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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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Abstract Despite mounting recognition of the importance of fishing-induced evolution, methods for quantifying selection pressures on multiple adaptive traits affected by size-selective harvesting are still scarce. We study selection differentials on three life-history traits—reproductive investment, size at maturation, and growth capacity—under size-selective exploitation of northern pike (*Esox lucius* L.) with recreational-fishing gear. An age-structured population model is presented that accounts for the eco-evolutionary feedback arising from density-dependent and frequency-dependent selection. By introducing minimum-length limits, maximum-length limits, and combinations of such limits (resulting in harvestable-slot length limits) into the model, we examine the potential of simple management tools for mitigating selection pressures induced by recreational fishing. With regard to annual reproductive investment, we find that size-selective fishing mortality exerts relatively small positive selection differentials. By contrast, selection differentials on size at maturation are large and consistently negative. Selection differentials on growth capacity are often large and positive, but become negative when a certain range of minimum-length limits are applied. In general, the strength of selection is reduced by implementing more stringent management policies, but each life-history trait responds differently to the introduction of specific harvest regulations. Based on a simple genetic inheritance model, we examine mid- and long-term evolutionary changes of the three

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life-history traits and their impacts on the size spectrum and yield of pike. Fishing-induced evolution often reduces sizes and yields, but details depend on a variety of factors such as the specific regulation in place. We find no regulation that is successful in reducing to zero all selection pressures on life-history traits induced by recreational fishing. Accordingly, we must expect that inducing some degree of evolution through recreational fishing is inevitable.

Introduction

Recently, questions regarding fishing-induced evolution have been attracting substantial attention in the literature (for reviews, see Dieckmann and Heino 2007; Hutchings and Fraser 2007; Jørgensen et al. 2007; Kuparinen and Merilä 2007; Heino and Dieckmann 2008; Andersen and Brander 2009; Dunlop et al. 2009a). As fisheries may impose remarkably high, and often size-selective, mortalities on fish populations, they have the potential to cause evolutionary changes in the life history, morphology, physiology, and behaviour of fish (Uusi-Heikkilä et al. 2008). Empirical evidence suggesting strong selection pressures and rapid evolutionary changes in life-history traits due to fishing is accumulating (e.g., Jørgensen et al. 2007; Darimont et al. 2009; Dieckmann et al. 2009; Dunlop et al. 2009a; Sharpe and Hendry 2009). Key future research questions are to quantify the strength of selection caused by specific fisheries on specific traits, the speed of the corresponding evolutionary changes, and the repercussions of these changes for fish populations and the ecological services they provide to society (Jørgensen et al. 2007; Dunlop et al. 2009a).

If current fishing practices cause substantial selection pressures on fish stocks, fisheries managers may want to identify effective ways to mitigate the strength of these pressures (Arlinghaus et al. 2009; Okamoto et al. 2009). In theoretical studies, different management policies have been examined by varying fishing selectivity between mature and immature fish (e.g., Heino 1998; Ernande et al. 2004), age classes (e.g., Law and Grey 1989; Grey 1993), size classes (e.g., Dunlop et al. 2009b), or by assuming representative shapes of size-selective exploitation (e.g., Jørgensen et al. 2009), in addition to changing harvest rates (e.g., Thériault et al. 2008; Enberg et al. 2009) and introducing marine reserves (e.g., Baskett et al. 2005; Dunlop et al. 2009c). However, more systematic investigations are required on a set of other management policies that have traditionally been used in, or are easily applicable to, fisheries. For example, some authors have suggested that saving large fish by applying maximum-length limits will mitigate fishing-induced evolution (Conover and Munch 2002; Law 2007), but so far only a few studies (Baskett et al. 2005; Williams and Shertzer 2005) have explored the benefits of applying maximum-length limits relative to other management tools.

Another important issue is to evaluate the influences of fishing-induced evolution of life-history traits on fisheries metrics. For example, large changes in life-history traits could cause small changes in yield, because of the confounding effects of density dependence, phenotypic plasticity, or other ecological processes. By contrast, even small life-history changes may have a critical impacts (Kinnison et al. 2009), for example, on stock recovery or stock stability (Enberg et al. 2009). Because of these uncertainties,

the importance of fishing-induced evolution for long-term population dynamics and fisheries yields remains controversial (Andersen and Brander 2009; Kinnison et al. 2009).

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

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

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

Materials and methods

We use an age-structured population model parameterized for northern pike (hereafter simply called pike) by integrating information available from various literature sources (Table 1). We extend the model by Arlinghaus et al. (2009) to the simultaneous

consideration of three important aspects of life history, i.e., reproduction, growth, and maturation. To promote generality and reduce the number of parameters, we remove some of the density-dependent processes considered by Arlinghaus et al. (2009) that were found to exert only small effects on estimates of the selection strength on reproductive investment caused by recreational fishing. For a specific level of fishing mortality, we calculate selection differentials on all three life-history traits, assuming that the population is at demographic equilibrium. Furthermore, we go beyond the original type of analysis conducted by Arlinghaus et al. (2009) by using our estimates of the strength of selection to model the resultant evolutionary dynamics (Hilborn and Minte-Vera 2008). Assuming a fixed heritability ($h^2 = 0.2$), we thus predict evolutionary changes in the three life-history traits caused by 100 years of fishing. In addition, we identify the evolutionary endpoints at which selection pressures on all three traits vanish.

Below, we explain the key ingredients of our model. For more details, please see Arlinghaus et al. (2009).

