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# Quantifying selection differentials caused by recreational fishing: development of modeling framework and application to reproductive investment in pike (*Esox lucius*)

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## Abstract

Methods for quantifying selection pressures on adaptive traits affected by size-selective fishing are still scarce, and none have as yet been developed for recreational fishing. We present an ecologically realistic age-structured model specifically tailored to recreational fishing that allows estimating selection differentials on adaptive life-history traits. The model accounts for multiple ecological feedbacks, which result in density-dependent and frequency-dependent selection. We study selection differentials on annual reproductive investment under size-selective exploitation in a highly demanded freshwater recreational fish species, northern pike (*Esox lucius* L.). We find that recreational angling mortality exerts positive selection differentials on annual reproductive investment, in agreement with predictions from life-history theory. The strength of selection increases with the intensity of harvesting. We also find that selection on reproductive investment can be reduced by implementing simple harvest regulations such as minimum-size limits. The general, yet computationally simple, methods introduced here allow evaluating and comparing selection pressures on adaptive traits in other fish populations and species, and thus have the potential to become a tool for evolutionary impact assessment of harvesting.

## Introduction

The potential for size-selective fishing to cause contemporary evolutionary changes in adaptive traits has attracted considerable interest in recent years (Jørgensen et al. 2007; Kuparinen and Merilä 2007). Fishing-induced selection has been identified as having the capacity to change various life-history traits as well as morphological, behavioral, and physiological traits (reviewed by Policansky 1993; Law 2000; Heino and Godø 2002; Dieckmann and Heino 2007; Hutchings and Fraser 2007; Kuparinen and Merilä 2007; Jørgensen et al. 2007; Uusi-Heikkilä et al. 2008; Hard et al. 2008). These changes can affect stock properties such as yield, average biomass, average value of harvested fish, catchability and stock recovery, and are also troublesome from the perspectives of conservation and management when genetic change, as opposed to merely phenotypic change, is involved (Heino 1998; Law 2000; Conover et al. 2005; Hutchings 2005; Jørgensen et al. 2007; Allendorf et al. 2008; Enberg et al. 2009; Philipp et al. 2009; Wang and Höök 2009).

Most studies estimating fishing-induced selection differentials acting on adaptive life-history traits have focused on commercially exploited species (Rowell et al. 1989; Rijnsdorp 1993a; Miller and Kapuscinski 1994; Sinclair et al. 2002; Williams and Shertzer 2005; Andersen et al. 2007; Hutchings and Rowe 2008). This is surprising given the popularity of recreational angling in all industrialized countries (Arlinghaus et al. 2002). Lewin et al. (2006) summarized current knowledge on recreational angling patterns and found that locally high annual exploitation rates of up to 80% and pronounced selectivity for species, size, age, sex, and behavioral traits are common. Therefore, recreational fishing might exert similar directional selection pressures on adaptive traits as previously identified for commercially exploited stocks (e.g., Heino 1998; Swain et al. 2007; Thériault et al. 2008; Darimont et al. 2009; Philipp et al. 2009; Redpath et al. 2009). Yet, little is known as to whether this is actually the case (Cooke and Cowx 2006; Lewin et al. 2006).

To appreciate the potential for recreational angling to induce evolutionary changes, methods are needed for estimating selection differentials acting on adaptive traits (Hutchings and Rowe 2008). Basic approaches developed to date can be broken down into empirical studies and theoretical models. Empirically, estimating selection differentials for adaptive traits depend on the availability of time series of individual phenotypic data, together with detailed knowledge about the ecology of, and the mortality regimes exerted on, the stock under investigation (Rowell et al. 1989; Miller and Kapuscinski 1994; Sinclair et al. 2002; Swain et al. 2007). Although these approaches are promising and have been applied to study fishing-induced selection responses in growth rate (e.g., Swain et al. 2007; Thomas and Eckmann 2007; Nusslé et al. 2009) and reproductive traits (e.g., Olsen et al. 2004; Thomas et al. 2009), they suffer from the possibility of confounding effects originating from joint evolution of correlated traits and from environmental influences such as density dependence in somatic growth and maturation schedules (Heino et al. 2008). The general paucity of long time series data on individual phenotypes for most angling fisheries (Post et al. 2002) limits the practical application of such approaches for recreational fisheries.

Alternatively, life-history models can be used to study selection differentials and responses to fishing. In commonly used evolutionary optimization models (Hutchings 1993a; Rijnsdorp 1993a; for other examples see Stokes et al. 1993), specific trait values are determined that maximize a chosen measure of fitness (usually, lifetime reproductive success or the population-level intrinsic rate of increase; Stearns 1992; Roff 2002). Such optimization models, however, usually do not incorporate density-dependent and frequency-dependent ecological feedback (e.g., Heino et al. 1998; Meszéna et al. 2001; Dieckmann and Ferrière 2004), which are crucial factors determining fisheries-induced selection. More recently, individual-based eco-genetic models (Dunlop et al. 2007, 2009; Thériault et al. 2008; Enberg et al. 2009; Wang and Höök 2009), other types of individual-based models (Kristiansen and Svåsand 1998; Martínez-Garmendia 1998; Williams and Shertzer 2005; Brown et al. 2008), and age-structured models (Hilborn and Minte-Vera 2008) have been used for investigating selection differentials and responses in adaptive traits induced by fishing. However, individual-based models in particular are computationally expensive, which could limit their application by a wider community of users including fisheries managers.

The aims of the present study were threefold: (1) to establish a class of age-structured population models capable of estimating selection differentials on adaptive life-history traits in recreationally exploited fish species, (2) to investigate the potential for standard harvest regulations to counteract recreational fishing-induced selection, and (3) to test the robustness of the proposed models to changes in model parameters and underlying assumptions about population dynamical processes. We were particularly interested in developing a modeling approach using classical age-structured models that can be easily applied by fisheries managers interested in estimating selection pressures on adaptive traits in response to recreational fisheries. In contrast to previous attempts to estimate selection responses to fishing (Rijnsdorp 1993a; Williams and Shertzer 2005; Andersen et al. 2007; Hilborn and Minte-Vera 2008), our modeling framework explicitly incorporates density dependence in growth, mortality, and fecundity to add realism. It also accounts for dynamic angler responses to changes in the density of vulnerable fish in a stock, and thus meets an important prerequisite for appropriate models of recreational fisheries (Radomski and Goeman 1996; Post et al. 2003).

After introducing the general framework, we apply our model to study the adaptation of annual reproductive investment in a hypothetical pike (*Esox lucius* L.) population. This fish species was chosen because pike is of high interest to anglers across the northern hemisphere (Pierce et al. 1995; Arlinghaus and Mehner 2004) and as it is highly vulnerable to angling (Paukert et al. 2001). Annual reproductive investment was chosen as the life-history trait under selection because less attention in the literature has as yet been given to this trait, compared to growth rate, age and size at maturation, or probabilistic maturation reaction norms (Jørgensen et al. 2007). We tested the prediction that angling selects for increased annual reproductive investment at age in size-selectively exploited pike populations. This is expected because individuals investing more of their surplus energy into reproduction at any age will have a selective advantage under conditions of reduced adult survival (Reznick et al. 1990; Hutchings 1993b).

## Materials and methods

### Modeling framework

We developed an age-structured population model for recreational fishing because demographic processes and selection pressures caused by fishing depend on the age and body size of individuals (e.g., Reznick et al. 1990;

Conover et al. 2005). Age-structured population models were chosen for this study because these have been widely accepted as the simplest representation of structured population dynamics in fisheries and are commonly used by fisheries managers (Hilborn and Walters 1992).

Realistic models concerned with fisheries-induced evolution must incorporate the eco-evolutionary feedback that determines how the fitness of a particular trait value is affected by a population's phenotypic composition and population density through frequency-dependent and density-dependent selection, respectively (Heino et al. 1998). For example, a realistic model has to capture the pathways along which the phenotypic composition of a population affects the environmental variables that describe the state of its ecological environment, such as those determining the density dependence of growth, cannibalism, or fishing effort. It is then important to specifically incorporate how a particular ecological state, as characterized by such environmental variables, influences a population's demographic properties and vital rates (such as those describing fecundity, growth, and mortality), and hence the fitness, of different phenotypes (Heino et al. 1998; Dieckmann and Ferrière 2004). To this end, our model for recreational fisheries incorporates multiple dimensions of eco-evolutionary feedback on fitness. For example, fish density influenced growth, fecundity, and natural mortality. In addition, the density of vulnerable fish, as opposed to the density of all fish, affected fishing effort, and catch rates of undersized fish influenced illegal harvest rates. The resulting multi-dimensional eco-evolutionary feedback results in nontrivial frequency-dependent selection that cannot be analyzed by traditional fitness optimization methods (Mylius and Diekmann 1995; Heino et al. 1998).

In the present model, the fish population is allowed to be polymorphic in the considered adaptive trait (here, annual reproductive investment) and is assumed to be at demographic equilibrium. At equilibrium, the density and the age and size composition reflect the density dependence of demographic processes such as fecundity, growth, and mortality, and the amount of fishing effort exerted for a given value of the adaptive trait, thus setting the population dynamical context and ecological environment for fishing-induced selection. The ecological environment, in turn, affects the current fitness landscape on which the adaptive trait evolves. The resulting fitness function becomes nonlinear as the result of the complex interaction of trait values and density-dependent processes. By calculating the fitness for each trait value at demographic equilibrium and weighing the distribution of trait values by their fitness, selection differentials are computed as the difference in mean trait value before and after selection (Fig. 1).

