the selection differentials S vanish for all
6 three traits, were identified by changing values of the three traits systematically. In
7 general, the procedure above was extended until the population reaches equilibrium.
8 Even when an evolutionary endpoint was identified, the procedure was repeated for
9 several different starting values because there may exist alternative equilibrium states.

10 Results

11 Evolutionary equilibria in the absence of fishing

12 To determine the initial conditions for studying fishing-induced evolution, we consider a fish
13 population that is not yet exposed to fishing pressures. Specifically, we assume that this popu-
14 lation has evolved to an evolutionary equilibrium, which implies that the selection pressures
15 on all three life-history traits vanish. We found two combinations of population means for the
16 three life-history traits that yield zero selection differentials (Table 2), representing alternative
17 possible evolutionary endpoints (EP). The first trait combination (EP-1) is characterised by
18 early maturation (at the age of 1 year), while the second trait combination (EP-2) is character-
19 ised by later maturation (at the age of 2 or 3 years). Accordingly, spawning occurs at the age
20 of 2 years in the EP-1 population and at the ages of 3 and 4 years in the EP-2 population. Al-
21 though selection differentials are zero in the EP-1 population with the default degree of phe-
22 notypic variation, individuals with the EP-2 population means can invade into the EP-1 popu-
23 lation, because their fitness is higher than that of the residents. By contrast, individuals with

1 the EP-1 population means cannot invade into the EP-2 population, because their fitness is
2 lower than that of the residents. In other words, only the EP-2 population is evolutionarily
3 stable. Therefore, we focus on EP-2 as a baseline condition for investigating the consequences
4 of fishing. The age and size at maturation in the EP-2 population agree well with empirical
5 values reported for pike populations (Raaf 1988).

6 Fishing-induced evolution in the absence of harvest regulations

7 We started our investigation by examining the situation without harvest regulation. As ex-
8 pected, the magnitude of selection differentials for the three traits increases with increasing
9 recreational-fishing mortality (Fig. 2a). Selection differentials for reproductive investment g
10 and growth capacity h_{\max} are both positive, so that the traits experience selection pressures
11 towards increasing reproductive investment and growth capacity. The standardized strength of
12 selection on growth is larger than that on reproductive investment, especially when the an-
13 gling intensity is high. The standardized selection differential on the size at maturation L_{p50} is
14 as large as that on h_{\max} , but the direction is opposite, so that this trait experiences selection
15 pressures towards decreasing size at maturation. The fishing yield (harvested biomass) from
16 the population is maximized at an instantaneous fishing mortality of $F \approx 0.4$ (Fig. 2b), and
17 selection differentials are relatively small when the population is not overexploited (Fig. 2a),
18 i.e., when fishing mortality remains below the fishing mortality at maximum sustainable yield.

19 Effects of harvest regulations on selection strengths

20 Next, we systematically investigated the effects of harvest regulations on selection differen-
21 tials. In general, increasing minimum-length limits (MinL-Ls) mitigate the magnitude of se-
22 lection differentials, but this effect differs greatly between the three evolving traits (Fig. 3a-c).
23 The magnitudes of selection differentials on reproductive investment g exhibit a peak at in-

1 intermediate MinL-Ls (Fig. 3a). MinL-Ls have a strong impact on selection differentials on
2 growth capacity h_{\max} (Fig. 3b): introduction of a MinL-L of 45 cm causes positive selection
3 differentials for this trait, but these change to negative at a MinL-L of about 50 cm, and val-
4 ues approach zero as the MinL-L is increased further. The magnitude of selection differentials
5 on the size L_{p50} at maturation first slightly increases as the MinL-L increases up to 60 cm, and
6 then decreases as the MinL-L is increased further (Fig. 3c).

7 We also investigated the effects of other types of harvest regulations, i.e., harvestable-
8 slot length limits (HSL-L; Fig. 3d-f) and maximum-length limits (MaxL-L; Fig. 3g-i). The
9 magnitude of selection differentials for g is generally smaller than in the absence of harvest
10 regulations. The curvatures of the relationships between selection differentials for g and the
11 tightness of harvest regulations are almost opposite to the MinL-L case, with the lowest selec-
12 tion differentials resulting for intermediate harvest regulations. The selection differentials for
13 h_{\max} are large and positive, and decline relatively suddenly for tight HSL-L harvest regula-
14 tions. Selection differentials for L_{p50} are usually negative, and their magnitude decreases as
15 regulations become stricter. They become even positive under the strictest HSL-L and MaxL-
16 L harvest regulations.

17 To understand regulation-specific differences in the mitigation of selection pressures
18 in more detail, we examined selection differentials for exploitation levels that result in identi-
19 cal reductions of spawner biomasses, as quantified by the spawning-potential ratio (Fig. 4).
20 For MinL-L regulations, selection pressures on g are larger, those on h_{\max} are generally
21 smaller, and those on L_{p50} are also smaller than without harvest regulations, because smaller
22 sizes have a selective advantage under MinL-L regulations. Opposite trends are found in the
23 selection pressures under HSL-L and MaxL-L regulations, because larger sizes have a selec-
24 tive advantage in these cases. It turned out that the selection strengths under harvest regula-

1 tions are often larger than those without harvest regulations for the same level of exploitation.
2 This means that the effects of harvest regulations on mitigating selection pressures, as seen in
3 Fig. 3, actually result from the reduction of exploitation levels rather than from altered selec-
4 tivity patterns in terms of vulnerable fish sizes. In fact, for the same exploitation levels, the
5 more pronounced selectivity patterns associated with harvest regulations result in stronger se-
6 lection pressures than the less selective exploitation patterns that apply in the absence of har-
7 vest regulations.

8 Evolutionary changes of traits and their consequences

9 We investigated evolutionary changes in the three life-history traits, and resultant changes in
10 population characteristics, when a fixed angling pressure was continuously applied for a
11 longer period (Fig. 5-7). Specifically, we followed changes in trait values, fish length at the
12 age of 4 years, and yield (harvested biomass) during 100 years of fishing (Fig. 5a). Essentially
13 linear changes in the values of the three life-history traits for 100 years imply that selection
14 pressures remain virtually constant during this period. Accordingly, the selection strengths at
15 the beginning of this period, represented by standardized selection differentials S_{std} and esti-
16 mated as described in the preceding section, are good predictors of the evolutionary outcomes
17 after 100 years. During this period, reproductive investment g and growth capacity h_{max} in-
18 crease by 5% and 10%, respectively, while size L_{p50} at maturation decreases by 8% when no
19 harvest regulation is adopted.

20 The evolutionary trait changes tend to increase (h_{max}) or decrease (g and L_{p50}) fish
21 length at age 4. As a result of these conflicting effects, adult fish length at the age of 4 years
22 increases by 5% after 100 years of harvesting without regulation (from 76.7 cm to 81.2 cm).
23 By contrast, the yield shows little change. When harvest regulations are introduced, adult fish
24 length at the age of 4 years becomes either larger (with MaxL-Ls or HSL-Ls) or smaller (with

1 MinL-Ls) than in the unexploited case. In some cases, yield drops by 10-20% as evolutionary
2 changes enable fish to escape the harvestable size ranges. Under HSL-Ls, increases in yield
3 result from increased fish length at the age of 4 years (from about 72 cm to about 78 cm),
4 while the number of harvested individuals decreases by more than 10%.

5 We also compared the values after 100 years with those at the possible evolutionary
6 endpoints (Fig. 6). At the evolutionary endpoint, fish length at the age of 4 years is ca. 50%
7 smaller when a MinL-L of 45 cm is applied than without fishing-induced evolution (Fig. 6a).
8 Evolution towards small size becomes less pronounced as MinL-Ls is increased. Applying
9 MaxL-Ls causes the opposite effect: in contrast to MinL-Ls, fish length at the evolutionary
10 endpoint is larger than without fishing-induced evolution (Fig. 6i). The largest evolutionary
11 change is observed for an intermediate MaxL-L of 75 cm. When HSL-Ls are introduced by
12 combining a MinL-L of 45 cm with various MaxL-Ls, two distinct outcomes occur depending
13 on whether the MaxL-L is large (≥ 80 cm) or small (≤ 75 cm) (Fig. 6e). Fish become consid-
14 erably smaller in the former case, whereas they become larger in the latter case.

