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

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19

20 **Abstract**

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

37

38 **Introduction**

39 The potential for size-selective fishing to cause contemporary evolutionary changes in
40 adaptive traits has attracted considerable interest in recent years (Jørgensen et al. 2007;
41 Kuparinen and Merilä 2007). Fishing-induced selection has been identified as having
42 the capacity to change various life-history traits as well as morphological, behavioral,
43 and physiological traits (reviewed by Policansky 1993; Law 2000; Heino and Godø
44 2002; Dieckmann and Heino 2007; Hutchings and Fraser 2007; Kuparinen and Merilä
45 2007; Jørgensen et al. 2007; Uusi-Heikkilä et al. 2008; Hard et al. 2008). These changes
46 can affect stock properties such as yield, average biomass, average value of harvested
47 fish, catchability and stock recovery, and are also troublesome from the perspectives of
48 conservation and management when genetic change, as opposed to merely phenotypic
49 change, is involved (Heino 1998; Law 2000; Hutchings 2005; Conover et al. 2005;
50 Jørgensen et al. 2007; Allendorf et al. 2008; Enberg et al. 2009; Philipp et al. 2009,
51 Wang and Höök 2009).

52 Most studies estimating fishing-induced selection differentials acting on
53 adaptive life-history traits have focused on commercially exploited species (Rowell et
54 al. 1989; Rijnsdorp 1993a; Miller and Kapuscinski 1994; Sinclair et al. 2002; Williams
55 and Shertzer 2005; Andersen et al. 2007; Hutchings and Rowe 2008). This is surprising
56 given the popularity of recreational angling in all industrialized countries (Arlinghaus et
57 al. 2002). Lewin et al. (2006) summarized current knowledge on recreational angling
58 patterns and found that locally high annual exploitation rates of up to 80% and
59 pronounced selectivity for species, size, age, sex, and behavioral traits are common.
60 Therefore, recreational fishing might exert similar directional selection pressures on
61 adaptive traits as previously identified for commercially exploited stocks (e.g., Heino

62 1998; Swain et al. 2007; Thériault et al. 2008; Darimont et al. 2009; Philipp et al. 2009;
63 Redpath et al. 2009). Yet, little is known as to whether this is actually the case (Cooke
64 and Cowx 2006; Lewin et al. 2006).

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

81 Alternatively, life-history models can be used to study selection differentials and
82 responses to fishing. In commonly used evolutionary optimization models (Hutchings
83 1993a; Rijnsdorp 1993a; for other examples see Stokes et al. 1993), specific trait values
84 are determined that maximize a chosen measure of fitness (usually, lifetime
85 reproductive success or the population-level intrinsic rate of increase; Stearns 1992;

86 Roff 2002). Such optimization models, however, usually do not incorporate density-
87 dependent and frequency-dependent ecological feedback (e.g., Heino et al. 1998;
88 Meszéna et al. 2001; Dieckmann and Ferrière 2004), which are crucial factors
89 determining fisheries-induced selection. More recently, individual-based eco-genetic
90 models (Dunlop et al. 2007, 2009; Thériault et al. 2008; Enberg et al. 2009; Wang and
91 Höök 2009), other types of individual-based models (Kristiansen and Svåsand 1998;
92 Martínez-Garmendia 1998; Williams and Shertzer 2005; Brown et al. 2008), and age-
93 structured models (Hilborn and Minto-Vera 2008) have been used for investigating
94 selection differentials and responses in adaptive traits induced by fishing. However,
95 individual-based models in particular are computationally expensive, which could limit
96 their application by a wider community of users including fisheries managers.

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

110 vulnerable fish in a stock, and thus meets an important prerequisite for appropriate
111 models of recreational fisheries (Radomski and Goeman 1996; Post et al. 2003).

112 After introducing the general framework, we apply our model to study the
113 adaptation of annual reproductive investment in a hypothetical pike (*Esox lucius* L.)
114 population. This fish species was chosen because pike is of high interest to anglers
115 across the northern hemisphere (Pierce et al. 1995; Arlinghaus and Mehner 2004) and
116 since it is highly vulnerable to angling (Paukert et al. 2001). Annual reproductive
117 investment was chosen as the life-history trait under selection because less attention in
118 the literature has as yet been given to this trait, compared to growth rate, age and size at
119 maturation, or probabilistic maturation reaction norms (Jørgensen et al. 2007). We
120 tested the prediction that angling selects for increased annual reproductive investment at
121 age in size-selectively exploited pike populations. This is expected because individuals
122 investing more of their surplus energy into reproduction at any age will have a selective
123 advantage under conditions of reduced adult survival (Reznick et al. 1990; Hutchings
124 1993b).