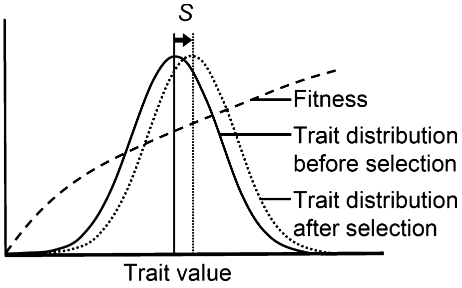

**Figure 1** Calculation of the selection differential *S* as the difference in trait means before and after selection. This is the last step in the general approach introduced in this article for estimating fishing-induced selection differentials from an age-structured life-history model. After compilation of life-history information and the specification of density dependences, the four steps involved are (A) determination of the demographic equilibrium and thereby of the ecological environment in which fitness is considered, (B) calculation of trait-specific fitness for the given ecological environment, (C) transformation of the trait distribution before selection (continuous curve) into the trait distribution after selection (dotted curve) by weighting the former by trait-specific fitness (dashed curve) and normalizing the resultant distribution, (D) calculation of the selection differential.

Below, we first present a general version of the discrete-time, age-structured model we used to quantify selection differentials in recreational fisheries. For simplicity, we assume a closed fish population (situated, e.g., in a lake) without immigration and emigration. We also assume an equal sex ratio and similar growth rates of males and females. The model is parameterized for a recreational fishery on pike (Appendix A). We start by describing the general model approach and explaining the methods used to estimate fishing-induced selection differentials. We then describe the underlying biological and angling fishery processes that determine the population dynamics, fishing intensity, exploitation patterns, and resulting selection pressures. We end this section by outlining our subsequent analyses.

## Population dynamics

We use deterministic Leslie-matrix population models because of their common application in fish population modeling and their ease of construction (Caswell 2001). Such models classify the individuals of a population into age classes and project the abundances in these classes in discrete time. The model detailed below is intended to be applied to fish species with a single breeding season per year, which is common in temperate regions (Wootton 1998), so that annual time steps can be used. We assume a polymorphic population in the considered adaptive trait $x$. Changes in the age structure and density of fish with trait value $x$ are thus described by $N'(x) = K(x, E)N(x)$ or

$$\begin{pmatrix} N_1'(x) \\ N_2'(x) \\ N_3'(x) \\ \cdots \\ N_{a_{\max}}'(x) \end{pmatrix} = \begin{pmatrix} f_1(x,E)s_0(x,E) & f_2(x,E)s_0(x,E) & \cdots & \cdots & f_{a_{\max}}(x,E)s_0(x,E) \\ s_1(x,E) & 0 & \cdots & \cdots & 0 \\ 0 & s_2(x,E) & \cdots & \cdots & 0 \\ \cdots & \cdots & \cdots & \cdots & \cdots \\ 0 & 0 & \cdots & s_{a_{\max}-1}(x,E) & 0 \end{pmatrix} \begin{pmatrix} N_1(x) \\ N_2(x) \\ N_3(x) \\ \cdots \\ N_{a_{\max}}(x) \end{pmatrix} \quad (1)$$

Here, the matrix $K$ is the population projection matrix (Leslie matrix) and the vectors $N$ and $N'$ represent the density of fish (i.e., the abundance of fish per area of the considered water body) across all age classes $a = 1,\ldots, a_{\max}$ in year $t$ and $t + 1$, respectively. Census time is chosen so that reproduction occurs at the beginning of each annual season. $f_a$ is the fecundity at age $a$ (i.e., the number of offspring produced per individual of age $a$ during a year), $s_a$ is the survival probability of individuals from age $a$ to age $a + 1$, and $a_{\max}$ is the maximum age considered in the model. The vital rates $f_a$ and $s_a$ differ for individuals with different values $x$ of the adaptive trait under investigation. They are also functions of the ecological environment $E$ and thus vary with time until reaching equilibrium. Accordingly, *K(x,E)* is a function of $x$ and $E$. In each time step, the survival of individuals in age class $a_{\max}$ is 0, whereas individuals at all other ages spawn if mature and experience natural and recreational fishing mortality as defined below. We assume that in a polymorphic resident population trait values $x$ are normally distributed with frequency $p(x)$, mean $\bar{x} = \int xp(x)dx$, and variance $\sigma_p^2 = \int (x - \bar{x})^2 p(x)dx$. The density of one age class in the entire resident population is described as $N_a = \int N_a(x)dx$.

For a given set of fishery parameters, describing angling effort or harvest regulations, the Leslie matrix $K$ is calculated each year $t$ and used to describe the dynamics of the polymorphic population. From the Leslie matrix $K$, we can infer the population's long term rate of increase, $\lambda$, as a fitness measure, which allows us to estimate selection differentials for the particular year (see description below).

### Selection differentials

Selection differentials measure the change of a population's mean trait value before and after selection (Fig. 1; Falconer and Mackay 1996). We compute selection differentials caused by size-selective recreational fisheries at demographic equilibria under various intensities of size-selective exploitation and for varying minimum-size limits (MSLs). On this basis, we analyze how variant phenotypes that differ in the adaptive trait (here reproductive investment, see the definition below) experience fitness advantages (disadvantages) and are therefore expected to increase (decrease) in abundance in a given ecological environment.

To estimate demographic equilibrium, we assume a polymorphic resident population with trait values $x$ being normally distributed around the population mean $\bar{x}$ with phenotypic variance $\sigma_p^2$. Compared with a monomorphic population with the same mean, a polymorphic population experiences different eco-evolutionary feedback and 'samples' the nonlinear fitness landscape over a range of trait values around the mean. Fitness is determined by the vital rates $f_a$ and $s_a$ in the Leslie matrix, which are functions of the trait value $x$, the total population biomass density $D$, and the resultant angling effort. The vital rates are thus varying with time until they reach demographic equilibrium.

To calculate trait-specific fitness values at demographic equilibrium (Fig. 1), the fitness of each phenotype (i.e., of each trait value) is estimated by calculating the dominant eigenvalue $\lambda$ of the corresponding Leslie matrix $K$ *(x,E)* (i.e., the eigenvalue that has the largest absolute value $|\lambda|$ among the $a_{\max}$ eigenvalues). This yields the long-term annual rate of increase in the phenotype's density under the considered ecological environment (for a review of Leslie models in the context of fisheries, see Gedamke et al. 2007). If $\lambda>1$, the phenotype's density grows exponentially with time; if $\lambda = 1$, it remains steady; whereas if $\lambda<1$, it decays exponentially. Hence, phenotypic trait values resulting in $\lambda>1$ experience a fitness advantage in the considered ecological environment, whereas trait values resulting in $\lambda<1$ experience a selective disadvantage. Note that the ecological conditions determining the fitness $\lambda(x, E)$ of trait values $x$ are shaped by the ecological environment $E$, and thus by the ecological state of the resident fish population, which in turn is shaped by the presence of anglers. The Leslie matrix *K*(*x*,*E*) describing the dynamics of the density of fish with trait value $x$ in the considered ecological environment is therefore affected by the density of resident fish and the density of vulnerable fish at demographic equilibrium (see details below). By weighing the fitness $\lambda(x)$ with the frequency $p(x)$ of trait values (Fig. 1), the selection differential $S$ is calculated as

$$S = \frac{\int x\lambda(x)p(x)dx}{\int \lambda(x)p(x)dx} - \overline{x}. \quad (2)$$

Over a single generation, the expected evolutionary response $R$ in a trait depends on the selection differential

$S$ and the heritability $h^2$ of the trait, which are related according to the breeder's equation $R = h^2S$ (Falconer and Mackay 1996). In the present study, however, the selection response $R$ is not calculated as we focus on the initial selection pressure.

To standardize the selection differentials, so as to facilitate comparisons of model predictions with field estimates and to allow comparisons of model predictions across different traits and stocks, three standardized measures are commonly applied: (1) proportional change in average trait value, $S_{\mathrm{std}}^{(1)} = S/\bar{x}$ (Roff 2002); (2) standard-deviation-standardized selection differential, $S_{\mathrm{std}}^{(2)} = S/\sigma_p$ (Lande and Arnold 1983; Kingsolver et al. 2001; alternatively termed variance-standardized selection gradient by Hereford et al. 2004); and (3) mean-and-variance-standardized selection differential, $S_{\mathrm{std}}^{(3)} = S\bar{x}/\sigma_p^2$ (alternatively termed mean-standardized selection gradient by Hereford et al. 2004). In the present study, we compute and report the mean-and-variance-standardized selection differential (hereafter termed standardized selection differential, $S_{\mathrm{std}}$). This measures the proportional change in fitness for a proportional change in trait value and thus provides an elasticity (i.e., proportional sensitivity) measure of the selection differential (Caswell 2001; Hereford et al. 2004).