15 It appears contradictory that in some cases fish length after 100 years is larger than
16 without fishing-induced evolution, even though fish length at the evolutionary endpoint is
17 considerably smaller than without fishing-induced evolution: this occurs for HSL-Ls with a
18 MinL-L of 45 cm and a large MaxL-L. The reason is that fish length increases for the first
19 few hundred years due to the positive selection on growth capacity (Fig. 7). Once the positive
20 selection on growth capacity stops, because its fitness advantage vanishes due to the trade-off
21 between growth and survival, adult fish length decreases continuously, mainly due to positive
22 selection on reproductive investment.

23 In most cases, yield at the evolutionary endpoint is much smaller than prior to fishing-
24 induced evolution (Fig. 6b, 6f, 6j). Exceptions appear for a MinL-L of 100 cm and for large
25 MaxL-Ls (≥ 80 cm), i.e., for cases in which the original yield is extremely small. In many

1 cases, also population biomass at the evolutionary endpoint is smaller than prior to fishing-
2 induced evolution (Fig. 6c, 6g, 6k). By contrast, if a MinL-L of 45 cm or HSL-Ls are applied,
3 population biomass can be twice as large as prior to fishing-induced evolution. In these cases,
4 the population contains a large number of fish that are smaller than 45 cm. At the evolution-
5 ary endpoint, the pristine population biomass, i.e., the equilibrium population biomass that is
6 attained when fishing is ceased, is considerably smaller (by up to 60%) than prior to fishing-
7 induced evolution (Fig. 6d, 6h, 6l).

8 Robustness analyses

9 The robustness of results of our model-based analysis was tested by altering the underlying
10 assumptions or default parameter values. According to our original assumption, almost all fish
11 at ages 2 years or older are equally vulnerable to angling (Fig. 1d, continuous line). In other
12 words, the difference in size selectivity on older fish is not very pronounced, in line with em-
13 pirical data for recreational pike fisheries, where only the very small juvenile fish (with a total
14 length of less than 20 cm) are not vulnerable to angling, while fish over 40-50 cm are equally
15 vulnerable (Pierce et al. 1995). We shifted the original vulnerability curve to the right, so that
16 target fish are restricted to much larger sizes than in the default case (Fig. 1d, dashed line).
17 Such a shift, to which we refer as trophy selectivity, may be expected, for example, when an-
18 glers start using large lures (Arlinghaus et al. 2008). Under such situations of more pro-
19 nounced size selectivity, large positive selection on growth capacity h_{\max} , which often occurs
20 for the original size selectivity, is not observed, even in the absence of harvest regulations
21 (Fig. 5b). Accordingly, fish size and yield decline during 100 years in the absence of harvest
22 regulation. Evolutionary changes become small for stringent harvest regulations (HSL-L of
23 45-60 cm or MaxL-L of 50 cm). This is because almost no legal harvest is possible under the
24 joint impact of these regulations and trophy selectivity.

1 Next, the phenotypic variability and heritability of the evolving traits are modified to
2 test the impact of these variables on the magnitude of evolutionary change (Fig. 8). As ex-
3 pected, this magnitude increases almost linearly with heritability. By contrast, the influence of
4 phenotypic variability on evolutionary change is more significant and complicated. When the
5 phenotypic coefficient of variation is 5%, evolutionary changes are almost negligible. When
6 the phenotypic coefficient of variation is 20%, considerably larger evolutionary changes are
7 observed, in particular in growth capacity. This large impact is a result of the fact that the de-
8 gree of phenotypic variability crucially affects whether or not variant individuals with trait
9 values that strongly depart from the current population means exist in the population: since,
10 due to the nonlinearity of the fitness landscape, these individuals may possess extremely high
11 fitness, they have a large impact on the resultant magnitude of evolutionary changes.

12 Results of sensitivity analyses for other parameters are summarized in Table 3. In gen-
13 eral, predictions about reproductive investment are more robust to changes in parameter val-
14 ues than those about growth capacity or size at maturation. The latter two life-history traits are
15 sensitive to the trade-off between growth and survival (described by the parameter τ). An in-
16 crease in t_1 , the age intercept of the pre-maturation growth curve, greatly intensifies selection
17 on growth, via changes in the vulnerability to angling around the age at first spawning. Other
18 parameters that relatively exert strong impacts on model predictions are the exponents in the
19 allometric length-weight regression (β), in the stock-recruitment relationship determining
20 density-dependent larval survival (λ and μ), and in the relationship between fish length and
21 vulnerability to fishing (η).

22 Discussion

23 The present study has demonstrated how recreational fishing causes considerable selection
24 pressures on multiple life-history traits under various types of fishing regimes. In the absence

1 of harvest regulations, these selection pressures elevate energy allocations to reproduction,
2 maturation, and growth. Selection strengths on maturation size and growth capacity exceed
3 those on reproductive investment. The present study has also illustrated the complex nature of
4 fishing-induced life-history selection: for example, the direction and magnitude of selection
5 on growth capacity changes drastically when the size-selectivity of harvesting is strengthened
6 by large minimum-length limits (MinL-Ls) or trophy-size-oriented recreational harvesting.

7 A primary goal of our work here was to systematically investigate the effects of differ-
8 ent types of harvest regulations on the strengths of fishing-induced selection on several life-
9 history traits. In addition to MinL-Ls, we therefore considered maximum-length limits
10 (MaxL-Ls) and harvestable-slot length limits (HSL-Ls), with the latter being designed to pro-
11 tect immature and large fish simultaneously (Arlinghaus et al. 2010).

12 Applying different MinL-Ls is one of the most common harvest regulations in recrea-
13 tional fisheries (Paukert et al. 2001). We find that MinL-Ls generally work well in mitigating
14 the strength of fishing-induced selection, in particular, on growth capacity and maturation size.
15 Although MinL-Ls strengthen the size-selectivity of harvesting, larger MinL-Ls usually re-
16 duce selection strengths. The direction of selection on growth capacity is positive for the
17 smallest considered MinL-L (45 cm), but becomes negative as MinL-Ls are raised. In inter-
18 preting these findings, it is crucial to remember that the mitigation of selection achieved by
19 MinL-Ls in our model largely results from the implied reduction of exploitation rates. If, in
20 contrast, fishing efforts are adjusted so as to keep yield (and income) constant, despite the al-
21 tered harvest regulations, larger MinL-Ls could instead intensify selection.

22 Application of MaxL-Ls has been suggested as an alternative to MinL-Ls to reduce the
23 strength of fishing-induced selection pressures (Conover and Munch 2002). It seems intui-
24 tively plausible to assume that MaxL-Ls might counteract the effects of positively size-
25 selective fishing. Corroborating this expectation, we find that selection strengths, in particular,

1 on maturation size, can indeed be reduced through MaxL-Ls. At the same time, however,
2 MaxL-Ls greatly increase the magnitude of positive selection on growth capacity.