Population dynamics

Using a Leslie population-projection matrix $\mathbf{K}(\mathbf{X}, \mathbf{E})$ that depends on life-history trait values $\mathbf{X}$ and environmental variables $\mathbf{E}$, together with vectors $\mathbf{N} = (N_1, N_2, \ldots, N_{a_{\max}})^{\mathrm{T}}$ that describe age-specific population densities (Caswell 2001), the population dynamics of a monomorphic fish population are given by

$$\mathbf{N}(t + 1) = \mathbf{K}\mathbf{N}(t), \tag{1a}$$

with

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

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

$$s_a = (1 - m_a)(1 - k_a), \tag{2}$$

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

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	$s_a = (1 - m_a)(1 - k_a)$ (2)	–	–
m_a	Annual natural mortality	$m_a = \tau h_{max}$ (8)	1	$\tau = 0.01429$ cm^{-1}
k_a	Annual angling morality	$k_a = \begin{cases} V_a[1 - \exp(-F)] & \text{if } L_{min} \leq L_a \leq L_{max} \\ V_a[1 - \exp(-\phi F)] & \text{otherwise} \end{cases}$ (9)	2,3	$\phi = 0.094$
f_a	Annual fecundity	$f_a = \psi \frac{G_a}{W_E} \exp(-\rho D)$ (6)	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)	$L_{a+1} = \frac{3}{g_a + 3}(L_a + h)$ (3); $L_1 = h(1 - t_1)$	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)	$G_a = gW_a/\omega$	8	$\omega = 1.73$
$P_{m,a}$	Probability of maturation	$P_{m,a} = \frac{1}{1 + \exp((-L_a - L_{p50})/d)}$ (4a)	–	–
V_a	Vulnerability to angling	$V_a = [1 - \exp(-\eta L_a)]^\theta$ (7)	2	$\eta = 0.25$ cm^{-1}; $\theta = 1300$
y	First year survival	$\log_e(y) = \lambda + \frac{\kappa B^\mu}{B^\mu + B^\mu_{1/2}}$ (7)	9	$\lambda = -7.65$; $\kappa = -31.73$; $\mu = 0.31$; $B_{1/2} = 1.68 \times 10^9$ ha^{-1}

Table 1 continued

Symbol	Description	Equation	Source	Value
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)	$h = \frac{h_{max}}{1+\gamma(D/D_u)^{\delta}}$ (5)	2	$\gamma = 0.1819$ $\delta = 0.5678$ $D_u = 1$ kg ha^{-1}
Parameters				
d		$d = \frac{vL_{p50}}{\mathrm{logit}p_u - \mathrm{logit}p_l}$ (4b)	1	$p_u = 0.75$ $p_l = 0.25$ $v = 0.2$
L_{min}	Minimum-length limit (cm)			Varied
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)

Growth and maturation

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

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

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

where g_a is the annual reproductive investment and $t_1 < 1$ is the age intercept of the pre-maturation growth curve. The annual reproductive investment g_a is represented as $g_a = \omega GSI$, with the gonado-somatic index GSI (the ratio of gonad weight to somatic weight) being weighted by a factor $\omega > 1$ that captures the higher caloric density of gonad tissue relative to somatic tissue. We define maturation as the start of energy allocation to reproduction, with first spawning occurring in the following year. In accordance with the original formulation by Lester et al. (2004), we assume a constant investment $g_a = g$ for all mature individuals, as opposed to $g_a = 0$ for all immature individuals. Consequently, the annual length increment equals h for juveniles ($g_a = 0$) and becomes smaller than h after maturation.

Following Dunlop et al. (2009a), the probability of becoming mature at age a is described as a function of the length L_a at age a,

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

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

where L_{p50} is the length at 50% maturation probability at age a and d determines the steepness of the change in maturation probability around L_{p50}. The probabilities p_u and p_1 define the upper and lower bounds of the probabilistic maturation envelope around L_{p50} (for example, 75 and 25%, respectively), and v determines the width of this envelope in units of L_{p50} (Fig. 1a).

Density dependence

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

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

where h_{max}, called growth capacity, is the maximum juvenile growth increment realized for $D = 0$, and D_u is a unit-standardizing constant.
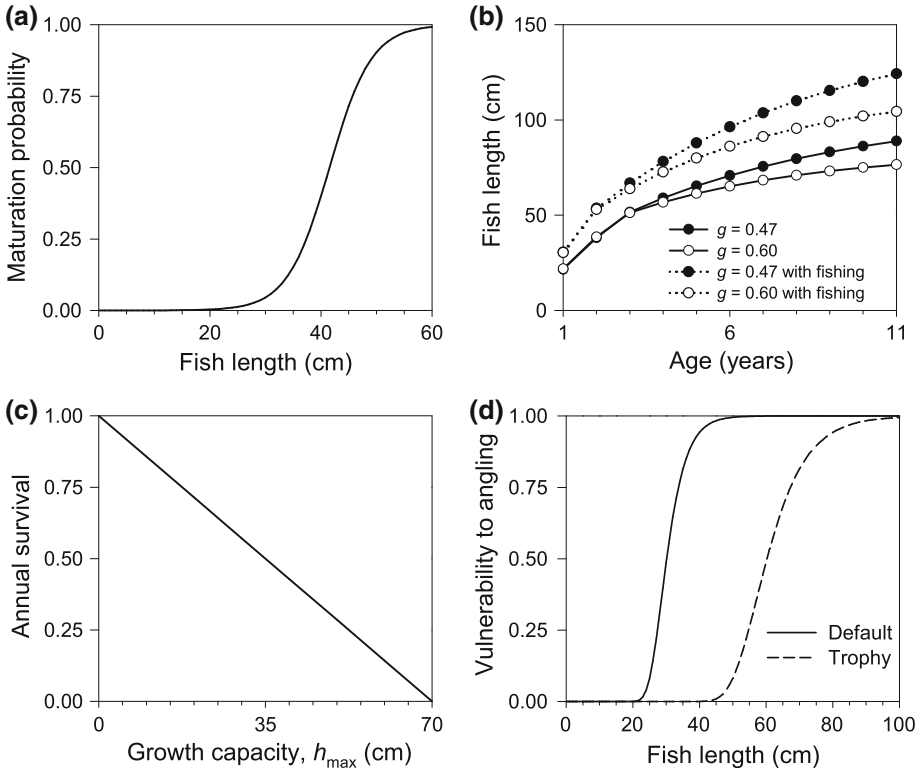
Fig. 1 **a** Probability of maturation in relation to size ($L_{p50} = 41.52$, $p_u = 0.75$, $p_1 = 0.25$, and $v = 0.2$).
b Examples of fish growth trajectories when annual reproductive investment $g = 0.47$ (the default value, *filled circles*) and $g = 0.6$ (*open circles*) in unexploited (*continuous 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*)