The method summarized above calculates selection differentials per year. When selection differentials per generation are needed, e.g., for comparison with field estimates of strength of selection, they can be calculated using the dominant eigenvalue of the matrix $K^{t_{\mathrm{G}}(x,E)}(x,E)$ instead of $K(x,E)$. $t_{\mathrm{G}}(x,E)$ is the population's generation time calculated as $t_{\mathrm{G}}(x,E) = \sum_{a=1}^{a_{\max}} l_a f_a a \Big/ \sum_{a=1}^{a_{\max}} l_a f_a$, where $l_a$ is the probability of survival until age $a$ and $f_a$ is fecundity as defined in equation (1).

### Biological processes

Biological processes determining the life history of a species include growth, fecundity, and mortality (Wootton 1998); the corresponding functions used in our model described below are depicted in Fig. S1.

Growth is modeled according to the biphasic growth model by Lester et al. (2004). This model explicitly considers the annual energetic demand imposed by reproduction, which is assumed to be constant across mature age classes. Lester et al. (2004) showed that the von Bertalanffy growth equation provides a good description of postmaturation somatic growth in freshwater fish. However, immature fish invest all surplus energy into somatic growth. Hence, growth does not follow the von Bertalanffy growth model across all ages, and instead is almost linear until the age $T$ at which allocation of energy to reproduction begins (Lester et al. 2004), resulting in an annual growth rate

$$L_{a+1} - L_a = \begin{cases} h & \text{for } a<T \\ h - \frac{g}{g+3}(L_a + h) & \text{for } a \geq T \end{cases}, \tag{3A}$$

$$L_0 = 0, \tag{3B}$$

where $L_a$ is length at age $a$, and $h$ is the annual length increment of immature fish (Lester et al. 2004; Fig. S1A). The annual reproductive investment $g$ is represented as an energy-weighed gonado-somatic index (GSI) calculated as gonad weight divided by somatic weight multiplied by a factor $\omega$ that accounts for the higher energy content of gonadic tissue relative to somatic tissue (Lester et al. 2004), $g = \omega GSI$. For conversions from length to weight, the empirical allometric relationship

$$W_a = \alpha(L_a/L_{\mathrm{u}})^{\beta} \tag{4}$$

is used, where $W_a$ is somatic weight at age $a$, $L_{\mathrm{u}}$ is a unit-standardizing constant, and $\alpha$ and $\beta$ are empirical parameters defining the relationship. Total biomass density $D$ of the population is the sum of biomasses across all age classes and phenotypes,

$$D = \sum_{a=1}^{a_{\max}} \int W_a(x) N_a(x) dx. \tag{5}$$

Growth in fish is typically density-dependent, due to increased competition for food when density rises (Lorenzen and Enberg 2002). This crucial population dynamical mechanism was included in the model by fitting empirical data to a variant of the competition equation described by Begon et al. (1996), to provide an estimation of the average immature annual length increment $h$ as a function of total population biomass density $D$,

$$h = \frac{h_{\max}}{1 + \gamma(D/D_{\mathrm{u}})^{\delta}}, \tag{6}$$

where $\gamma$ and $\delta$ define the relationship, $D_{\mathrm{u}}$ is a unit-standardizing constant, and $h_{\max}$ is the maximum immature annual length increment at $D = 0$ (Fig. S1B). As seen from equation (3A), density-dependent immature growth also determines postmaturation growth.

We assume that fecundity diminishes with population density, as elevated food competition with increasing fish density can reduce surplus energy and energy invested in gonad development (Craig and Kipling 1983; Edeline et al. 2007). Maximum fecundity at $D = 0$ depends on reproductive investment $g$, because $g$ sets an upper limit on the production of eggs (Roff 1983; Lester et al. 2004). The age-specific fecundity, $f_a$, expressed in terms of hatched larvae, is 0 for $a \leq T$ and is defined for $a >$ T as

$$f_a = \psi \frac{gW_a}{2\omega W_\mathrm{E}} \exp(-\rho \tilde{D}), \tag{7}$$

where $\psi$ is the survival until hatching, $\omega$ is the relative caloric density of eggs compared to soma, $W_\mathrm{E}$ is the average egg weight, and $\exp(-\rho\tilde{D})$ describes a decrease of fecundity with increasing fish population density $\tilde{D}$ (Fig. S1C). The tilde indicates that $f_a$ is influenced by $\tilde{D}$ with a time lag of $t_\mathrm{L}$ years (Appendix A). $(gW_a)/(\omega W_\mathrm{E})$ is the maximum number of eggs produced by a female at $\tilde{D} = 0$, which is divided by 2 because only half of a particular age class are assumed to be females. Total hatched egg density (i.e., larval density) $B$ of the population is the sum of age-specific fecundities across all age classes and trait values,

$$B = \sum\nolimits_{a=T+1}^{a_\mathrm{max}} \int f_a(x) N_a(x) dx. \tag{8}$$

Recruitment from egg hatching to age 1 is assumed to be density-dependent as a result of competition and cannibalism. Following an empirical relationship reported by Minns et al. (1996) for our species of interest (pike), the survival rate $s_0$ from egg hatching to age 1 is assumed to depend on the density of hatched larvae following a dome-shaped relationship with overcompensation (Fig. S1D),

$$s_0 = s_{0,\mathrm{max}} \exp(-\kappa G(B)), \tag{9}$$

where $s_{0,\mathrm{max}}$ is the maximum survival rate and $\kappa$ is a constant that specifies the minimum survival rate $s_{0,\mathrm{min}} = s_{0,\mathrm{max}} \exp(-\kappa)$ as a fraction of $s_{0,\mathrm{max}}$. The function $G(B)$ determines the relationship between the density of hatched larvae and their survival,

$$G(B) = \frac{B^\mu}{B^\mu + B_{1/2}^\mu}, \tag{10}$$

where $\mu$ is an exponent determining the rapidity of the transition between $s_{0,\mathrm{max}}$ and $s_{0,\mathrm{min}}$ through changes in hatched larvae density, and $B_{1/2}$ is the density of hatched larvae at which $s_0 = s_{0,\mathrm{max}} \exp(-\kappa/2)$.

Annual survival rates $s_a$ at age are calculated by combining age-specific instantaneous natural mortality rates $M_a$ with instantaneous fishing mortality rates $F_a$. Instantaneous natural mortality rates at age $a$ for the age classes 1 and older are calculated as

$$M_a = \begin{cases} M_\mathrm{b} & \text{for } a<T \\ M_\mathrm{b} + \tau g & \text{for } a \geq T \end{cases}, \tag{11}$$

where $\tau$ is a constant (Fig. S1E). The rationale in including $\tau g$ is an assumed trade-off between reproductive investment and survival that can result for example from an inverse relation between current reproductive effort and postreproduction condition and survival (Hirshfield 1980; Wootton 1998). For the baseline mortality $M_\mathrm{b}$, we use empirical relationships representing density-dependent and size-dependent mortalities (e.g., due to cannibalism) reported by Haugen et al. (2007) for our focal species, pike (Appendix A). It follows that $s_a$ is given by

$$s_a = \exp(-(M_a + F_a)). \tag{12}$$

In each time step, the survival of individuals in age class $a_\mathrm{max}$ is 0, whereas individuals at all other ages spawn if mature and subsequently experience recreational fishing mortality as defined below.

## Angling processes

The angling fishery model constitutes a modified version of the model described by Post et al. (2003). The vulnerability of individual age classes by the fishery is represented by a sigmoid relationship with length and scaled from 0 (completely invulnerable) to 1 (completely vulnerable),

$$V_a = [1 - \exp(-\eta L_a)]^\theta, \tag{13}$$

where $V_a$ is the vulnerability of fish of age $a$ with length $L_a$, and $\eta$ and $\theta$ describe the shape of the relationship (Fig. S1F). The total density $N_\mathrm{V}$ of vulnerable fish in the population is then given by summing across all age classes and trait values,

$$N_\mathrm{V} = \sum\nolimits_{a=1}^{a_\mathrm{max}} \int V_a(x) N_a(x) dx. \tag{14}$$

A realistic expectation about angler behavior is a response of angling effort $A$ to the perceived quality of the fishery (Johnson and Carpenter 1994; Cox and Walters 2002). As the quality of fishing measured in terms of angler satisfaction is often catch-dependent (Arlinghaus and Mehner 2005; Arlinghaus 2006), increasing numbers of vulnerable fish are expected to increase the number of anglers spending effort on a particular fishery (Cox et al. 2003). As empirical information on this effort dynamic is not available for many fisheries, a generic sigmoid numerical response of angling effort density $A$ to fish availability, modified from Post et al. (2003), was chosen,

$$A = u\left(p + \frac{N_\mathrm{V}^\xi}{N_\mathrm{V}^\xi + N_{\mathrm{V},1/2}^\xi}(1-p)\right), \tag{15}$$

where $u$ is the maximum effort density, $p$ is the effort proportion of $u$ that is always present, $N_{\mathrm{V},1/2}$ is the density of vulnerable fish that elicits one-half of the effort density, and $\xi$ is an exponent that characterizes the steepness of the effort-response curve (Fig. S1G). Note that this model ignores regional angler dynamics, i.e., anglers here choose a particular water body depending only on the quality of its fishery (Post et al. 2003).