3 Also HSL-Ls have been suggested for mitigating fishing-induced evolution (Law
4 2007). The present study has shown that HSL-Ls change fishing-induced selection pressures
5 similar to MaxL-Ls. Selection on reproductive investment can be reduced effectively, while
6 selection on growth capacity is considerably strengthened, and is usually positive just as for
7 high MinL-Ls. Nevertheless, HSL-Ls have been shown to be effective in reducing selection
8 on maturation size, both in our model and elsewhere (Baskett et al. 2005). Similarly, Jørgen-
9 sen et al. (2009) have argued that bell-shaped size-selectivity, which obviously is akin to
10 HSL-Ls, better mitigates fishing-induced evolution than sigmoid size-selectivity. Arlinghaus
11 et al. (2010) reported additional advantages of HSL-Ls over MinL-Ls for managing pike, in-
12 cluding increased harvest biomass, elevated abundance of trophy fish, and reduced truncation
13 of the population's age structure. Based on these findings, further investigations of the poten-
14 tial of HSL-Ls as a tool of recreational-fisheries management are warranted.

15 Our findings on either positive or negative growth-capacity evolution in response to
16 harvesting clearly underscore that one should not trust the often-reported intuition that fish-
17 ing-induced evolution will necessarily reduce the growth rates of fish in response to positively
18 size-selective fishing (*sensu* Walters and Martell 2004). Despite some empirical studies (e.g.,
19 Ricker 1981; Conover and Munch 2002; Swain et al. 2007; Nusslé et al. 2008), only few theo-
20 retical investigations have so far examined growth evolution caused by size-selective fishing
21 (William and Schertzer 2005; Hilborn and Minte-Vera 2008). In agreement with our study,
22 recent empirical investigations have reported less-than-straightforward patterns in fishing-
23 induced selection on growth. In particular, using an individual-based eco-genetic model,
24 Dunlop et al. (2009b) predicted positive evolutionary changes in genetic growth capacity for
25 small MinL-Ls, although they found negative changes for other MinL-Ls. Also the present

1 model predicts such changes in the direction of selection pressures on growth capacity: al-
2 though selection is positive and strong for small MinL-Ls (45 cm), it becomes negative and
3 weak for larger MinL-Ls. It seems clear that the direction of selection on growth capacity de-
4 pends not only on the size-selectivity of fishing, but also on the life history of the fished spe-
5 cies. If the species matures at small sizes, while fishing is limited to very large fish (as im-
6 plied by large MinL-Ls), the number of reproductive opportunities increases for fish staying
7 below MinL-L. Thus, slow growth will be favoured by evolution. This is not the case if fish-
8 ing also targets small fish (as implied by small MinL-Ls or non-selective exploitation). Under
9 such conditions, fast growth may be favoured by evolution, because growing as quickly as
10 possible and having a single successful spawning event might then be advantageous. Given
11 the life history of pike (early maturation at small size) and considering its typical exposure to
12 steep size-selectivity curves (Pierce et al. 1995), positive selection on growth must be ex-
13 pected when pike is managed by small MinL-Ls of 45-50 cm.

14 MaxL-Ls must also be expected to favour faster-growing fish, because these increase
15 their chances of avoiding harvesting by growing into the protected size range. Therefore, if
16 the baseline harvesting scheme in the absence of harvest regulations causes negative selection
17 on growth, as in the case examined by William and Schertzer (2005), MaxL-Ls might coun-
18 teract the baseline selection, and thus decrease the strength of selection on growth. However,
19 if the baseline selection on growth is positive, as in the present study, MaxL-Ls further in-
20 crease the strength of selection on growth.

21 Surely the argument above is sensitive to assumptions of size-dependent mortality and
22 fecundity (Thygesen et al. 2005). Except for the first year of life, our model considered a con-
23 stant, size-independent natural mortality, which was assumed to be a function of growth rate
24 to represent the theoretically sound idea of a growth-survival trade-offs (Stamps 2007). How-
25 ever, positively size-dependent survival resulting from higher chances of escaping cannibal-

1 ism as body size increases might also be found in adult pike (Haugen et al. 2007). Further-
2 more, our model assumed a constant gonado-somatic index after maturation, even though it is
3 known that it increases with the size of mature female pike (Edeline et al. 2007). Structural
4 changes to our model will therefore be needed to examine the implications of size dependence
5 in natural mortality and gonado-somatic index for estimates of fishing-induced evolution.

6 It is worth highlighting that, in terms of the practical consequences of fishing-induced
7 evolution, positive selection on growth in the present study had a large effect on pike yield as
8 measured by harvested biomass. To date, there have only been a few attempts to quantify
9 yield changes resulting from fishing-induced evolution, and most of them predicted yield to
10 decline (Law and Grey 1989; Heino 1998; Andersen and Brander 2009; Okamoto et al. 2009).
11 Also experiments have demonstrated declining yields in response to size-selective exploita-
12 tion (Conover and Munch 2002). In the present study, however, fishing-induced life-history
13 evolution increased yield for some harvest regulations such as HSL-Ls. The difference be-
14 tween previous results and our findings arises from evolutionary trends in fish size caused by
15 fishing. In many previous models, only maturation age could evolve, with its decline in re-
16 sponse to fishing resulting in smaller fish. In our study, adult fish size often increased as the
17 effects of increased growth capacity outweighed those of smaller maturation size and elevated
18 reproductive investment.

19 The three life-history traits examined here exhibited considerable evolutionary
20 changes. For example, we found an increase in growth capacity of up to 13% within 100 years
21 of fishing with an instantaneous mortality of 0.67 year^{-1} . During those 100 years, evolutionary
22 changes were almost linear in time, which implies that the direction and strength of direc-
23 tional selection were almost constant. The initial selection strength represented by S_{std} thus
24 appears to be a good predictor of the amount of evolutionary changes accruing during 100
25 years. Based on the maximum value of S_{std} on growth, which occurs for very high angling in-

1 densities, growth capacity may evolutionarily increase by up to 40% during 100 years of fish-
2 ing. A 13-40% increase during 100 years corresponds to an evolutionary rate of $1.2-3.4 \times 10^3$
3 Darwin. This rate is modest compared to values reported for fishing-induced evolution in
4 commercial fisheries (Jørgensen et al. 2007; Sharpe and Hendry 2009). Andersen and Brander
5 (2009) concluded in a modelling study that the rate of fishing-induced evolution is slow, but
6 their estimates ($\approx 0.1-0.6\%$ change in phenotypes per year, which is equivalent to $1.0-$
7 6.0×10^3 Darwin) are well in line with our estimated evolutionary rates here. Therefore, dis-
8 cussions of whether fishing-induced evolution is “fast” or “slow” are not overly meaningful
9 without establishing a natural baseline against which to judge evolutionary rates. Moreover,
10 as our robustness analysis has shown, the rate of evolution is influenced by the degree of phe-
11 notypic variance and heritability. Unfortunately, good estimates of these parameters are ex-
12 ceedingly rare for wild fish stocks. Moreover, genetic and phenotypic variances, and hence
13 the corresponding heritabilities, might readily change during the course of evolution (Edeline
14 et al. 2009), with obvious consequences for the speed of fishing-induced evolution.

15 How do our estimated rates of life-history evolution in response to recreational fishing
16 compare with field observations for pike? Qualitatively, our prediction that exploitation of
17 pike results in increased reproductive investment well agrees with field observations of pike
18 populations exposed to differential angling mortality (Diana 1983). Diana (1983) also ob-
19 served pike populations to mature earlier when exposed to high adult mortality through an-
20 gling, which again agrees with our findings, but the empirical study did not control for a po-
21 tential compensatory response, which provides an alternative explanation of earlier matura-
22 tion through relaxed competition for food.