125 **Materials and Methods**

126 **Modeling framework**

127 We developed an age-structured population model for recreational fishing because
128 demographic processes and selection pressures caused by fishing depend on the age and
129 body size of individuals (e.g., Reznick et al. 1990; Conover et al. 2005). Age-structured
130 population models were chosen for this study because these have been widely accepted

131 as the simplest representation of structured population dynamics in fisheries and are
132 commonly used by fisheries managers (Hilborn and Walters 1992).

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

152 In the present model, the fish population is allowed to be polymorphic in the
153 considered adaptive trait (here, annual reproductive investment) and is assumed to be at
154 demographic equilibrium. At equilibrium, the density and the age and size composition

155 reflect the density dependence of demographic processes such as fecundity, growth, and
156 mortality, and the amount of fishing effort exerted for a given value of the adaptive trait,
157 thus setting the population dynamical context and ecological environment for fishing-
158 induced selection. The ecological environment, in turn, affects the current fitness
159 landscape on which the adaptive trait evolves. The resulting fitness function becomes
160 nonlinear as the result of the complex interaction of trait values and density-dependent
161 processes. By calculating the fitness for each trait value at demographic equilibrium and
162 weighing the distribution of trait values by their fitness, selection differentials are
163 computed as the difference in mean trait value before and after selection (Fig. 1).

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

174 **Population dynamics**

175 We use deterministic Leslie-matrix population models because of their common
176 application in fish population modeling and their ease of construction (Caswell 2001).
177 Such models classify the individuals of a population into age classes and project the
178 abundances in these classes in discrete time. The model detailed below is intended to be

179 applied to fish species with a single breeding season per year, which is common in
 180 temperate regions (Wotton 1998), so that annual time steps can be used. We assume a
 181 polymorphic population in the considered adaptive trait x . Changes in the age structure
 182 and density of fish with trait value x are thus described by $N'(x) = K(x, E)N(x)$ or

$$\begin{matrix}
 183 \\
 184
 \end{matrix}
 \begin{pmatrix}
 N'_1(x) \\
 N'_2(x) \\
 N'_3(x) \\
 \dots \\
 N'_{a_{\max}}(x)
 \end{pmatrix}
 =
 \begin{pmatrix}
 f_1(x, E)s_0(x, E) & f_2(x, E)s_0(x, E) & \dots & \dots & f_{a_{\max}}(x, E)s_0(x, E) \\
 s_1(x, E) & 0 & \dots & \dots & 0 \\
 0 & s_2(x, E) & \dots & \dots & 0 \\
 \dots & \dots & \dots & \dots & \dots \\
 0 & 0 & \dots & s_{a_{\max}-1}(x, E) & 0
 \end{pmatrix}
 \begin{pmatrix}
 N_1(x) \\
 N_2(x) \\
 N_3(x) \\
 \dots \\
 N_{a_{\max}}(x)
 \end{pmatrix}
 \quad (1)$$

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

199 variance $\sigma_p^2 = \int (x - \bar{x})^2 p(x) dx$. The density of one age class in the entire resident
200 population is described as $N_a = \int N_a(x) dx$.

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

206 **Selection differentials**

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

215 To estimate demographic equilibrium, we assume a polymorphic resident
216 population with trait values x being normally distributed around the population mean
217 \bar{x} with phenotypic variance σ_p^2 . Compared with a monomorphic population with the
218 same mean, a polymorphic population experiences different eco-evolutionary feedback
219 and "samples" the nonlinear fitness landscape over a range of trait values around the
220 mean. Fitness is determined by the vital rates f_a and s_a in the Leslie matrix, which are

221 functions of the trait value x , the total population biomass density D , and the resultant
222 angling effort. The vital rates are thus varying with time until they reach demographic
223 equilibrium.

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

$$242 \quad S = \frac{\int x\lambda(x)p(x)dx}{\int \lambda(x)p(x)dx} - \bar{x}. \quad (2)$$

243 Over a single generation, the expected evolutionary response R in a trait depends on
244 the selection differential S and the heritability h^2 of the trait, which are related
245 according to the breeder's equation $R = h^2 S$ (Falconer and Mackay 1996). In the
246 present study, however, the selection response R is not calculated since we focus on the
247 initial selection pressure.