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

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

where ψ is the hatching probability, W_E is the egg weight, and G_a is the gonad weight of individuals at age a ($GSI = G_a/W_a$). Parameters determining density-dependent relationships above are determined based on studies on pike in Lake Windermere, UK (Craig and Kipling 1983; Kipling 1983a, b; see Table 1 and Arlinghaus et al. 2009 for details).

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

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

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

Trade-offs and natural mortality

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

$$m_a = \begin{cases} \tau h_{\max} & \text{if } h_{\max} \leq 1/\tau, \\ 1 & \text{if } h_{\max} 1/\tau, \end{cases} \tag{8}$$

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

Fishing mortality

We consider three types of harvest regulations, which are widely used in recreational fisheries: minimum-length limits (MinL-Ls), maximum-length limits (MaxL-Ls), and a combination of these (harvestable-slot length limits, HSL-Ls). The annual fishing mortality k_a represents the proportion of fish removed from the population by recreational fishing, and is calculated as

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

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

Selection differentials

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

$$S = \frac{\int X\lambda(X)p(X)\mathrm{dx}}{\int \lambda(X)p(X)\mathrm{dX}} - \frac{\int Xp(X)\mathrm{dX}}{\int p(X)\mathrm{dX}}, \tag{10}$$

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

Since the selection differential is not dimensionless, it must be standardized for comparing the selection strengths among traits or populations. In the present study, the mean-and-variance-standardized selection differential (Arlinghaus et al. 2009), which has been referred to in the literature as the mean-standardized selection gradient (Hereford et al. 2004), is calculated as

$$S_{\mathrm{std}} = \bar{X}\frac{S}{\sigma_X^2}, \tag{11}$$

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

Outline of analysis

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

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

   - We focused on the type and strength of selection that a pristine pike population experiences at the commencement of harvesting. The default set of population means of the three life-history traits was determined assuming that the present

population is at evolutionary equilibrium in the absence of harvesting. Annual selection differentials S for the three traits were then calculated for the default resident population.

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

- Using the annual selection differential S and heritability h^2 for each trait, its selection response was obtained as $R = h^2 S$ (Falconer and Mackay 1996). The trait's population mean for the next year was then obtained by adding the selection response to the current population mean.
- This procedure was repeated for 100 years. The rate of evolution, in the unit Darwin, 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 means at the beginning (t_1) and end (t_2) of the considered period and the duration $t_2 - t_1$ was measured in millions of years.
- Possible evolutionary endpoints, where the selection differentials S vanish for all three traits, were identified by changing values of the three traits systematically. In general, the procedure above was extended until the population reaches equilibrium. Even when an evolutionary endpoint was identified, the procedure was repeated for several different starting values because there may exist alternative equilibrium states.

Results

Evolutionary equilibria in the absence of fishing

To determine the initial conditions for studying fishing-induced evolution, we consider a fish population that is not yet exposed to fishing pressures. Specifically, we assume that this population has evolved to an evolutionary equilibrium, which implies that the selection pressures on all three life-history traits vanish. We found two combinations of population means for the three life-history traits that yield zero selection differentials (Table 2), representing alternative possible evolutionary endpoints (EP). The first trait combination (EP-1) is characterised by early maturation (at the age of 1 year), while the second trait combination (EP-2) is characterised by later maturation (at the age of 2 or 3 years).

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*)

	g	h_{max}(cm)	L_{p50}(cm)	At equilibrium		
				Fish density (ha^{-1})	Biomass density (kg ha^{-1})	Age at first 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%)

The default parameter values (Table 1) are used. The densities and age at first spawning are also shown. The densities represent fish at age 1 year and older

* 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%

Accordingly, spawning occurs at the age of 2 years in the EP-1 population and at the ages of 3 and 4 years in the EP-2 population. Although selection differentials are zero in the EP-1 population with the default degree of phenotypic variation, individuals with the EP-2 population means can invade into the EP-1 population, because their fitness is higher than that of the residents. By contrast, individuals with the EP-1 population means cannot invade into the EP-2 population, because their fitness is lower than that of the residents. In other words, only the EP-2 population is evolutionarily stable. Therefore, we focus on EP-2 as a baseline condition for investigating the consequences of fishing. The age and size at maturation in the EP-2 population agree well with empirical values reported for pike populations (Raat 1988).