23 The only empirical estimates of fishing-induced evolution in the growth rate of pike
24 stems from long-term demographic analyses of the pike population in Lake Windermere
25 (Carlson et al. 2007; Edeline et al. 2007, 2009). This population experienced relatively mild

1 experimental exploitation with gill nets, with a maximum annual exploitation fraction of 8%
2 (Edeline et al. 2007). One must be careful, however, when trying to directly compare the em-
3 pirical findings from Windermere with our model predictions. This is for two reasons. First,
4 exploitation levels, types of fishing gears, and the implied size-selectivity in Windermere
5 strongly differed from the simpler assumptions made in our recreational-fisheries pike model.
6 Second, interpreting any observed phenotypic changes in adult growth rates (as provided by
7 the Windermere studies) is complicated by the potential joint evolution of growth capacity,
8 maturation schedule, and reproductive investment. Yet, it is noteworthy that natural and fish-
9 ing-induced selection on body size in Windermere pike appeared to act in opposite directions:
10 small adult pike are disfavoured by natural selection, but favoured by fishing-induced selec-
11 tion (Carlson et al. 2007; Edeline et al. 2009). Consequently, somatic growth of adult pike de-
12 creased when the experimental gill-net fishery was intensified, but increased after experimen-
13 tal fishing was relaxed (Edeline et al. 2007, 2009). The evolution of slower growth in Win-
14 dermere pike agrees with our model predictions for a MinL-L of 60 cm (Windermere pike be-
15 low 60 cm were not intensively exploited, so the experimental fishery may be viewed as ef-
16 fectively exploiting adult pike according to a MinL-L of 60 cm).

17 Another important insight from the Windermere studies is that the gill-net fishery re-
18 sulted in disruptive selection favouring both small- and large-sized pike through a bell-shaped
19 selectivity curve (Carlson et al. 2007; Edeline et al. 2009). This disruptive selectivity appears
20 to have increased the genetic variability for somatic growth of adult pike, thus enabling the
21 rapid evolutionary rebound observed in somatic growth after fishing intensity was relaxed
22 (Edeline et al. 2009). Even though the HSL-Ls in the present study resemble the disruptive se-
23 lectivity caused by gill nets in Windermere, we cannot immediately use our model to investi-
24 gate the rapid evolutionary rebound, because we only considered a constant genetic variance.

1 Including the effects of fishing on genetic variability thus provides a natural and interesting
2 extension of our model.

3 The present study showcases the complexity exploited fish populations can exhibit in
4 response to fishing activities and regulations. It underscores the need for the development and
5 analyses of stock-specific models, to fully understand observed ecological and evolutionary
6 responses to fishing. When applied to pike, future stock-specific models could include size-
7 dependent mortality processes in general, and size-dependent cannibalism in particular. De-
8 spite these opportunities for extension, our study clearly demonstrates that no regulation can
9 reduce to zero all selection pressures induced by size-selective recreational fishing. Thus,
10 managers will likely have to cope with recreational fishing-induced evolution in all inten-
11 sively exploited pike populations. Independently of whether such evolution is beneficial (e.g.,
12 when it increases fish size) or detrimental (e.g., when it reduces yield), its existence should no
13 longer be ignored in recreational-fisheries management.

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Table 1. Symbols and parameter values in a life-history model of pike (*Esox lucius*).

Symbol	Description	Equation	Source	Value
Evolving traits				
h_{\max}	Growth capacity (cm)	---	---	---
L_{p50}	Midpoint of size at maturation (cm)	---	---	---
g	Annual reproductive investment	---	---	---
Variables				
N_a	Fish density (ha^{-1})	(1)	---	---
s_a	Annual survival probability	(2) $s_a = (1 - m_a)(1 - k_a)$	---	---
m_a	Annual natural mortality	(8) $m_a = \tau h_{\max}$	1	$\tau = 0.01429 \text{ (cm}^{-1}\text{)}$
k_a	Annual angling mortality	(9) $k_a = \begin{cases} V_a [1 - \exp(-F)] & \text{if } L_a \geq \text{MinL-L} \cap L_a \leq \text{MaxL-L} \\ V_a [1 - \exp(-\phi F)] & \text{if } L_a < \text{MinL-L} \cup L_a > \text{MaxL-L} \end{cases}$	2,3	$\phi = 0.094$

f_a	Annual fecundity	(6) $f_a = \psi \frac{G_a}{W_E} \exp(-\rho D)$	2,4,5	$\psi = 0.735$
				$W_E = 6.37 \times 10^{-6}$ (kg)
				$\rho = 0.04818$ (ha kg ⁻¹)
L_a	Individual fish length (cm)	(3) $\begin{cases} L_{a+1}(t+1) = \frac{3}{g_a + 3} (L_a(t) + h) \\ L_1 = h(1 - t_1) \end{cases}$	2,6	$t_1 = -0.423$
W_a	Individual fish weight (kg)	$W_a = \alpha (L_a / L_u)^\beta$	7	$\alpha = 4.8 \times 10^{-6}$ (kg)
				$\beta = 3.059$
				$L_u = 1$ (cm)
G_a	Gonad weight (kg)	$G_a = g W_a / \omega$	8	$\omega = 1.73$
$P_{m,a}$	Probability of maturation	(4a) $P_{m,a} = \frac{1}{1 + \exp(-(L_a - L_{p50}) / d)}$		
V_a	Vulnerability to angling	$V_a = [1 - \exp(-\eta L_a)]^\theta$	2	$\eta = 0.25$ (cm ⁻¹)
				$\theta = 1300$

y	First year survival	$(7) \log_e(y) = \lambda + \frac{\kappa B^\mu}{B^\mu + B_{1/2}^\mu}$	9	$\lambda = -7.65$ $\kappa = -31.73$ $\mu = 0.31$ $B_{1/2} = 1.68 \times 10^9 \text{ (ha}^{-1}\text{)}$
D	Biomass density (kg ha ⁻¹)	$D = \sum_{a=1}^{a_{\max}} W_a N_a$		
B	Hatched egg density (ha ⁻¹)	$B = \sum_{a=1}^{a_{\max}} f_a N_a$		
h	Annual juvenile growth increment (cm)	$(5) h = \frac{h_{\max}}{1 + \gamma(D/D_u)^\delta}$	2	$\gamma = 0.1819$ $\delta = 0.5678$ $D_u = 1 \text{ (kg ha}^{-1}\text{)}$

Parameters

d		$(4b) d = \frac{\nu L_{p50}}{\text{logit}(p_u) - \text{logit}(p_l)}$	1	$p_u = 0.75$ $p_l = 0.25$ $\nu = 0.2$ varied
L_{\min}	Minimum-length limit (cm)			

L_{max}	Maximum-length limit (cm)		varied
CV_p	coefficient of phenotypic variation	1	0.15
h^2	heritability	1	0.2

1: own calculation/definition; 2: Arlinghaus et al. 2009; 3: Munoeke and Childress 1994; 4: Franklin and Smith 1963; 5: Craig and Kipling 1983; 6: Lester et al. 2004; 7: Willis 1989; 8: Diana 1983; 9: Minns et al. 1996

Table 2. Population means of the three life-history traits (reproductive investment, growth capacity, and size at maturation) at evolutionary equilibrium in the absence of angling pressures in pike (*Esox lucius*). The default parameter values (Table 1) are used. The densities and age at first spawning are also shown.

	g	h_{\max} (cm)	L_{p50} (cm)	At equilibrium		
				fish density	biomass density	age at first
				(ha^{-1})	(kg ha^{-1})	spawning (yr)
EP-1	0.433	30.0	<12*	12.0	7.8	2 (100 %)
EP-2	0.471	27.1	39.4	13.4	9.0	3 (42 %), 4 (57 %)

* Individuals with L_{p50} of less than 12 cm are phenotypically equivalent because they mature (i.e., start investing to reproduction) at the age of 1 year with a probability of 100 %.

Table 3. Sensitivity analysis in terms of percent changes in selection differentials on the three life-history traits when the default value of each parameter is altered by $\pm 10\%$. Changes in response variables $\geq |10\%|$ (i.e., sensitive or elastic changes) are highlighted in bold. We chose an intermediate angling intensity ($F = 0.67$) with no harvest regulation.