In most recreational fisheries, some variants of size-based harvest regulations are used to maintain recruitment, manipulate the size structure of the fish stocks, or distribute the harvest more equitably among anglers (Arlinghaus et al. 2002). Therefore, anglers may voluntarily or mandatorily release a certain proportion of fish (Arlinghaus et al. 2007). In our model, a MSL is assumed, above which every caught fish is removed for consumption. This situation is characteristic for purely consumptive recreational fisheries in countries such as Germany, where catch-and-release fishing is often not tolerated (Arlinghaus 2007). However, the situation is different in many other fisheries in which large percentages of legally sized fish are released (Arlinghaus et al. 2007). In our model, catch-and-release fishing only applies to undersized fish. However, anglers may also illegally harvest undersized fish (Sullivan 2002). Therefore, in our model three sources of fishing mortality are considered (Post et al. 2003): harvest mortality of fish exceeding the MSL, hooking mortality of fish caught undersized and then released, and noncompliance mortality from illegal harvest of undersized fish. On this basis, the density of dead fish $D_\mathrm{a}$ at age $a$ is given by

$$D_a = \begin{cases} V_a N_a[1-\exp(-qA)] & \text{for } L_a \geq MSL \\ V_a N_a[1-\exp(-qAU)] & \text{for } L_a < MSL\text{'} \end{cases} \tag{16}$$

where $q$ is a constant catchability coefficient, $A$ is angling effort, and

$$U = \phi + Q - \phi Q, \tag{17}$$

where $\varphi$ is the proportion of fish below the MSL that experience hooking mortality from catch-and-release fishing, and $Q$ is the proportion of fish below the MSL that are harvested illegally. The noncompliance mortality $Q$ was treated as a dynamic variable following Sullivan (2002), who found that in walleye (*Sander vitreum*) angling it was inversely related to the angling catch rate $C_\mathrm{r}$ of undersized fish,

$$Q' = \varepsilon(C_\mathrm{r}/C_\mathrm{u})^{\zeta}, \tag{18}$$

where ε and $\zeta$ are empirically derived constants defining the relationship and $C_\mathrm{u}$ is a unit-standardizing constant. As the prime indicates, we assume that the catch rate of undersized fish influences the noncompliance mortality by anglers in the following year. Note that the parameter $\zeta$ is negative, so that the noncompliance mortality declines as the catch rate $C_\mathrm{r}$ of undersized fish increases (Fig. S1H). The catch rate $C_\mathrm{r}$ of undersized fish,

$$C_\mathrm{r} = A^{-1}\sum_{a=1}^{a_{\max}} \int c_a(x)dx, \tag{19}$$

was calculated based on the number of undersized fish $c_a$ caught at age $a$,

$$c_a = \begin{cases} 0 & \text{for } L_a \geq MSL \\ D_a/U & \text{for } L_a < MSL\text{'} \end{cases} \tag{20}$$

where $A$ is angling effort density and $U$ is the proportion of fish below the MSL that experience either hooking mortality or noncompliance mortality. The instantaneous angling mortality $F_\mathrm{a}$ at age $a$ is then

$$F_a = -\ln(1 - D_a/N_a). \tag{21}$$

### Outline of analysis

To address the three principal objectives of the present work, numerical investigations were carried out for a parameter set chosen to describe size-selective recreational fishing on a hypothetical pike stock (Table A1). Population dynamics were computed for 100 years. The initial population densities for the considered 12 age classes were derived from Kipling and Frost (1970).

The analysis then proceeded in three steps:

1 First, selection differentials were computed for populations with different average trait values $\bar{x}$ for annual reproductive investment $g$ and different angling intensities. We assumed the logarithm ln$g$ of the adaptive trait $g$ to be normally distributed in the population because $g$ is always positive. The average value of annual reproductive investment $g$ was increased from a baseline of $\bar{x} = 0.10$ (with $\sigma_p = 0.015$), at which the selection differential on $g$ is zero in the absence of angling pressure, representing an evolutionarily stable strategy (ESS). Angling intensity was varied by changing the parameter $u$ (maximum angling effort per area) in equation (15). This enables investigating how the direction of selection on $g$ changes with increasing mean trait values of the population and to analyze how the ESS in $g$ depends on angling intensity.

2 Second, the MSL was varied for different angling intensities to investigate the potential of simple standard harvest regulations to counteract angling-induced selection on reproductive investment.

3 Lastly, we conducted a series of analyses to estimate the robustness of our model to examine how the results are affected by some of the most critical underlying assumptions. We first examined how incorporation of density dependence in relative fecundity, somatic growth, and natural mortality affected predicted

selection differentials. We then examined how selection differentials changed over time rather than only examining the situation at demographic equilibrium. We also relaxed the assumption of deterministic population dynamics by incorporating stochasticity in recruitment and examining the resultant impact on the predicted selection differentials. Finally, the sensitivity of results to individual parameters was assessed by varying parameters by 5% and calculating the resultant percentage of change in the predicted selection differentials.

## Results

Pike populations size-selectively exploited by anglers equilibrate after about 20 years at much reduced abundance density as compared with the unexploited case (Fig. 2). This corresponds to a biomass density between 4.5 and 9.9 kg $ha^{-1}$ compared to 15.8 kg $ha^{-1}$ in the unexploited case. Increasing angling effort results in monotonically increasing annual angling exploitation rates of up to 66.5% of fish larger than the MSL and of up to 22.4% for fish aged 1 or older (Table 1). Note that in Table 1 $A$ (total angling effort per area at demographic equilibrium) differs from $u$ (maximum angling effort per area) owing to the density dependence of angling effort. The resulting demographic equilibrium represents the ecological environment that determines the selection differentials on reproductive investment exerted by size-selective recreational fishing.

At demographic equilibrium, size-selective angling induces positive selection differentials on annual reproductive investment for wide ranges of average reproductive investment values (Fig. 3A). Selection differentials increase with angling intensity and the associated higher annual exploitation rates (Fig. 3A; Table 1). Positive selection differentials would cause the mean phenotype to increase, whereas negative selection differentials would cause it to decrease. The phenotype at which such directional selection ceases (and only stabilizing selection remains) is the ESS. It occurs where the curve of selection differentials intersects with the horizontal axis (Fig. 3A). These intersections thus describe the expected endpoints of angling-induced evolution for different angling intensities. Accordingly, intensive recreational angling selects for increased annual reproductive investment, with evolutionary endpoints ranging from $g = 0.10$ in the absence of angling to $g = 0.23$ at $u = 150$ h $ha^{-1}$ $year^{-1}$ (Fig. 3A) and up to $g = 0.44$ under extreme exploitation (Fig. 3B).

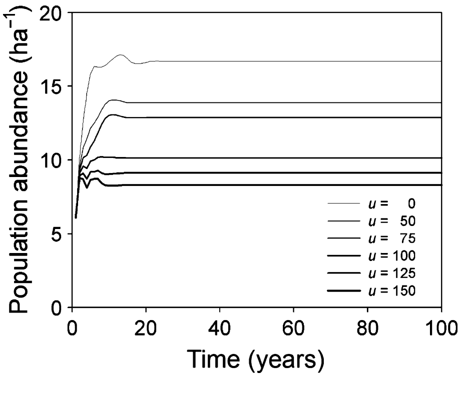

**Figure 2** Population dynamics of pike at age 1 year and older exploited at different intensities by anglers. Curves show the equilibration of abundance density over time for different levels of maximum angling effort per area and year ($u$; unit h $ha^{-1}$ $year^{-1}$), with thicker curves corresponding to higher efforts. The corresponding annual exploitation rates at equilibrium are shown in Table 1 and default parameter values are listed in Table A1.

Note that at particular conditions the selection differential exhibits jumps, for example, at a mean reproductive investment of 0.14 and 0.17 for $u = 125$ h $ha^{-1}$ $year^{-1}$ and $u = 150$ h $ha^{-1}$ $year^{-1}$, respectively (Fig. 3A). This can be understood by appreciating the complex interplay among the size variation caused by polymorphism in $g$, size-dependent angling, and density-dependent growth. For example, when the population mean $g$ takes a particular value, a component of a particular age class comprising fish with high $g$ values can remain below the MSL, resulting in positive selection differentials. However, this situation is limited to a small range of the population's mean $g$. As the population mean of $g$ increases, a greater component of the considered age class stays smaller than the MSL. This in turn results in an increase of the population biomass, which further reduces the size of some phenotypes due to density-dependent growth. Eventually, all individuals of one particular age class may remain smaller than the MSL, causing the selection differential to decrease. As shown in Fig. 3A, however, these irregular patterns for particular situations do not change the general result of stabilizing selection on reproductive investment in response to varying levels of angling intensity.