Fishing-induced evolution in the absence of harvest regulations

We started our investigation by examining the situation without harvest regulation. As expected, the magnitude of selection differentials for the three traits increases with increasing recreational-fishing mortality (Fig. 2a). Selection differentials for reproductive investment g and growth capacity h_{max} are both positive, so that the traits experience selection pressures towards increasing reproductive investment and growth capacity. The standardized strength of selection on growth is larger than that on reproductive investment, especially when the angling intensity is high. The standardized selection differential on the
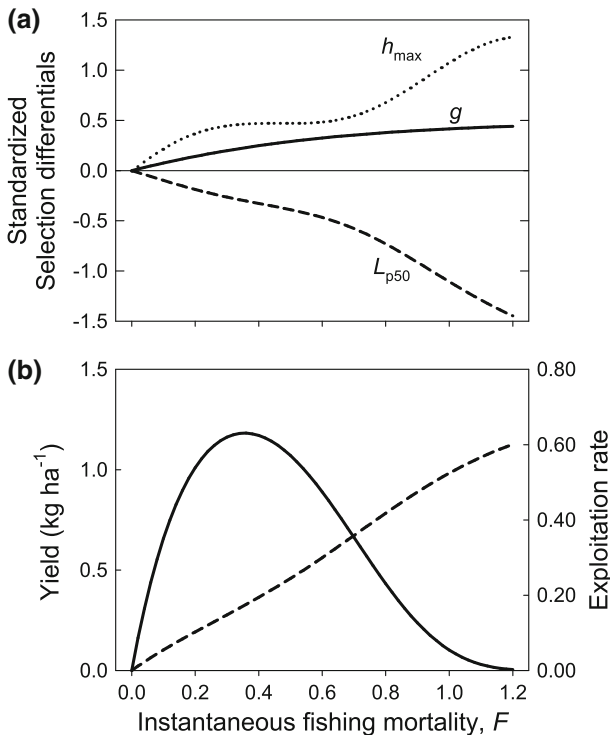

Fig. 2 a Standardized selection differentials (S_{std}) on annual reproductive investment (g), growth capacity (h_{max}), and size at maturation (L_{p50}) in relation to the instantaneous fishing mortality (F). b Yield and exploitation rate (among fish of age 1 year or older) in relation to the instantaneous fishing mortality (F)
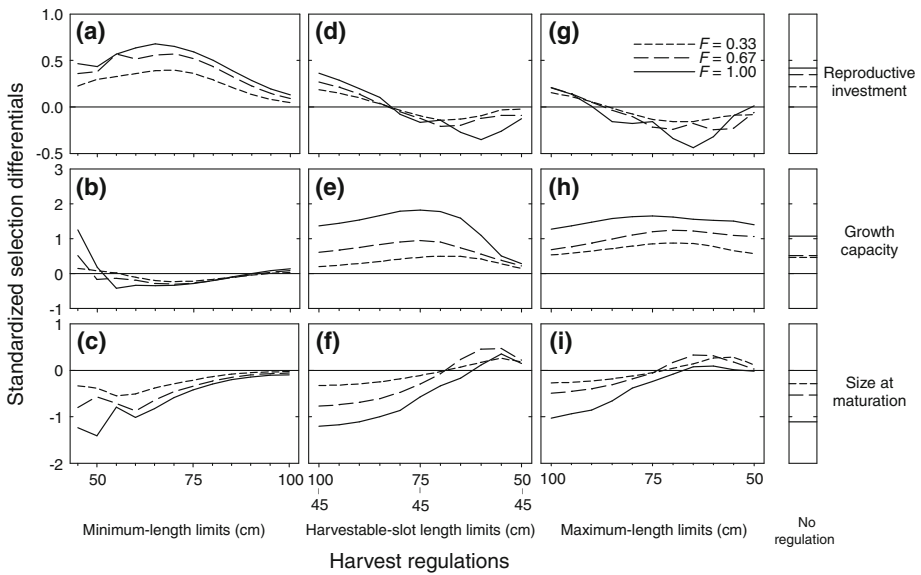
Fig. 3 Influence of different harvest regulation on standardized selection differentials (S_{std}) on annual reproductive investment (g, *top*), growth capacity (h_{max}, *middle*), and size at maturation (L_{p50}, *bottom*). In the right, *small plots* show the baseline case with no harvest regulation. 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*)

size at maturation L_{p50} is as large as that on h_{max}, but the direction is opposite, so that this trait experiences selection pressures towards decreasing size at maturation. The fishing yield (harvested biomass) from the population is maximized at an instantaneous fishing mortality of $F \approx 0.4$ (Fig. 2b), and selection differentials are relatively small when the population is not overexploited (Fig. 2a), i.e., when fishing mortality remains below the fishing mortality at maximum sustainable yield.

Effects of harvest regulations on selection strengths

Next, we systematically investigated the effects of harvest regulations on selection differentials. In general, increasing minimum-length limits (MinL-Ls) mitigate the magnitude of selection differentials, but this effect differs greatly between the three evolving traits (Fig. 3a–c). The magnitudes of selection differentials on reproductive investment g exhibit a peak at intermediate MinL-Ls (Fig. 3a). MinL-Ls have a strong impact on selection differentials on growth capacity h_{max} (Fig. 3b): introduction of a MinL-L of 45 cm causes positive selection differentials for this trait, but these change to negative at a MinL-L of about 50 cm, and values approach zero as the MinL-L is increased further. The magnitude of selection differentials on the size L_{p50} at maturation first slightly increases as the MinL-L increases up to 60 cm, and then decreases as the MinL-L is increased further (Fig. 3c). We also investigated the effects of other types of harvest regulations, i.e., harvestable-slot length limits (HSL-L; Fig. 3d–f) and maximum-length limits (MaxL-L; Fig. 3g–i).

The magnitude of selection differentials for g is generally smaller than in the absence of harvest regulations. The curvatures of the relationships between selection differentials for g and the tightness of harvest regulations are almost opposite to the MinL-L case, with the lowest selection differentials resulting for intermediate harvest regulations. The selection differentials for h_{max} are large and positive, and decline relatively suddenly for tight HSL-L harvest regulations. Selection differentials for L_{p50} are usually negative, and their magnitude decreases as regulations become stricter. They become even positive under the strictest HSL-L and MaxL-L harvest regulations.