Parameters	Reproductive investment g		Growth capacity h_{\max}		Size at maturation L_{p50}	
	+10%	-10%	+10%	-10%	+10%	-10%
α	0.2	-0.3	-4.7	8.4	1.1	-0.3
β	-17.5	10.2	99.1	52.3	39.7	13.4
γ	0.1	-0.1	-2.6	3.5	0.4	-0.2
δ	0.0	0.0	0.2	-0.2	0.0	0.0
t_1	0.0	-0.1	13.3	-8.7	4.4	-3.8
ω	-0.2	0.2	5.6	-4.1	-0.3	0.8
w_E	-0.2	0.2	5.6	-4.1	-0.3	0.8
ψ	0.2	-0.2	-3.8	6.3	0.7	-0.3
ρ	0.0	0.0	0.2	-0.2	0.0	0.0
λ	-2.4	1.7	90.2	28.1	5.5	30.5
κ	-0.2	0.2	5.6	-4.2	-0.3	0.9
μ	0.6	-0.7	-5.9	29.1	5.2	0.9
$B_{1/2}$	0.1	-0.1	-1.4	1.7	0.2	-0.1
ν	-0.2	0.2	2.4	-3.0	1.4	-2.0
τ	-5.0	4.8	22.5	-8.1	-9.6	16.9
η	-0.5	0.9	54.1	12.6	-0.8	4.6
θ	0.1	-0.1	-3.3	5.2	0.3	-0.3
ϕ	0.0	0.0	0.0	0.0	0.0	0.0

Figure captions

Fig. 1. a) Probability of maturation in relation to size ($L_{p50} = 41.52$, $p_u = 0.75$, $p_l = 0.25$, and $\nu = 0.2$). **b)** Examples of fish growth trajectories when annual reproductive investment $g = 0.4709$ (the default value, filled circles) and $g = 0.6$ (open circles) in unexploited (continuous lines) and exploited populations (dotted lines). **c)** Default trade-off relationship between growth capacity (h_{\max}) and annual survival probability ($1 - \tau h_{\max}$). **d)** Vulnerability to angling in relation to fish size. In addition to the default vulnerability curve (continuous line), an alternative trophy vulnerability curve used in robustness analysis is shown (dashed line).

Fig. 2. a) Standardized selection differentials (S_{std}) on annual reproductive investment (g), growth capacity (h_{\max}), and size at maturation (L_{p50}) in relation to the instantaneous fishing mortality (F). **b)** Yield and exploitation rate (among fish of age 1 year or older) in relation to the instantaneous fishing mortality (F).

Fig. 3. Influence of different harvest regulation on standardized selection differentials (S_{std}) on annual reproductive investment (g , top), growth capacity (h_{\max} , middle), and size at maturation (L_{p50} , bottom). In the right, small plots show the baseline case with no harvest regulation. In the left three plots (a-c), minimum-length limits are changed between 45 and 100 cm. In the central three plots (d-f), maximum-length limits are changed between 100 and 50 cm in combination with a minimum-length limit of 45 cm (i.e., harvestable-slot length limits). In the right three plots (g-i), maximum-length limits are changed between 100 and 50 cm. In every plot, regulations are getting tighter from left to right. Three different degrees of instantaneous fishing

morality (F) are used: 0.33 (dotted lines), 0.67 (dashed lines) and 1.0 (continuous lines).

Fig. 4. Influence of different harvest regulation on standardized selection differentials (S_{std}) on annual reproductive investment (g , top), growth capacity (h_{max} , middle), and size at maturation (L_{p50} , bottom). Selection differentials are shown when the population is exploited towards different levels of SPR (spawning potential ratio), 0.50 (dotted lines), 0.35 (dashed lines), or 0.2 (continuous lines). The SPR index indicates the degree of reduction of the exploited spawner biomass relative to the unexploited case, and a value ≤ 0.35 is supposed to indicate recruitment overfishing (Mace 1994). In the right small plots show the baseline case with no harvest regulation. In the left three plots (a-c), minimum-length limits are changed between 45 and 100 cm. In the central three plots (d-f), maximum-length limits are changed between 100 and 50 cm in combination with a minimum-length limit of 45 cm (i.e., harvest-able-slot length limits). In the right three plots (g-i), maximum-length limits are changed between 100 and 50 cm. In every plot, regulations are getting tighter from left to right.

Fig. 5. Changes of the population means of the life-history traits (top), fish length at the age of 4 years (middle), and yield (harvest biomass) (bottom) during 100 years of consistent exploitation with particular harvest regulations. Instantaneous mortality is fixed to $F = 0.67$. In (a), the default selectivity is assumed. In (b), “trophy” or large-size targeting selectivity is assumed (see Fig. 1d).

Fig. 6. Influence of different harvest regulation on fish length at the age of 4 years (top), yield (upper middle), population biomass (lower middle), and population pristine biomass (bottom). The values after 100 years of the evolution (continuous line) and

at the evolutionary endpoints (dashed line) are shown. In the right, small plots show the baseline case with no harvest regulation. In the left four plots (a-d), minimum-length limits are changed between 45 and 100 cm. In the central four plots (e-h), maximum-length limits are changed between 100 and 50 cm in combination with a minimum-length limit of 45 cm (i.e., harvestable-slot length limits). In the right four plots (i-l), maximum-length limits are changed between 100 and 50 cm. Instantaneous mortality is fixed to $F = 0.67$.

Fig. 7. Long-term changes of the population means of the life-history traits (top) and fish length at the age of 4 years (bottom) during 1500 years of consistent exploitation. A minimum-length limit of 45 cm is applied, and instantaneous mortality is fixed to $F = 0.67$.

Fig. 8. Changes of the population means of the life-history traits after 100 years of consistent exploitation with no harvest regulation. Heritability and phenotypic variability are systematically varied. Instantaneous mortality is fixed to $F = 0.67$.