To address the second objective of our study (i.e., to investigate the potential for standard harvest regulations to counteract recreational fishing-induced selection), we analyzed the effects of changing harvest regulations on the selection differentials acting on annual reproductive investment (Fig. 4). Increasing MSLs decrease the strength of angling-induced evolution. Although MSLs generally reduce selection pressures, some irregular patterns with increases in selection differentials are visible in Fig. 4, for example, at a maximum angling effort level of $u = 50$ h $ha^{-1}$ $year^{-1}$and a MSL of 70 cm. The increase in the selection differential at this parameter combination is caused by part of an age class being saved from harvest as described before, which does not change the general observation that increasing MSLs reduce selection pres-

**Table 1.** Relationships between the maximum annual angling effort per area ($u$; unit h ha$^{-1}$ year$^{-1}$) and the resultant annual angling effort per area ($A$; unit h ha$^{-1}$ year$^{-1}$), annual exploitation rate, and standardized selection differentials (per year and per generation) for annual reproductive investment in a size-selectively exploited pike population at demographic equilibrium. Default values are given in Table A1. The average value of annual reproductive investment $g$ was the default value 0.1 at which the standardized selection differential $S_{\mathrm{std}}$ on $g$ vanishes in the absence of angling pressure.

| Maximum annual angling effort per area, $u$ | Annual angling effort per area, $A$ | Annual exploitation rate | | Selection differential, $S_{\mathrm{std}}$ | |
|---|---|---|---|---|---|
| | | Pike older than 1 year | Pike larger than minimum-size limit | per year | per generation |
| 0 | 0.0 | 0.000 | 0.000 | 0.00 | 0.00 |
| 10 | 6.3 | 0.025 | 0.087 | 0.01 | 0.08 |
| 20 | 12.5 | 0.045 | 0.163 | 0.02 | 0.15 |
| 30 | 18.4 | 0.061 | 0.232 | 0.03 | 0.22 |
| 40 | 24.2 | 0.075 | 0.292 | 0.04 | 0.27 |
| 50 | 29.8 | 0.087 | 0.347 | 0.05 | 0.32 |
| 60 | 35.2 | 0.098 | 0.396 | 0.06 | 0.36 |
| 70 | 40.6 | 0.107 | 0.440 | 0.07 | 0.39 |
| 80 | 45.8 | 0.115 | 0.481 | 0.08 | 0.42 |
| 90 | 51.0 | 0.122 | 0.518 | 0.09 | 0.44 |
| 100 | 56.1 | 0.128 | 0.552 | 0.09 | 0.46 |
| 110 | 57.3 | 0.195 | 0.559 | 0.11 | 0.52 |
| 120 | 62.1 | 0.203 | 0.588 | 0.12 | 0.55 |
| 130 | 66.9 | 0.210 | 0.615 | 0.13 | 0.57 |
| 140 | 71.7 | 0.217 | 0.641 | 0.14 | 0.58 |
| 150 | 76.6 | 0.222 | 0.665 | 0.15 | 0.60 |

sures. These findings are strongly dependent on levels of angling effort. Increasing MSLs at high angling effort leads to more drastic reductions in the selection differentials than it does at low angling effort. It is important to note that even under extremely high MSLs (corresponding to total catch-and-release fishing) there are always positive selection differentials on annual reproductive investment, so that recreational fishing-induced selection cannot be avoided by standard harvest regulations alone.

To examine the robustness of our model and to provide justification for the incorporation of density- and frequency-dependent selection, we removed the assumptions of density-dependent relative fecundity, density-dependent somatic growth, or density-dependent natural mortality. The predicted selection differentials on reproductive investment are essentially similar for situations with and without density-dependent relative fecundity (Fig. 5). The same applies to density-dependent natural mortality. This suggests that our pike model could be simplified by removing density-dependence in relative fecundity and natural mortality without jeopardizing the estimation of selection differentials.

The situation is different for density-dependent growth. In simulations without density-dependent growth, the predicted selection differentials and evolutionary endpoints are larger or smaller than in simulations with density-dependent growth. The direction of change depends on whether the density-independent immature growth rate is higher or lower than the one in the density-dependent case at equilibrium. What is particularly noticeable is that jumps in the selection differentials are more prominent under density-independent growth than under density-dependent growth. Large selection differentials occur when there is a large fitness advantage for part of an age class to stay below the MSL by increasing reproductive investment and thus reducing growth. Under density-dependent growth, ecological feedback resulting from increased population density in response to some fish escaping harvest reduces growth further, eventually saving an entire age class from harvest. This reduces selection differentials on reproductive investment. Such feedback mechanisms do not occur under density-independent growth, which explains the more pronounced increases in selection pressures in Fig. 5. Our model is thus sensitive to assumptions about density-dependent growth. Ignoring density dependence in growth may thus result in erroneous predictions about the strength of selection and the predicted evolutionary endpoints.

Support for our deterministic approach to estimate selection differentials in response to size-selective recreational fishing was obtained when stochasticity in recruitment was introduced to the model and the resulting dynamics in selection differentials were examined. As shown in Fig. 6, stochastic recruitment results in largely constant selection differentials, except for short-term irregularities that are not correlated with population

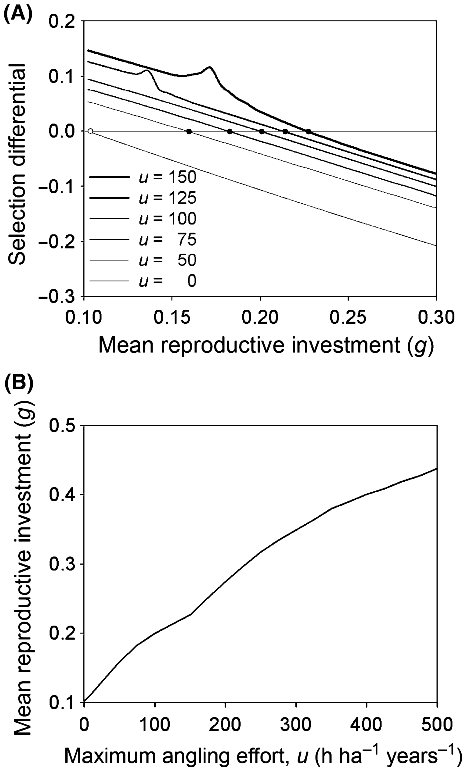

**Figure 3** (A) Dependence of the standardized selection differential for annual reproductive investment $g$ on the mean of $g$ in a pike population size-selectively exploited by anglers at varying intensities (Table 1). Positive (negative) selection pressures are expected to increase (decrease) annual reproductive investment. Filled circles along the horizontal axis indicate the evolutionarily stable strategies at which selection pressures vanish. These vary with the maximum angling effort per area ($u$; unit h ha$^{-1}$ year$^{-1}$), with thicker curves corresponding to higher efforts. (B) Dependence of the evolutionarily stable strategy for $g$ on the maximum angling effort per area. Default parameter values are listed in Table A1.

abundance (Pearson product-moment correlation coefficient $r = -0.09$, with $P = 0.35$). The largely constant selection pressures provide support for the simplifying assumption of deterministic population dynamics.

Finally, we examined the model's sensitivity to individual parameters. For most parameters, model predictions were robust to changes in parameter values (Fig. 7). 5% changes in each of the parameters resulted in changes in the predicted standardized selection differential of less than 5% in all parameters except $\beta$, $\tau$, and $\mu$. $\beta$ is the exponent in the length-weight regression, $\mu$ is the exponent in the stock-recruitment relationship determining density-dependent larval survival, and $\tau$ is a parameter determining the relationship between reproductive investment and natural mortality, which represents the immediate cost of reproduction. Changes of these parameters thus influence fecundity and/or mortality, and in turn fitness and selection differentials. Among the parameters characterizing the angling fishery, $q$ (catchability) and $p$ (proportion of maximum angling effort always present) were found to be particularly sensitive for prediction of selection pressures. This calls for more accurate determination of these parameters if our model is to be applied to real fisheries.

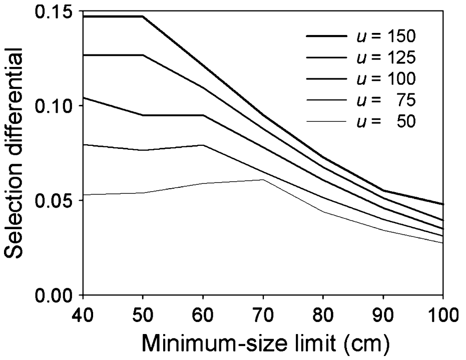

**Figure 4** Influence of different minimum-size limits on the standardized selection differential for annual reproductive investment in a pike population size-selectively exploited by anglers. These vary with the maximum angling effort per area ($u$; unit h ha$^{-1}$ year$^{-1}$), with thicker curves corresponding to higher efforts. In the figure, the average value of annual reproductive investment $g$ was the default value 0.1 at which the selection differential on $g$ vanishes in the absence of angling pressure.