To understand regulation-specific differences in the mitigation of selection pressures in more detail, we examined selection differentials for exploitation levels that result in identical reductions of spawner biomasses, as quantified by the spawning-potential ratio (Fig. 4). For MinL-L regulations, selection pressures on g are larger, those on h_{max} are generally smaller, and those on L_{p50} are also smaller than without harvest regulations, because smaller sizes have a selective advantage under MinL-L regulations. Opposite trends are found in the selection pressures under HSL-L and MaxL-L regulations, because larger sizes have a selective advantage in these cases. It turned out that the selection strengths under harvest regulations are often larger than those without harvest regulations for the same level of exploitation. This means that the effects of harvest regulations on mitigating selection pressures, as seen in Fig. 3, actually result from the reduction of
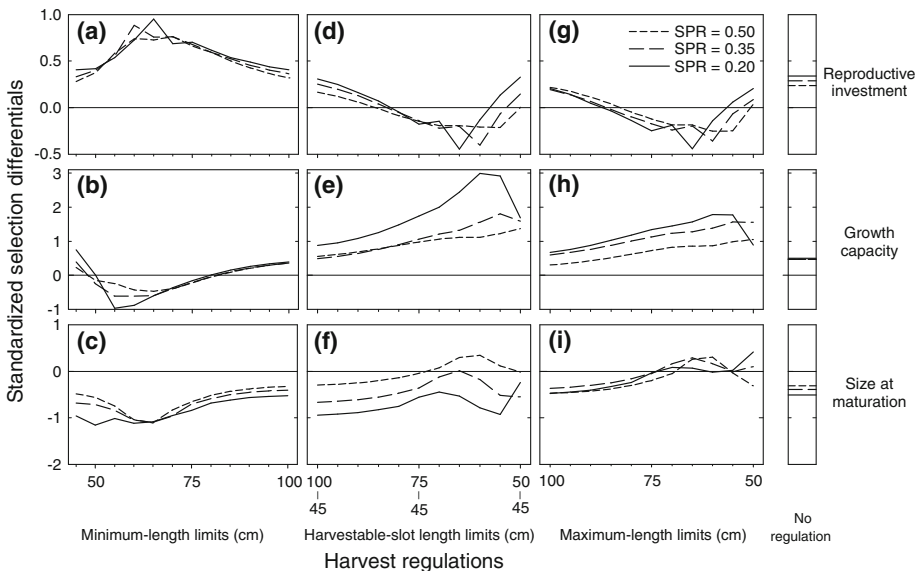

Fig. 4 Influence of different harvest regulation on standardized selection differentials (S_{std}) on annual reproductive investment (g, *top*), growth capacity (h_{max}, *middle*), and size at maturation (L_{p50}, *bottom*). Selection differentials are shown when the population is exploited towards 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., 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

exploitation levels rather than from altered selectivity patterns in terms of vulnerable fish sizes. In fact, for the same exploitation levels, the more pronounced selectivity patterns associated with harvest regulations result in stronger selection pressures than the less selective exploitation patterns that apply in the absence of harvest regulations.

Evolutionary changes of traits and their consequences

We investigated evolutionary changes in the three life-history traits, and resultant changes in population characteristics, when a fixed angling pressure was continuously applied for a longer period (Figs. 5, 6, 7). Specifically, we followed changes in trait values, fish length at the age of 4 years, and yield (harvested biomass) during 100 years of fishing (Fig. 5a). Essentially linear changes in the values of the three life-history traits for 100 years imply that selection pressures remain virtually constant during this period. Accordingly, the selection strengths at the beginning of this period, represented by standardized selection differentials S_{std} and estimated as described in the preceding section, are good predictors of the evolutionary outcomes after 100 years. During this period, reproductive investment g and growth capacity h_{max} increase by 5 and 10%, respectively, while size L_{p50} at maturation decreases by 8% when no harvest regulation is adopted.

The evolutionary trait changes tend to increase (h_{max}) or decrease (g and L_{p50}) fish length at age 4. As a result of these conflicting effects, adult fish length at the age of 4 years increases by 5% after 100 years of harvesting without regulation (from 76.7 to
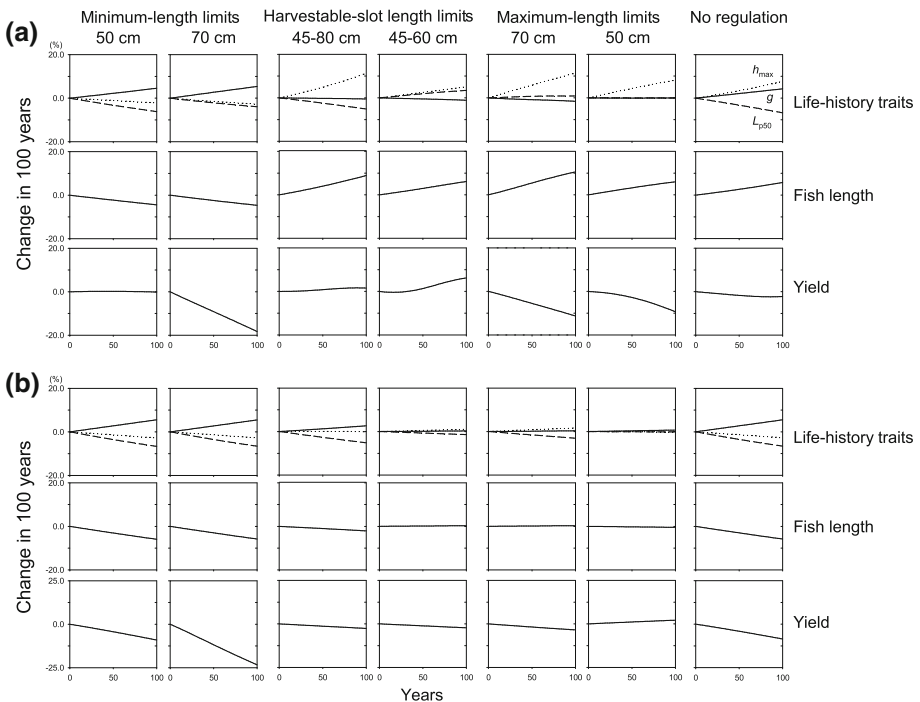