Fig.1

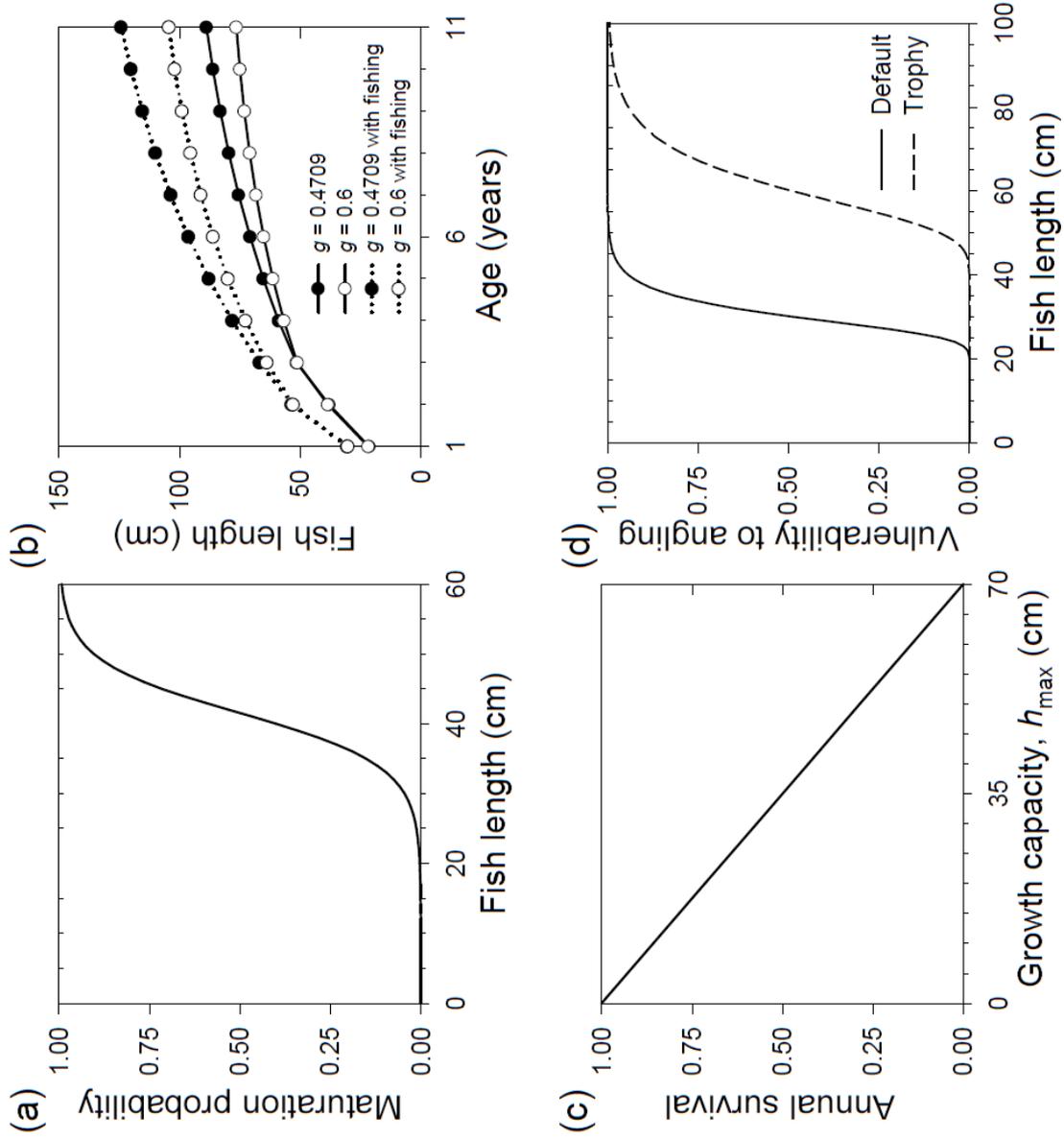


Fig.2

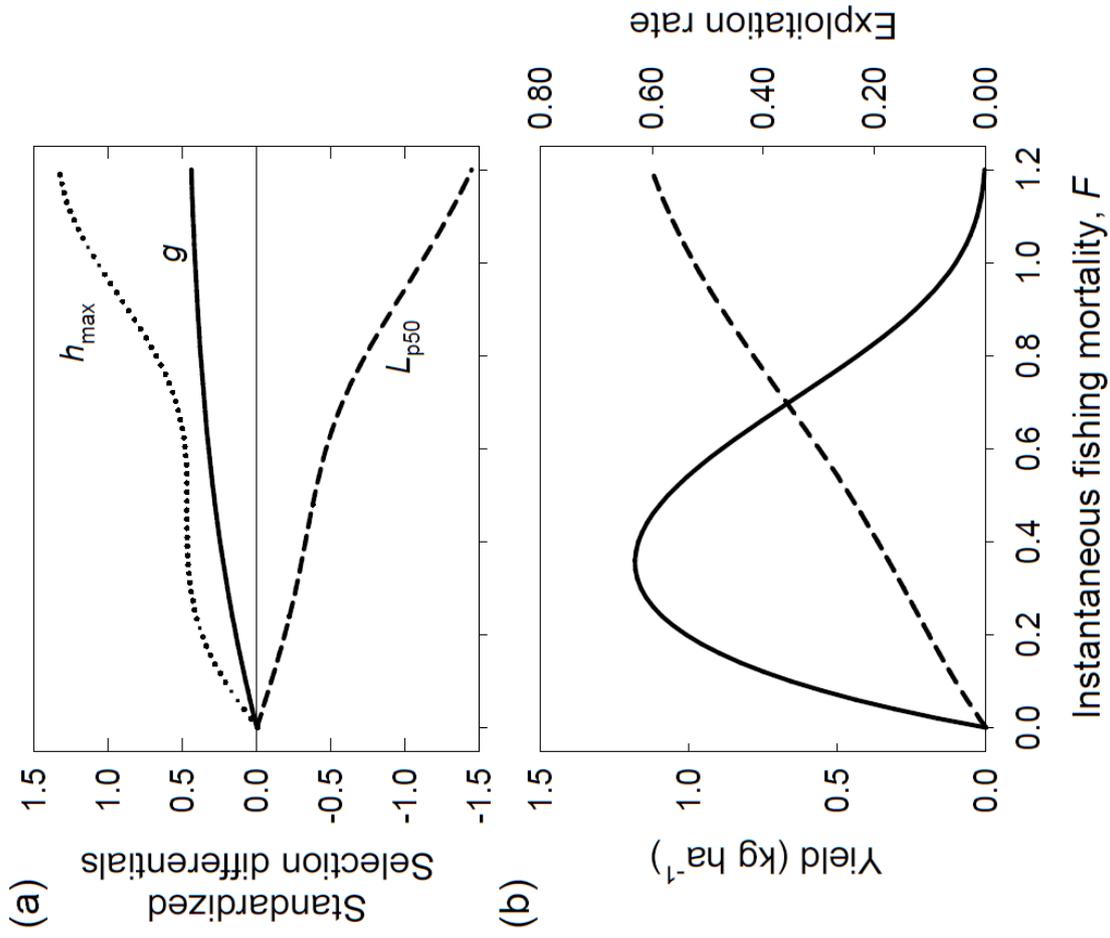


Fig. 3