## Discussion

The primary purpose of this study was to demonstrate how an age-structured fish population model incorporating density dependence as a crucial aspect of population dynamics can be used to estimate selection differentials caused by size-selective recreational angling. We illustrated our model's applicability with a hypothetical size-selective angling fishery for pike, investigating reproductive investment as the adaptive trait under selection. We showed that angling mortality exerts a positive directional selection pressure on annual reproductive investment and analyzed how the strength and direction of standardized selection strength depends on the pattern of exploitation, the level of angling mortality, and the mean trait value. The selection differential is positive and largest in a population with low average reproductive investment and rises with increased angling mortality and decreased MSL. Model predictions are sensitive to assumptions about density dependence in growth, a common process in most fish stocks (Lorenzen and Enberg 2002). This justifies the methodological choice of including multiple eco-evolutionary feedbacks for estimating ecology-driven fitness functions. Inclusion of multidimensional density

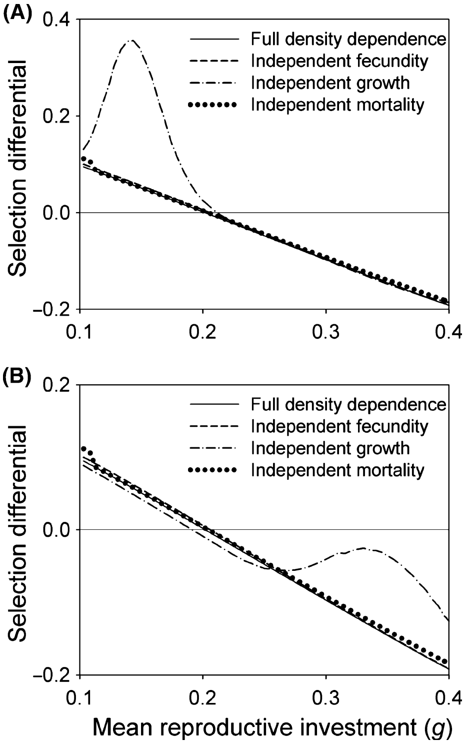

**Figure 5** Influence of removed density dependence of either somatic growth (equation 6), relative fecundity (equation 7), or natural mortality (equations 11 and A1) relative to the baseline case with density dependence. Average values from empirical studies (Craig and Kipling 1983; Kipling 1983a) were used in density-independent cases, assuming (A) $h = 18.0$ cm and (B) $h = 16.0$ cm in equation (6), $\exp(-\rho\tilde{D}) = 0.79$ in equation (7), or $M_b = 0.23$ in equation (11). As in Fig. 3, the influence of the mean annual reproductive investment $g$ in the resident condition on the standardized selection differential in a pike population size-selectively exploited by anglers was examined. The maximum angling effort per area was set at $u = 100$ h ha$^{-1}$ year$^{-1}$.

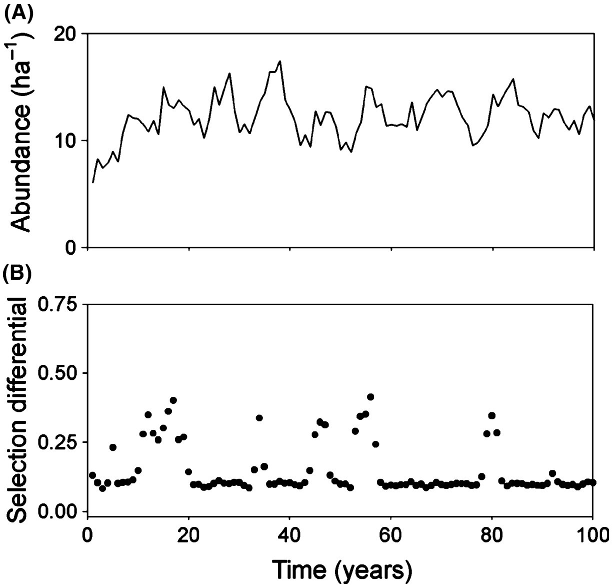

**Figure 6** Influence of stochastic variations in the stock-recruitment relationship on (A) abundances of pike aged 1 year and older and (B) standardized selection differentials. We assumed multiplicative lognormally distributed fluctuations around the deterministic recruitment in equation (8), $B = \exp(v)\sum_{a=T+1}^{a_{\max}}\int f_a(X)N_a(X)dX$, where $v$ is drawn randomly from a normal distribution with mean 0 and standard deviation $\sigma_v = 0.5$. The maximum angling effort per area was set at $u = 100$ h ha$^{-1}$ year$^{-1}$.

dependence renders the problem intractable through fitness optimization principles. Therefore, a numerical approach to estimate fishing-induced selection is needed and justified. It is important to note that our model estimates initial selection strength and not subsequent evolutionary rates. Determining evolutionary rates would depend on the calculation of selection responses, which are the product of selection differentials and heritabilities (Hilborn and Minte-Vera 2008).

Our results are qualitatively similar to those reported by Rijnsdorp (1993a) in his pioneering study on estimating selection differentials for reproductive investment under size-selective commercial fishing. In agreement with our results, he showed that in North Sea plaice (*Pleuronectes platessa*) size-selective fishing induces a positive selection differential on reproductive investment. However, Rijnsdorp (1993a) assumed, in contrast to our analysis, the absence of eco-evolutionary feedback on fitness through density dependence. In our life-history model of pike, fecundity and annual length increments depend on total pike density, and natural survival depends on larval density until age 1 and on the density of older pike thereafter. Further density dependences in our model arise from variations of angling effort with the density of vulnerable fish and of noncompliance mortality with the density of under-sized fish. This multidimensional eco-evolutionary feedback enables a more realistic representation of natural life histories in fish than density-independent models can achieve. We showed that our model predictions were indeed sensitive to assumptions about density-dependent growth. Estimating selection differentials exerted by size-selective fishing without accounting for density dependence might thus lead to misleading predictions.

Increased reproductive investment as an evolutionary response to angling results from the life-history trade-off between investing surplus energy into either current or future reproduction. One of the costs associated with investment into current reproduction is decelerated somatic growth, which reduces future reproductive output (Roff 1983; Lester et al. 2004). However, in an

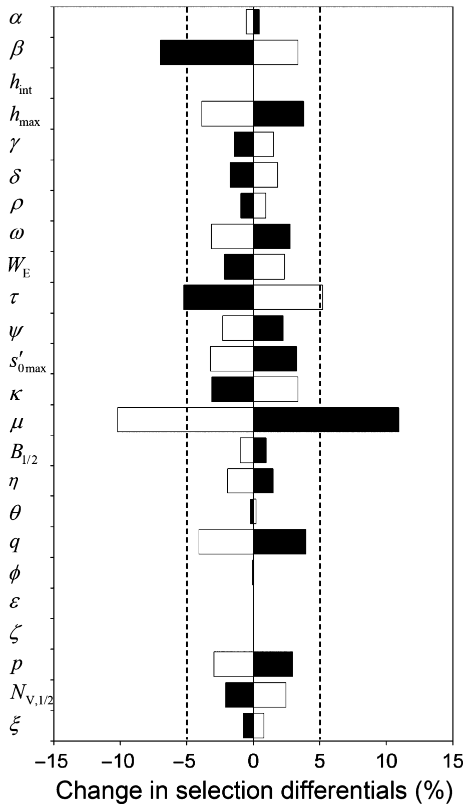

**Figure 7** Sensitivity analysis of standardized selection differentials with respect to parameters that determine the dynamics of a pike population size-selectively exploited by anglers. Black (white) bars depict the relative change in standardized selection differentials when the corresponding parameter is increased (decreased) by 5%. For easier reference, the dashed vertical lines indicate the ±5% range for the relative change in standardized selection differentials. Default parameter values are listed in Table A1.

environment in which larger or older fish face high mortalities, as when anglers heavily crop a stock of pike in a size-selective manner, betting on future reproduction by investing surplus energy into growth may not pay off. Instead, individual fitness can be raised by investment into current reproduction, through gonads and/or spawning and mating behavior. Reduced somatic growth due to such investment may even further reduce exposure to size-selective angling. Indeed, theoretical studies have shown that increased annual reproductive investment is expected under conditions of elevated adult mortality (Law 1979; Roff 1992), and empirical evidence in various fish species (Reznick et al. 1990; Hutchings 1993b; Rijnsdorp 1993b; Rochet et al. 2000; Yoneda and Wright 2004; Rijnsdorp et al. 2005; Thomas et al. 2009), including pike (Diana and Mackay 1979; Diana 1983; Edeline et al. 2007), has supported this. Such adaptive changes increase the fitness of individual fish in the exploited stock, but – in the long run – may be harmful to the population as a whole, because these changes can be maladaptive with regard to natural selection pressures (Conover et al. 2005). They may also reduce the socio-economic value of the fishery, because the size of harvested fish may shrink (Jørgensen et al. 2007).

Our results indicate that saving a greater proportion of adult fish through increased MSLs can greatly reduce the selective pressures exerted by anglers. This is good news for the fisheries manager and is in agreement with other research on fishing-induced evolution pointing to the possibility of counteracting fishing-induced adaptive changes through appropriate harvest regulations (Conover and Munch 2002; Ernande et al. 2004; Baskett et al. 2005) or gear choices (Jørgensen et al. 2009). However, it is also important to realize that selection differentials were positive even when the MSL was high, thus mimicking a total regulatory catch-and-release fishery. The reason why some selective pressures persist even under such very restrictive harvest regulations is that unwanted hooking mortality (Arlinghaus et al. 2007; Coggins et al. 2007) and/or illegal harvest (Sullivan 2002) will still take place. Both of these common types of 'cryptic' (Coggins et al. 2007) angling mortalities were incorporated into our model of a recreational fishery, resulting in positive directional selection on reproductive investment being predicted even for a total catch-and-release pike fishery.