Fig. 5 Changes of the population means of the life-history traits (*top*), fish length at the age of 4 years (*middle*), and yield (harvest biomass) (*bottom*) during 100 years of consistent exploitation with particular harvest regulations. Instantaneous mortality is fixed to $F = 0.67$. In **a**, the default selectivity is assumed. In **b**, "trophy" or large-size targeting selectivity is assumed (see Fig. 1d)
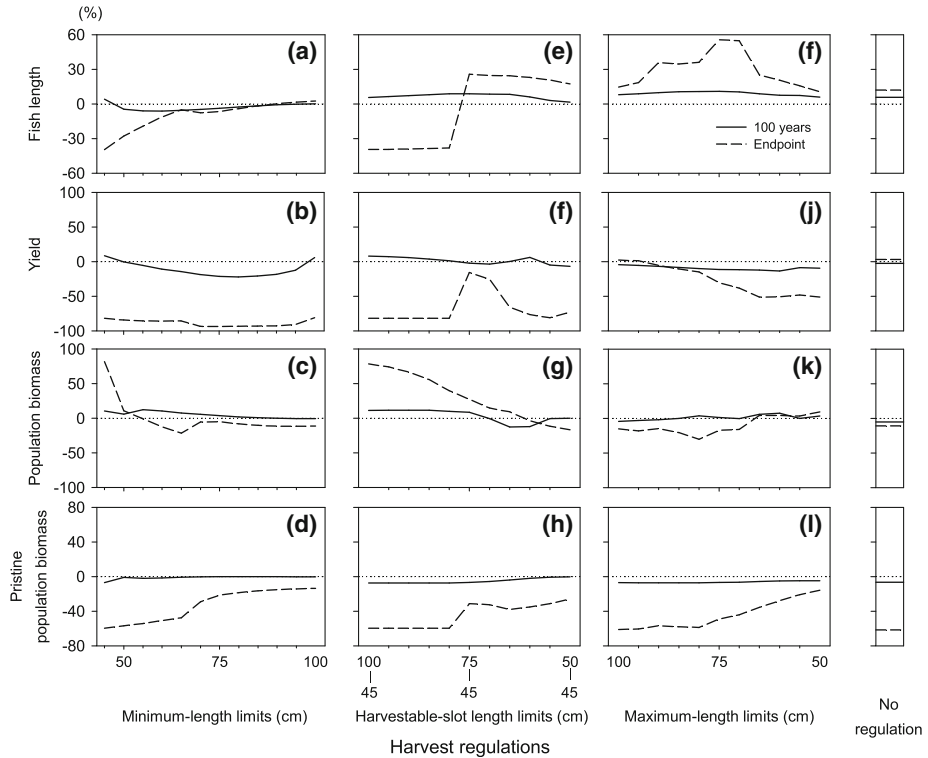
Fig. 6 Influence of different harvest regulation on fish length at the age of 4 years (*top*), yield (*upper middle*), population biomass (*lower middle*), and population pristine biomass (*bottom*). The values after 100 years of the evolution (*continuous line*) and at the evolutionary endpoints (*dashed 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 morality is fixed to $F = 0.67$

81.2 cm). By contrast, the yield shows little change. When harvest regulations are introduced, adult fish length at the age of 4 years becomes either larger (with MaxL-Ls or HSL-Ls) or smaller (with MinL-Ls) than in the unexploited case. In some cases, yield drops by 10–20% as evolutionary changes enable fish to escape the harvestable size ranges. Under HSL-Ls, increases in yield result from increased fish length at the age of 4 years (from about 72 cm to about 78 cm), while the number of harvested individuals decreases by more than 10%.

We also compared the values after 100 years with those at the possible evolutionary endpoints (Fig. 6). At the evolutionary endpoint, fish length at the age of 4 years is ca. 50% smaller when a MinL-L of 45 cm is applied than without fishing-induced evolution (Fig. 6a). Evolution towards small size becomes less pronounced as MinL-Ls is increased. Applying MaxL-Ls causes the opposite effect: in contrast to MinL-Ls, fish length at the evolutionary endpoint is larger than without fishing-induced evolution (Fig. 6i). The largest evolutionary change is observed for an intermediate MaxL-L of 75 cm. When HSL-Ls are introduced by combining a MinL-L of 45 cm with various MaxL-Ls, two distinct
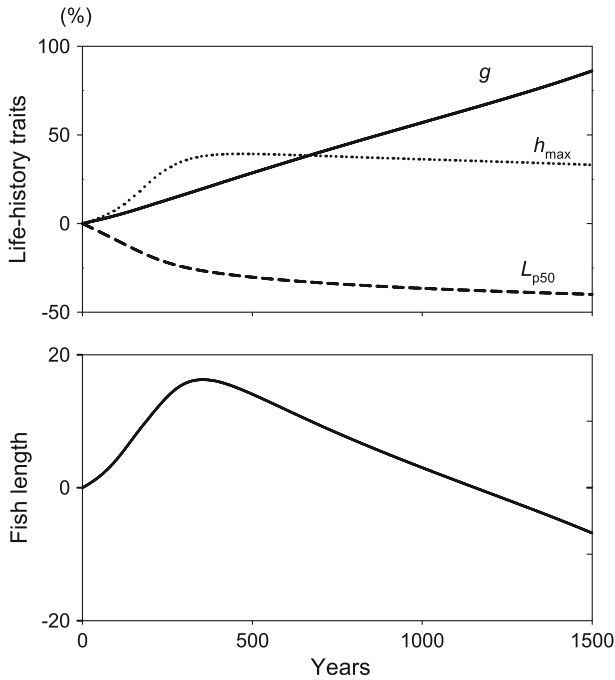
Fig. 7 Long-term changes of the population means of the life-history traits (*top*) and fish length at the age of 4 years (*bottom*) during 1500 years of consistent exploitation. A minimum-length limit of 45 cm is applied, and instantaneous morality is fixed to $F = 0.67$

outcomes occur depending on whether the MaxL-L is large (≥ 80 cm) or small (≤ 75 cm) (Fig. 6e). Fish become considerably smaller in the former case, whereas they become larger in the latter case.