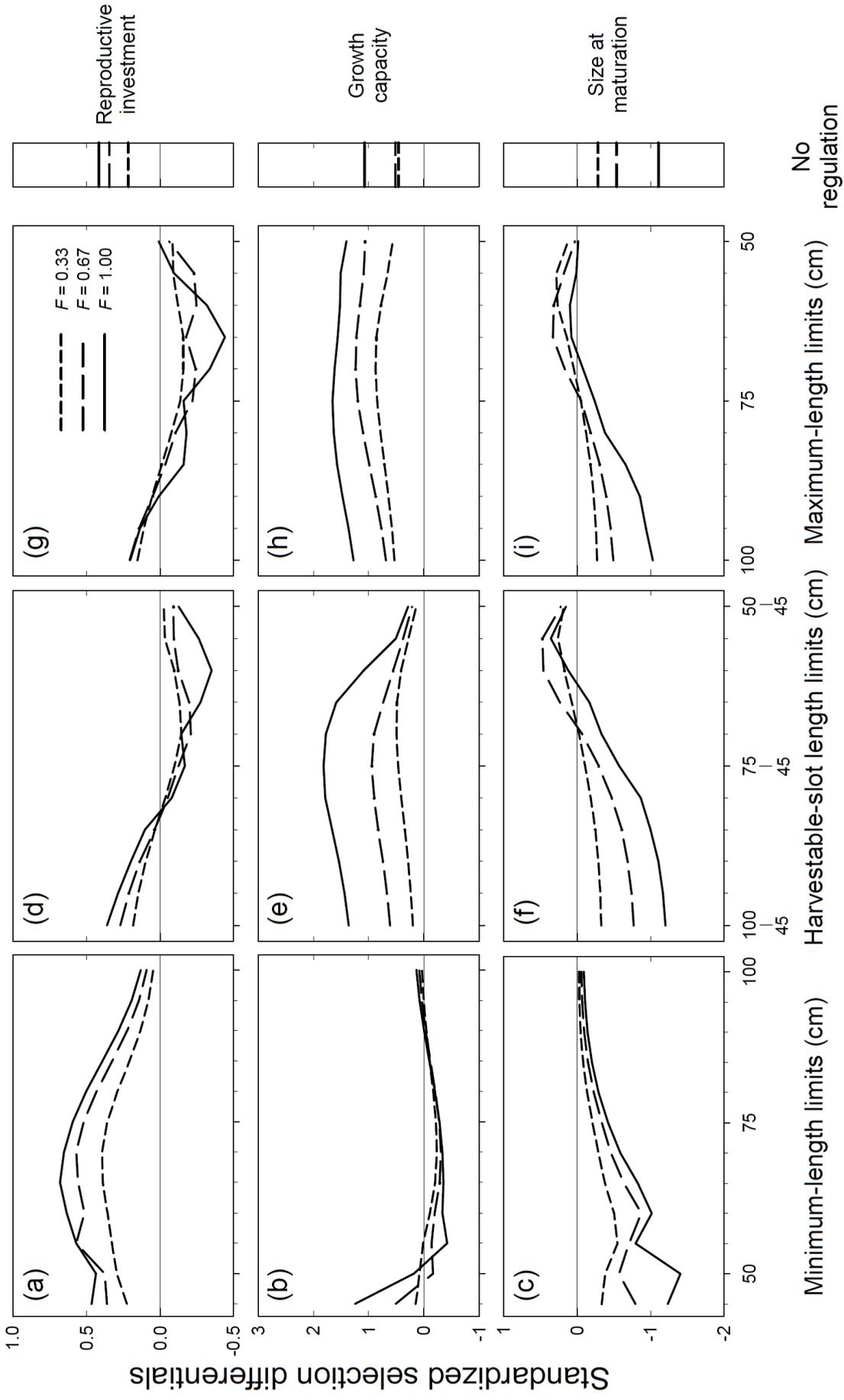


Fig.4

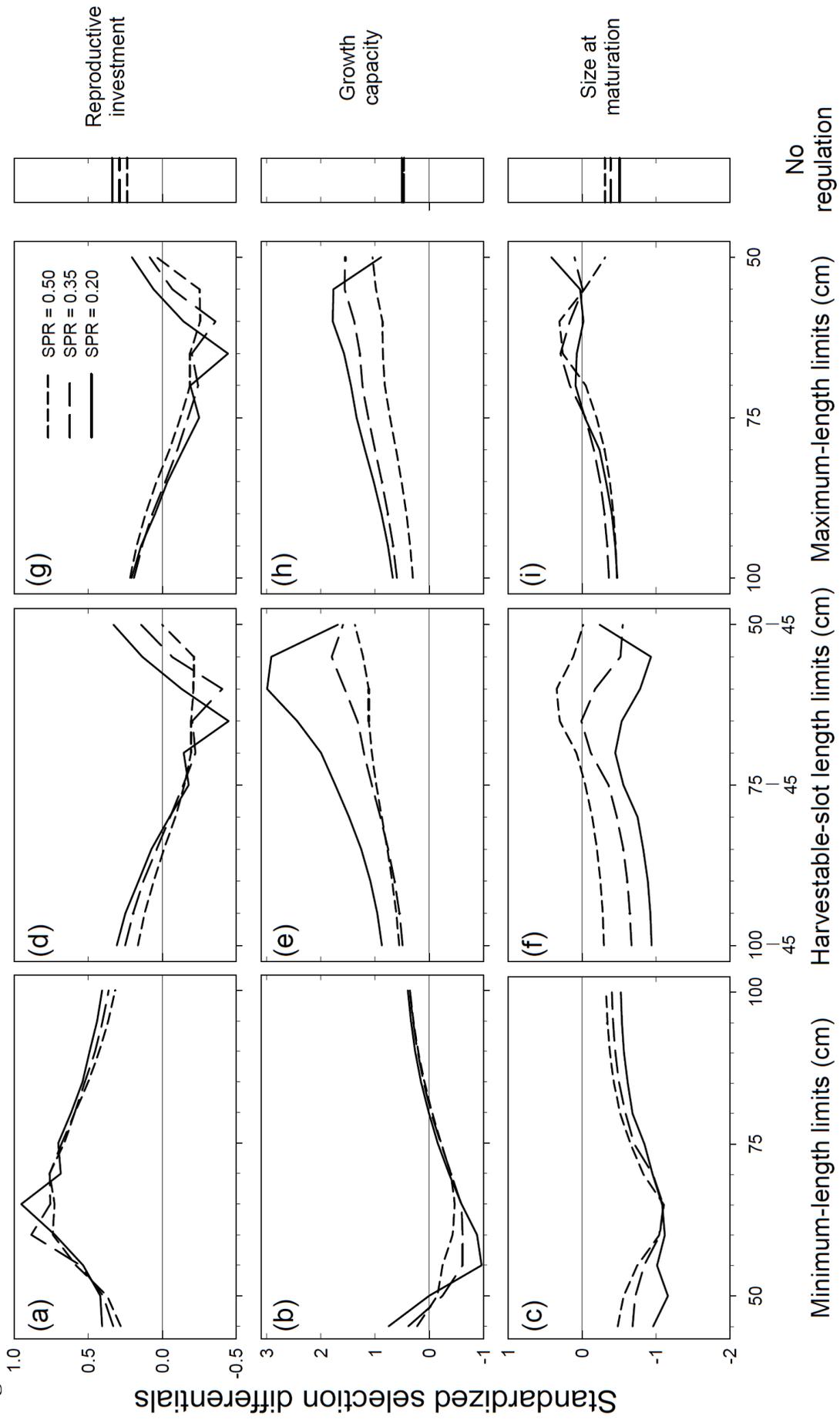


Fig.5

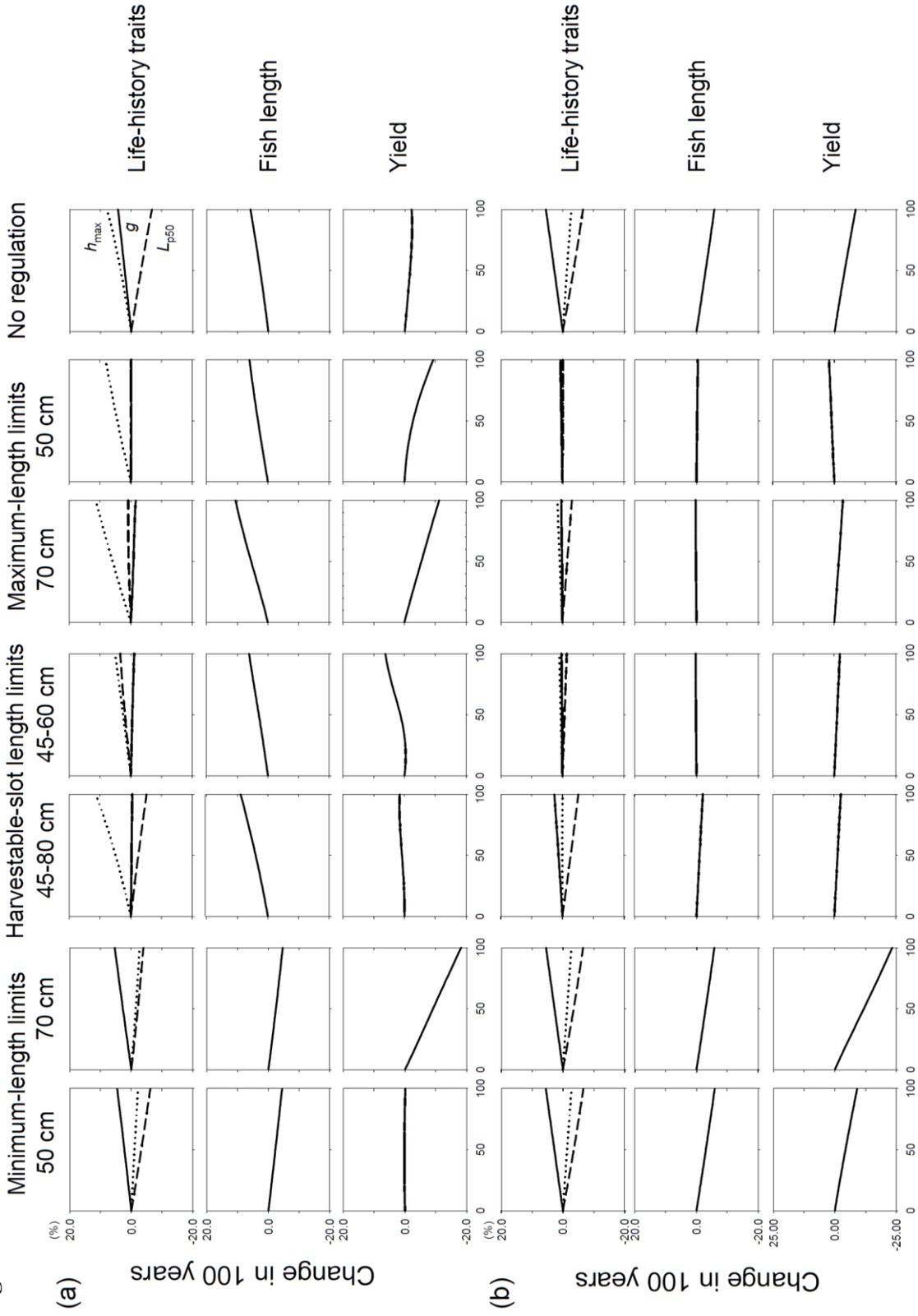