How strong are the selection pressures induced by a recreational angling fishery relative to natural selection pressures? Hereford et al. (2004) and Stinchcombe (2005) suggested that the mean-and-variance-standardized selection differential $S_{\text{std}} = S\bar{x}/\sigma_p^2$ is an appropriate measure of the strength of selection on adaptive traits, as this dimensionless measure is insensitive to changes in a trait's variability. This measure, $S_{\text{std}}$, has also an intuitive interpretation in terms of elasticity: changing the considered trait value by a fraction $f$ of the mean trait value causes fitness to increase by $S_{\text{std}}f$ (Hereford et al. 2004). For annual angling exploitation rates of legally sized pike of up to 67%, we estimated mean-and-variance-standardized selection differentials of up to 0.60 per generation (Table 1). This means that doubling annual reproductive investment would increase fitness by up to 60%. Hereford et al. (2004) conducted a meta-analysis of available mean-and-variance-standardized selection differentials and reported a median value of 0.48 for univariate traits. The strength of angling-induced selection on annual reproductive investment reported here is thus comparable in magnitude to natural selection pressures, neither being unusually low or unusually high. This observation seems to disagree with a recent meta-analysis on phenotypic changes by Darimont et al. (2009), who reported that human predators in general exerted significantly greater phenotypic changes compared with both natural and nonexploitative anthropogenic environmental changes. However, direct comparison of our model with the findings by Darimont et al. (2009) is difficult for two reasons. First, the meta-analysis by Darimont et al. (2009) includes many other traits in addition to reproductive investment. The selection responses of those different traits to fishing will very likely differ considerably, limiting the usefulness of grand averages across traits. Second, Darimont et al. (2009) compared rates of long-term phenotypic changes in the wild, which are jointly determined by evolutionary and/or ecological processes, while we estimated initial selection strength on reproductive investment and did not analyze the expected resultant long-term phenotypic changes.

Our analysis suggests that angling-induced selection on reproductive investment in pike is moderately strong and positive, but we confined our analysis to this trait only. Other studies on fisheries-induced evolution of life-history traits suggest that, in addition to reproductive investment, other traits such as age and size at maturation can evolve. In iteropareous species, evolution towards maturation at younger age and smaller size in response to size-selective harvesting is likely and has been documented repeatedly for various species (reviewed in Dieckmann and Heino 2007; Jørgensen et al. 2007; Hard et al. 2008). The room for evolution of age at maturation is limited for an early maturing fish such as pike. However, Diana (1983) reported that in pike populations exploited by anglers pike tended to mature earlier than in unexploited reference lakes, but no attempt was made to control for the impact of relaxed density dependence in high-exploitation lakes on age at maturation. Our model can and should be extended in further studies to investigate selection on other traits, such as age and size at maturation.

Our results on the selection differentials of fishing-induced evolution in annual reproductive investment depend on five critical assumptions, which warrant some discussion. First, we assumed a constant annual reproductive investment throughout adult age classes. However, GSI, which is a fairly accurate estimator of annual reproductive investment when gonadic biomass constitutes the vast majority of annual reproductive investment (Diana 1983; Lester et al. 2004), may increase with age in some fish species (Roff 1983; Heino and Kaitala 1999). In pike, the GSI was found to be independent of total body weight in an early study by Mann (1976). A recent study by Edeline et al. (2007), however, showed that the GSI was positively size-dependent within mature age classes in pike in Lake Windermere (UK). Without developing and analyzing a specific model that accounts for this dependence, it is not known whether relaxing the assumption of constant GSI with age affects selection differentials on this trait. However, it is unlikely that the general findings reported in our paper would change qualitatively, because selection for greater reproductive investment would provide selective advantages to pike whenever adult mortality is high.

Second, many models of life-history evolution assume, like we did, that the main trade-off in energy allocation is that between gonadic and somatic growth (Roff 1983; Law and Grey 1989; Rowell 1993; see Heino and Kaitala 1999 for a review). Our model incorporates an additional trade-off, between reproduction and survival, which may arise, e.g., from intraspecific interactions on a spawning site or poor condition after reproduction (Wootton 1998). Although this trade-off cannot be readily quantified for pike populations, we considered its incorporation crucial as it is expected to imply selection pressures naturally counteracting those originating from angling (Edeline et al. 2007). As expected, we found that this trade-off affects the dependence of the ESS for annual reproductive investment on angling mortality predicted by our model (Fig. 3).

Third, we did not incorporate into our model any assumption about egg size and its influence on total egg number at a given reproductive investment. In some fish species, egg size allometrically increases with body size, and hence age, and is positively correlated with fry survival (Hutchings 1993a; Einum and Fleming 2000). Although egg size in pike is known to increase with size and age (Schäperclaus 1940; Anwand 1968; but see Goedmakers and Verboom 1974 for a report on a nonsignificant correlation), Wright and Shoesmith (1988) did not detect a significant correlation between egg size and fry size, or between fry size and adult length, supporting our assumptions in the present model for pike.

Fourth, we used an empirical dome-shaped stock-recruitment function that resembles a Ricker-type stock-recruitment relationship (Minns et al. 1996). Empirically estimated parameter values for this function in pike were associated with large standard errors (Minns et al. 1996). This uncertainty is an issue if our model is to be applied to predicting selection differentials for a real fishery, as we found that the selection differentials estimated with our model were sensitive to the exponent $\mu$ determining density-dependent larval survival in the stock-recruitment relationship. There is thus a need for improved long-term monitoring to reduce the uncertainty in parameter estimates for stock-recruitment relationships in pike (and other fish species). Similarly, when our model is applied to a particular fishery there is a need for a thorough assessment of the exponent $\beta$ in the length-weight regression, as this parameter exerts a large influence on the predicted strength of selection. Fortunately, this is one of the biological parameters that is most accurately estimated for a given population, considering the high regression coefficients reported in the literature (0.95–0.99, Willis 1989).

Finally, we examined a range of angling intensities and very high annual exploitation rates. A recent review showed that anglers can indeed remove up to 80% of a target population within a single angling season (Lewin et al. 2006). The angling efforts used in our model are well in accord with field studies on pike (Kempinger and Carline 1978; Pierce et al. 1995; Margenau et al. 2003), and the maximum annual exploitation rates we have used, up to 67%, are in close agreement with empirical data of annual exploitation rates for pike, ranging between 47% and 74% (T. Klefoth et al., Leibniz-Institute of Freshwater Ecology and Inland Fisheries, Berlin, unpublished). We thus did not simulate an artificially intensive angling fishery, but used realistic values that can be expected in many pike fisheries world-wide.

To conclude, this study is the first attempt to estimate selection differentials on life-history traits caused by recreational angling based on an ecologically realistic model incorporating density-dependent effects resulting in density- and frequency-dependent selection. Compared with traditional optimization models used for studying fishing-induced selection (see examples in Stokes et al. 1993), the fitness function in our approach is dynamically determined by the ecological environment through density-dependent growth, survival, fecundity, angling effort, and noncompliance mortality. Our model thus captures key ecological and fisheries-related mechanisms that optimization models by definition cannot incorporate. Once some crucial biological and fishery-related processes have been quantified from field data or compiled from the literature, our approach is applicable to evaluate the vulnerability of a particular recreational fishery to fishing-induced evolution. In the absence of long-term data to quantify density dependence in recreationally exploited fish stocks, our model could be further simplified by the omission of density-dependent mortality or fecundity, as our analysis has shown that this would still yield valid approximations of the selection differentials for reproductive investment induced by angling. Our approach may also be valuable as an educational tool for managers, as a quantitative approach to evolutionary impact assessment, and as an antidote to the belief that anglers are neither persistent nor efficient enough to act as an evolutionary force.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Figure S1.** (A) Age-specific length as described by equation (3). The continuous and dashed curves correspond to annual reproductive investments of $g = 0.10$ and $g = 0.25$, respectively, in an unexploited population. (B) Density-dependent growth as described by equation (6). (C) Density-dependent fecundity as described by equation (7). The curve shows the fecundity of a female weighing 2 kg. (D) Density-dependent recruitment to age 1 year as described by equations (9) and (10). (E) Trade-off between annual survival and reproductive investment g as described by equation (11). (F) Vulnerability to angling in dependence on fish length as described by equation (13). (G) Density-dependent angling effort as described by equation (15). (H) Density-dependent non-compliance mortality as described by equations (18)–(20).

## Appendix A: Parameterization of the model for pike (*Esox lucius* L.)

The parameter set used in our analysis (Table A1) was developed to represent a hypothetical lake population of northern pike. Constants determined by empirical studies were represented by Greek letters, except when following popular notations (e.g., catchability $q$). Recreational fishing patterns (e.g., annual exploitation rates, size-selectivity, angling-effort dynamic) resembled those typical for consumptive anglers targeting top predatory fish such as pike (reviewed in Lewin et al. 2006). The parameter set is a compilation of literature data. No study was available that reported all the needed information in a single source; thus, parameter values were collected from different sources. Studies from the pike population in Lake Windermere (UK) were favored, due to the availability of long-term data sets on population demography from this lake (Haugen et al. 2007). It was assumed that the modeled fishery reflected common effects on the population dynamics of pike exerted by the presence and actions of pike anglers. The aim of this study was not to provide a precise and accurate description of a particular pike population and a particular angling fishery. Instead, the present study mainly aimed at elucidating the general modeling approach and its utility for estimating selection pressures acting on adaptive life-history traits. This objective justifies the more general compilation of pike parameters and demographic processes. Table A1 reports parameter values and references. Below, we comment on those parameter values that deserve special clarification.

To determine the parameter value for $h$, time series data published in Kipling (1983a) on early growth of female pike until age-at-maturation from 1939 to 1978 in Lake Windermere (UK) were used (her Table 1). Prematuration growth is supposed to be linear with the slope of the age-length regression being given by $h$ (Lester et al. 2004). Kipling (1983a) did not report length-based growth-rate data from age 0 year to age 1 year. We thus calculated average length data from age 1 year to age 2 years in the published time series. Density-dependent early pike growth rate $h$ was determined by combining data in Kipling (1983a) with data in Kipling (1983b) (her Table 3) on total density of pike aged 2–18 in Lake Windermere for the years 1944–1978 and fitting this data to equation (6) to determine the parameter values $h_{\max}$, $\gamma$, and $\delta$ by minimizing the sum of squares of the residuals ($r^2 = 0.279$, $F = 12.37$, $P < 0.01$).