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

In most cases, yield at the evolutionary endpoint is much smaller than prior to fishing-induced evolution (Fig. 6b, f, j). Exceptions appear for a MinL-L of 100 cm and for large MaxL-Ls (≥ 80 cm), i.e., for cases in which the original yield is extremely small. In many cases, also population biomass at the evolutionary endpoint is smaller than prior to fishing-induced evolution (Fig. 6c, g, k). By contrast, if a MinL-L of 45 cm or HSL-Ls are applied, population biomass can be twice as large as prior to fishing-induced evolution. In these cases, the population contains a large number of fish that are smaller than 45 cm. At the evolutionary endpoint, the pristine population biomass, i.e., the equilibrium population biomass that is attained when fishing is ceased, is considerably smaller (by up to 60%) than prior to fishing-induced evolution (Fig. 6d, h, l).
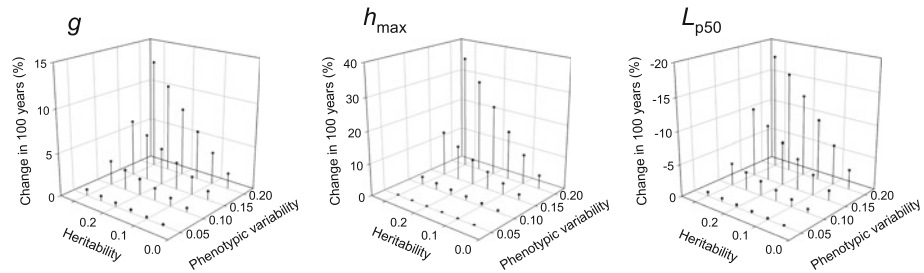
Fig. 8 Changes of the population means of the life-history traits after 100 years of consistent exploitation with no harvest regulation. Heritability and phenotypic variability are systematically varied. Instantaneous morality is fixed to $F = 0.67$

Robustness analyses

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

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

Results of sensitivity analyses for other parameters are summarized in Table 3. In general, predictions about reproductive investment are more robust to changes in parameter values than those about growth capacity or size at maturation. The latter two life-history traits are sensitive to the trade-off between growth and survival (described by the

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 ± 10%

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
v	−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

Change in response variables that are larger than 10% in absolute value (i.e., sensitive or elastic changes) are highlighted in bold. We chose an intermediate angling intensity ($F = 0.67$) with no harvest regulation

parameter τ). An increase in t_1, the age intercept of the pre-maturation growth curve, greatly intensifies selection on growth, via changes in the vulnerability to angling around the age at first spawning. Other parameters that relatively exert strong impacts on model predictions are the exponents in the allometric length-weight regression (β), in the stock-recruitment relationship determining density-dependent larval survival (λ and μ), and in the relationship between fish length and vulnerability to fishing (η).

Discussion

The present study has demonstrated how recreational fishing causes considerable selection pressures on multiple life-history traits under various types of fishing regimes. In the absence of harvest regulations, these selection pressures elevate energy allocations to reproduction, maturation, and growth. Selection strengths on maturation size and growth capacity exceed those on reproductive investment. The present study has also illustrated the complex nature of fishing-induced life-history selection: for example, the direction and magnitude of selection on growth capacity changes drastically when the size-selectivity of harvesting is strengthened by large minimum-length limits (MinL-Ls) or trophy-size-oriented recreational harvesting.

A primary goal of our work here was to systematically investigate the effects of different types of harvest regulations on the strengths of fishing-induced selection on several

life-history traits. In addition to MinL-Ls, we therefore considered maximum-length limits (MaxL-Ls) and harvestable-slot length limits (HSL-Ls), with the latter being designed to protect immature and large fish simultaneously (Arlinghaus et al. 2010).

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

Application of MaxL-Ls has been suggested as an alternative to MinL-Ls to reduce the strength of fishing-induced selection pressures (Conover and Munch 2002). It seems intuitively plausible to assume that MaxL-Ls might counteract the effects of positively size-selective fishing. Corroborating this expectation, we find that selection strengths, in particular, on maturation size, can indeed be reduced through MaxL-Ls. At the same time, however, MaxL-Ls greatly increase the magnitude of positive selection on growth capacity.

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

Our findings on either positive or negative growth-capacity evolution in response to harvesting clearly underscore that one should not trust the often-reported intuition that fishing-induced evolution will necessarily reduce the growth rates of fish in response to positively size-selective fishing (sensu Walters and Martell 2004). Despite some empirical studies (e.g., Ricker 1981; Conover and Munch 2002; Swain et al. 2007; Nusslé et al. 2008), only few theoretical investigations have so far examined growth evolution caused by size-selective fishing (Williams and Shertzer 2005; Hilborn and Minte-Vera 2008). In agreement with our study, recent empirical investigations have reported less-than-straightforward patterns in fishing-induced selection on growth. In particular, using an individual-based eco-genetic model, Dunlop et al. (2009b) predicted positive evolutionary changes in genetic growth capacity for small MinL-Ls, although they found negative changes for other MinL-Ls. Also the present model predicts such changes in the direction of selection pressures on growth capacity: although selection is positive and strong for small MinL-Ls (45 cm), it becomes negative and weak for larger MinL-Ls. It seems clear that the direction of selection on growth capacity depends not only on the size-selectivity of fishing, but also on the life history of the fished species. If the species matures at small

sizes, while fishing is limited to very large fish (as implied by large MinL-Ls), the number of reproductive opportunities increases for fish staying below MinL-L. Thus, slow growth will be favoured by evolution. This is not the case if fishing also targets small fish (as implied by small MinL-Ls or non-selective exploitation). Under such conditions, fast growth may be favoured by evolution, because growing as quickly as possible and having a single successful spawning event might then be advantageous. Given the life history of pike (early maturation at small size) and considering its typical exposure to steep size-selectivity curves (Pierce et al. 1995), positive selection on growth must be expected when pike is managed by small MinL-Ls of 45-50 cm.