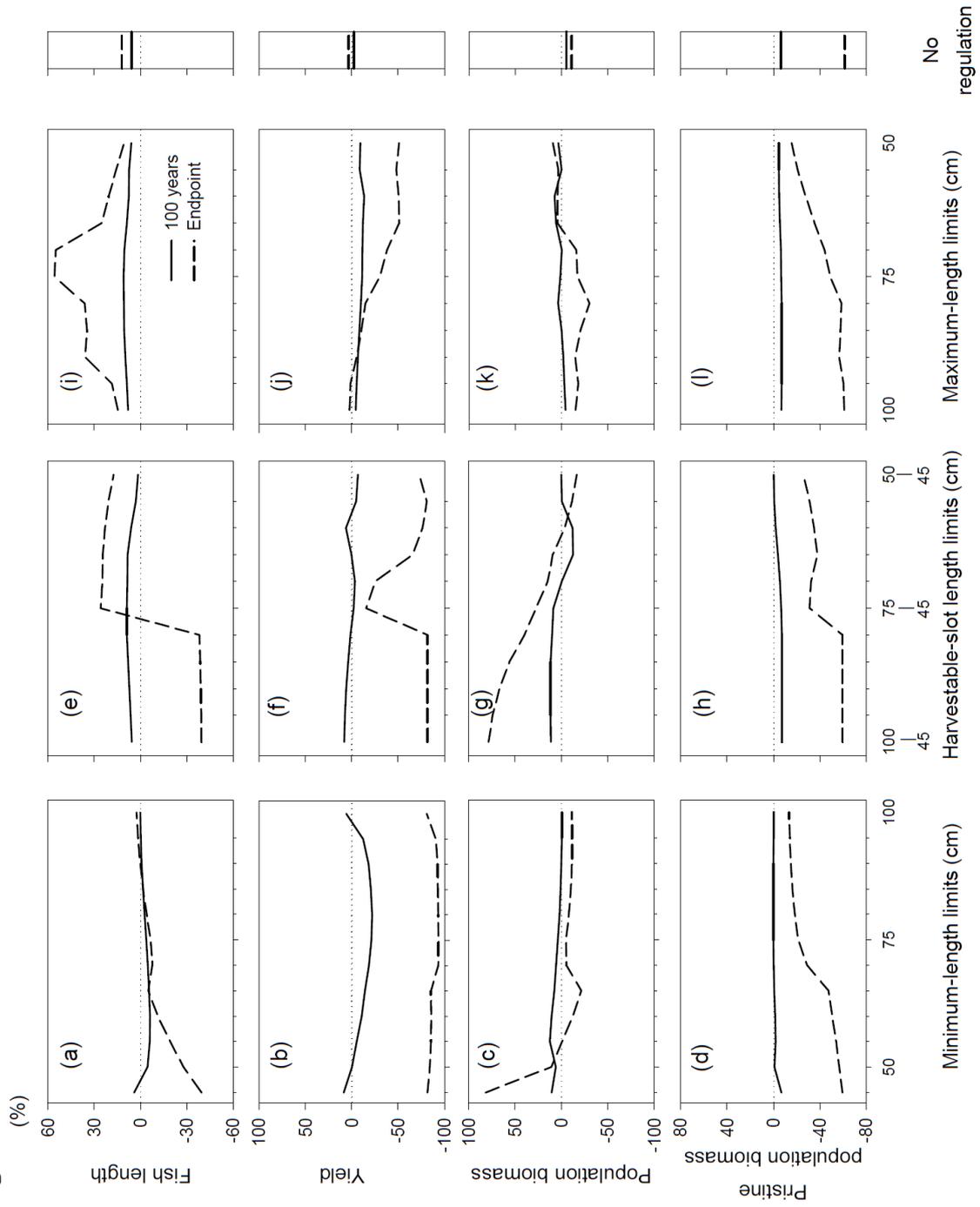


Fig.6



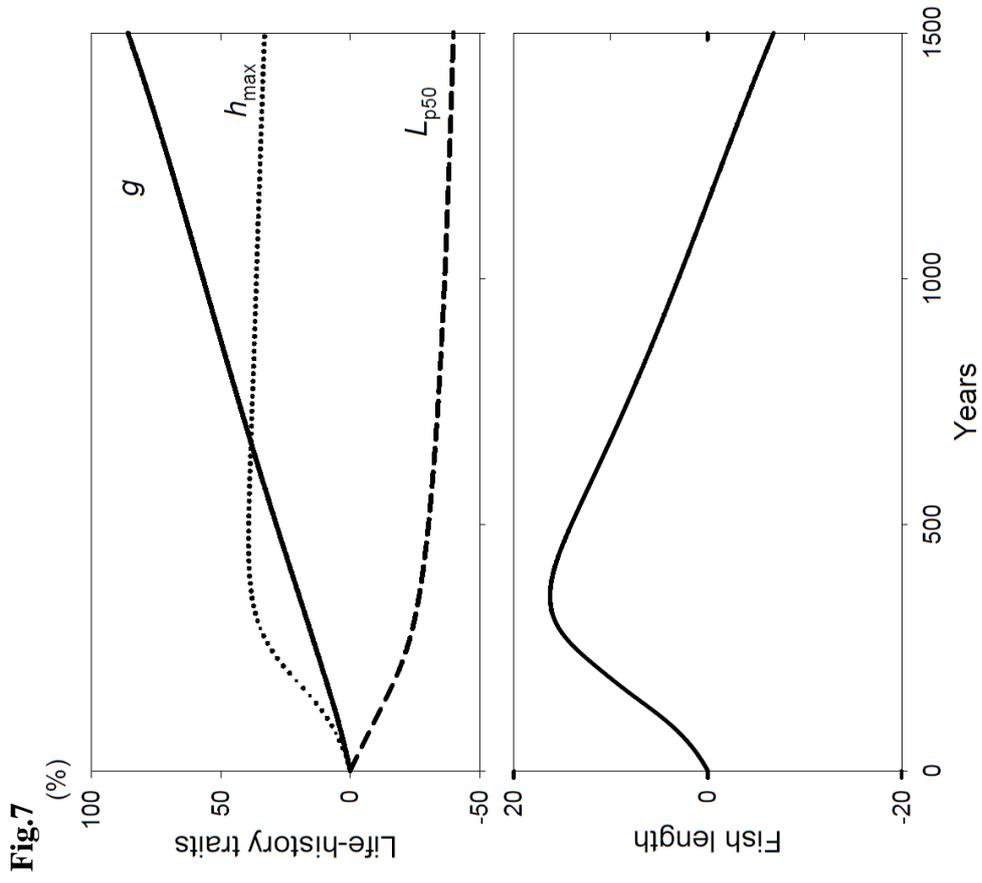


Fig.8