To estimate density-dependent relative fecundity, the parameters in the original function by Craig and Kipling (1983) for pike in Lake Windermere were recalculated from their Fig. 1 to derive a function relating fecundity to fish biomass density $D$ two years before spawning ($t_{\mathrm{L}} = 2$). The baseline for recalculation was an area of littoral pike habitat of 550 ha in Lake Windermere according to Raat (1988). Relative caloric equivalents of gonads relative to soma were calculated as means of the values published in Table 2 in Diana (1983) taking March as the reference month. Mean egg weight was calculated taking the mean egg diameter value (2.3 mm) from Frost and Kipling (1967) assuming a spherical shape and a specific density of 1.0 g cm$^{-3}$. For the age at which energy is first diverted to reproduction, we used $T = 1$, so that fish start spawning at age 2. In our model, the length of fish of age 2 years was usually larger than 40 cm (the smallest length was 36 cm in the unexploited case). These values agree well with common literature reports on the age and size at first spawning in female pike (Raat 1988).

Cannibalism and associated density-dependent recruitment is a well-known process in pike populations (Raat 1988; Haugen et al. 2007). Empirical relationships relating density-dependent first-year survival of pike to the density of hatched eggs were taken from Minns et al. (1996) and converted into a more common representation of a dome-shaped stock-recruitment function. The baseline instantaneous natural mortality rate $M_{\mathrm{b}}$ of older pike was determined according to an empirical model for predicting the half-year survival probability $s_{1/2}$ for 'small' and 'large' Lake Windermere pike as reported by Haugen et al. (2007),

$$s_{1/2} = \frac{\exp(\beta_0 + \beta_X X + \beta_Y Y + \beta_L L)}{1 + \exp(\beta_0 + \beta_X X + \beta_Y Y + \beta_L L)}, \qquad (A1)$$

where $X$ and $Y$ are densities of 'small' (age 2 years) and 'large' pike (older than 2 years), respectively, and $L$ denotes the length of fish, and $\beta_0$, $\beta_X$, $\beta_Y$, and $\beta_L$ are empirically determined coefficients. Values of $\beta_0$, $\beta_X$, $\beta_Y$, and $\beta_L$ for 'small' and 'large' pike were calculated from Table 3 in Haugen et al. (2007), assuming no specific basin of the study lake and no sex structure. As Haugen et al. (2007) did not report survival rate of age-1 pike, we applied the survival rate estimated for small pike (i.e., age-2) also to age-1 individuals. The half-year survival rates were translated into instantaneous mortality rates,

$$M_{\mathrm{b}} = -\log s_{1/2}^2. \qquad (A2)$$

It is reasonable to assume a potential trade-off between reproductive investment and postreproduction survival in pike. No empirical data were available to parameterize this trade-off (Wootton 1998). We determined $\tau$ so that the total instantaneous natural mortality rate $M$ ranges between 0.3 year$^{-1}$ and 0.5 year$^{-1}$, which is typical for many pike populations (Raat 1988).

Anglers generally exploit fish stocks size-selectively (Lewin et al. 2006). For describing size-selectivity in pike fisheries, the parameters $\eta$ and $\theta$ were set to reflect empirical data on length-specific vulnerability of pike in angling fisheries (Pierce et al. 1995; Pierce and Cook 2000). Accordingly, pike smaller than 20 cm in total length were invulnerable and pike larger than 50 cm were assumed to be fully vulnerable. Catchability $q$ in pike is density-independent (Pierce and Tomcko 2003). The value of $q$ in the present model was determined from a field study on pike recreational angling conducted by Arlinghaus et al. (unpublished data) that also utilized natural baits to capture pike. The value found in this study ranged among the highest values for $q$ reported by Pierce and Tomcko (2003). However, Pierce and Tomcko (2003) only used artificial lures. Catchability of pike is typically higher for natural baits, which are commonly used in many pike fisheries (Beukema 1970; Arlinghaus et al.

2008). This justifies our choice for the catchability parameter. Hooking mortality rate $\varphi$ was estimated conservatively based on the maximum value published in Munoeke and Childress (1994) for esocids. Noncompliance rate was treated as a dynamic variable depending on the catch rate of undersized fish following Sullivan (2002). He found that $Q$ was inversely related to the anglers' catch rate of undersized walleye (*Sander vitreum*). No investigations were available for pike. Therefore, the same functional relationship was assumed for pike fisheries as anecdotal evidence suggests similar relationships in many fisheries.

Anglers respond dynamically to changing catch qualities (Post et al. 2003). Without quantitative information available to model the effort-response curve in pike fisheries, the coefficients in the modified model of Post et al. (2003) were chosen to correspond with published work on absolute annual angling effort density $u$ in typical pike fisheries (Kempinger and Carline 1978; Pierce et al. 1995; Margenau et al. 2003). Accordingly, the maximum value for $u$ was set at 150 h ha$^{-1}$ year$^{-1}$. The sigmoid effort-response curve describes a relatively steep rise in effort with increased fish abundance (resulting from the positive effects of elevated catch rates on angler satisfaction, Arlinghaus 2006) and a flattening at high effort rates (resulting from the negative effect of crowding on angling experience). Exploitation of pike was modeled under different minimum-size limits *MSL*s a standard harvest regulation in pike fisheries world-wide.

**Table A1.** Life-history parameters for a pike (*Esox lucius* L.) population size-selectively exploited by anglers. Parameters for biological processes and for angling processes are presented in groups. Parameters with units indicated by '–' are dimensionless. Unit standardizing constants were included to remove units in empirically estimated relationships.

| Symbol | Value | Unit | Source |
|---|---|---|---|
| Biological processes | | | |
| $a_{\max}$ | 12 | year | Raat (1988) |
| Length-weight relationship | | | |
| $\alpha$ | $4.8 \times 10^{-6}$ | kg | Willis (1989) |
| $\beta$ | 3.059 | – | Willis (1989) |
| $L_u$ | 1 | cm | Standard unit |
| Growth | | | |
| $h$ | 16.725 (initial value in year $t$ = 1) | cm | Own calculations |
| $T$ | 1 | year | Raat (1988) |
| $h_{\max}$ | 27.094 | cm | Own calculations |
| $\gamma$ | 0.18190 | – | Own calculations |
| $\delta$ | 0.56783 | – | Own calculations |
| $D_u$ | 1 | kg ha$^{-1}$ | Standard unit |
| Fecundity | | | |
| $g$ | Default mean = 0.10 and SD = 0.015 | – | See text |
| $\rho$ | 0.04818 | ha kg$^{-1}$ | Craig and Kipling (1983) |
| $t_L$ | 2 | year | Craig and Kipling (1983) |
| $\omega$ | 1.22 | – | Diana (1983) |
| $W_E$ | $6.37 \times 10^{-6}$ | kg | Own calculations |
| Hatching rate | | | |
| $\psi$ | 0.735 | – | Franklin and Smith (1963) |
| Natural mortality | | | |
| $\tau$ | 1.0 | – | Own calculations |
| $\beta_0$ | 2.37 (small pike),<br>1.555 (large pike) | – | Haugen et al. (2007) |
| $\beta_X$ | −0.02 (small pike),<br>0.40 (large pike) | – | Haugen et al. (2007) |
| $\beta_Y$ | −0.29 (small pike),<br>−0.88 (large pike) | – | Haugen et al. (2007) |
| $\beta_L$ | 0.25 (small pike),<br>0.00 (large pike) | – | Haugen et al. (2007) |
| $s_{0,\max}$ | $4.76 \times 10^{-4}$ | – | exp($f_a$) in Minns et al. (1996) |
| $\kappa$ | 31.73 | – | $-f_b$ in Minns et al. (1996) |
| $\mu$ | 0.31 | – | $f_c$ in Minns et al. (1996) |
| $B_{1/2}$ | $1.68362 \times 10^9$ | ha$^{-1}$ | $f_d^{1/f_c}$ in Minns et al. (1996) |

| Symbol | Value | Unit | Source |
|---|---|---|---|
| Angling processes | | | |
| $\eta$ | 0.25 | $cm^{-1}$ | See text |
| $\theta$ | 1300 | – | See text |
| Catchability | | | |
| $q$ | 0.01431 | $ha\ h^{-1}$ | Own empirical value |
| Other fishing mortalities | | | |
| $\varphi$ | 0.094 | – | Munoeke and Childress (1994) |
| $Q$ | 0 (initial value in year $t = 1$) | – | Own calculations |
| $\varepsilon$ | 1.25 | – | Sullivan (2002) |
| $\zeta$ | −0.84 | – | Sullivan (2002) |
| Angling effort | | | |
| $u$ | varied up to 150 (default 100, if not varied) | $h\ ha^{-1}\ year^{-1}$ | See text |
| $p$ | 0.5 | – | See text |
| $N_{V,1/2}$ | 10 | $ha^{-1}$ | See text |
| $\xi$ | 5 | – | See text |
| $C_u$ | 1 | $h^{-1}$ | Standard unit |
| $MSL$ | varied (default 50, if not varied) | cm | See text |