MaxL-Ls must also be expected to favour faster-growing fish, because these increase their chances of avoiding harvesting by growing into the protected size range. Therefore, if the baseline harvesting scheme in the absence of harvest regulations causes negative selection on growth, as in the case examined by Williams and Shertzer (2005), MaxL-Ls might counteract the baseline selection, and thus decrease the strength of selection on growth. However, if the baseline selection on growth is positive, as in the present study, MaxL-Ls further increase the strength of selection on growth.

Surely the argument above is sensitive to assumptions of size-dependent mortality and fecundity (Thygesen et al. 2005). Except for the first year of life, our model considered a constant, size-independent natural mortality, which was assumed to be a function of growth rate to represent the theoretically sound idea of a growth-survival trade-offs (Stamps 2007). However, positively size-dependent survival resulting from higher chances of escaping cannibalism as body size increases might also be found in adult pike (Haugen et al. 2007). Furthermore, our model assumed a constant gonado-somatic index after maturation, even though it is known that it increases with the size of mature female pike (Edeline et al. 2007). Structural changes to our model will therefore be needed to examine the implications of size dependence in natural mortality and gonado-somatic index for estimates of fishing-induced evolution.

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

The three life-history traits examined here exhibited considerable evolutionary changes. For example, we found an increase in growth capacity of up to 13% within 100 years of fishing with an instantaneous mortality of 0.67 year^{-1}. During those 100 years, evolutionary changes were almost linear in time, which implies that the direction and strength of directional selection were almost constant. The initial selection strength represented by S_{std} thus appears to be a good predictor of the amount of evolutionary changes accruing during 100 years. Based on the maximum value of S_{std} on growth, which occurs for very high angling intensities, growth capacity may evolutionarily increase by up to 40% during 100 years of fishing. A 13–40% increase during 100 years corresponds to an evolutionary

rate of 1.2–3.4 × 10³ Darwin. This rate is modest compared to values reported for fishing-induced evolution in commercial fisheries (Jørgensen et al. 2007; Sharpe and Hendry 2009). Andersen and Brander (2009) concluded in a modelling study that the rate of fishing-induced evolution is slow, but their estimates (≈ 0.1–0.6% change in phenotypes per year, which is equivalent to 1.0–6.0 × 10³ Darwin) are well in line with our estimated evolutionary rates here. Therefore, discussions of whether fishing-induced evolution is "fast" or "slow" are not overly meaningful without establishing a natural baseline against which to judge evolutionary rates. Moreover, as our robustness analysis has shown, the rate of evolution is influenced by the degree of phenotypic variance and heritability. Unfortunately, good estimates of these parameters are exceedingly rare for wild fish stocks. Moreover, genetic and phenotypic variances, and hence the corresponding heritabilities, might readily change during the course of evolution (Edeline et al. 2009), with obvious consequences for the speed of fishing-induced evolution.

How do our estimated rates of life-history evolution in response to recreational fishing compare with field observations for pike? Qualitatively, our prediction that exploitation of pike results in increased reproductive investment well agrees with field observations of pike populations exposed to differential angling mortality (Diana 1983). Diana (1983) also observed pike populations to mature earlier when exposed to high adult mortality through angling, which seems to agree with our findings because age and size are usually correlated, but the empirical study did not control for a potential compensatory response, which provides an alternative explanation of earlier maturation through relaxed competition for food.

The only empirical estimates of fishing-induced evolution in the growth rate of pike stems from long-term demographic analyses of the pike population in Lake Windermere (Carlson et al. 2007; Edeline et al. 2007, 2009). This population experienced relatively mild experimental exploitation with gill nets, with a maximum annual exploitation fraction of 8% (Edeline et al. 2007). One must be careful, however, when trying to directly compare the empirical findings from Windermere with our model predictions. This is for two reasons. First, exploitation levels, types of fishing gears, and the implied size-selectivity in Windermere strongly differed from the simpler assumptions made in our recreational-fisheries pike model. Second, interpreting any observed phenotypic changes in adult growth rates (as provided by the Windermere studies) is complicated by the potential joint evolution of growth capacity, maturation schedule, and reproductive investment. Yet, it is noteworthy that natural and fishing-induced selection on body size in Windermere pike appeared to act in opposite directions: small adult pike are disfavoured by natural selection, but favoured by fishing-induced selection (Carlson et al. 2007; Edeline et al. 2009). Consequently, somatic growth of adult pike decreased when the experimental gill-net fishery was intensified, but increased after experimental fishing was relaxed (Edeline et al. 2007, 2009). The evolution of slower growth in Windermere pike agrees with our model predictions for a MinL-L of 60 cm (Windermere pike below 60 cm were not intensively exploited, so the experimental fishery may be viewed as effectively exploiting adult pike according to a MinL-L of 60 cm).

Another important insight from the Windermere studies is that the gill-net fishery resulted in disruptive selection favouring both small- and large-sized pike through a bell-shaped selectivity curve (Carlson et al. 2007; Edeline et al. 2009). This disruptive selectivity appears to have increased the genetic variability for somatic growth of adult pike, thus enabling the rapid evolutionary rebound observed in somatic growth after fishing intensity was relaxed (Edeline et al. 2009). Even though the HSL-Ls in the present study resemble the disruptive selectivity caused by gill nets in Windermere, we cannot

immediately use our model to investigate the rapid evolutionary rebound, because we only considered a constant genetic variance. Including the effects of fishing on genetic variability thus provides a natural and interesting extension of our model.

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

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