248 To standardize the selection differentials, so as to facilitate comparisons of
249 model predictions with field estimates and to allow comparisons of model predictions
250 across different traits and stocks, three standardized measures are commonly applied:
251 (1) proportional change in average trait value, $S_{\text{std}}^{(1)} = S / \bar{x}$ (Roff 2002); (2) standard-
252 deviation-standardized selection differential, $S_{\text{std}}^{(2)} = S / \sigma_p$ (Lande and Arnold 1983;
253 Kingsolver et al. 2001; alternatively termed variance-standardized selection gradient by
254 Hereford et al. 2004); and (3) mean-and-variance-standardized selection differential,
255 $S_{\text{std}}^{(3)} = S\bar{x} / \sigma_p^2$ (alternatively termed mean-standardized selection gradient by Hereford et
256 al. 2004). In the present study, we compute and report the mean-and-variance-
257 standardized selection differential (hereafter termed standardized selection differential,
258 S_{std}). This measures the proportional change in fitness for a proportional change in trait
259 value and thus provides an elasticity (i.e., proportional sensitivity) measure of the
260 selection differential (Caswell 2001; Hereford et al. 2004).

261 The method summarized above calculates selection differentials per year. When
262 selection differentials per generation are needed, e.g., for comparison with field
263 estimates of strength of selection, they can be calculated using the dominant eigenvalue
264 of the matrix $K^{t_G(x,E)}(x, E)$ instead of $K(x, E)$. $t_G(x, E)$ is the population's generation

265 time calculated as $t_G(x, E) = \sum_{a=1}^{a_{\max}} l_a f_a a / \sum_{a=1}^{a_{\max}} l_a f_a$, where l_a is the probability of
 266 survival until age a and f_a is fecundity as defined in equation (1).

267 **Biological processes**

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

271 Growth is modeled according to the biphasic growth model by Lester et al.
 272 (2004). This model explicitly considers the annual energetic demand imposed by
 273 reproduction, which is assumed to be constant across mature age classes. Lester et al.
 274 (2004) showed that the von Bertalanffy growth equation provides a good description of
 275 post-maturation somatic growth in freshwater fish. However, immature fish invest all
 276 surplus energy into somatic growth. Hence, growth does not follow the von Bertalanffy
 277 growth model across all ages, and instead is almost linear until the age T at which
 278 allocation of energy to reproduction begins (Lester et al. 2004), resulting in an annual
 279 growth rate

$$280 \quad L_{a+1} - L_a = \begin{cases} h & \text{for } a < T \\ h - \frac{g}{g+3}(L_a + h) & \text{for } a \geq T \end{cases}, \quad (3a)$$

$$281 \quad L_0 = 0, \quad (3b)$$

282 where L_a is length at age a , and h is the annual length increment of immature fish
 283 (Lester et al. 2004, Fig. S1a). The annual reproductive investment g is represented as
 284 an energy-weighted gonado-somatic index (GSI) calculated as gonad weight divided by

285 somatic weight multiplied by a factor ω that accounts for the higher energy content of
 286 gonadic tissue relative to somatic tissue (Lester et al. 2004), $g = \omega GSI$. For conversions
 287 from length to weight, the empirical allometric relationship

$$288 \quad W_a = \alpha(L_a / L_u)^\beta \quad (4)$$

289 is used, where W_a is somatic weight at age a , L_u is a unit-standardizing constant, and
 290 α and β are empirical parameters defining the relationship. Total biomass density D
 291 of the population is the sum of biomasses across all age classes and phenotypes,

$$292 \quad D = \sum_{a=1}^{a_{\max}} \int W_a(x) N_a(x) dx . \quad (5)$$

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

$$299 \quad h = \frac{h_{\max}}{1 + \gamma(D / D_u)^\delta}, \quad (6)$$

300 where γ and δ define the relationship, D_u is a unit-standardizing constant, and h_{\max} is
 301 the maximum immature annual length increment at $D = 0$ (Fig. S1b). As seen from
 302 equation (3a), density-dependent immature growth also determines post-maturation
 303 growth.

304 We assume that fecundity diminishes with population density, as elevated food
 305 competition with increasing fish density can reduce surplus energy and energy invested

306 in gonad development (Craig and Kipling 1983; Edeline et al. 2007). Maximum
 307 fecundity at $D=0$ depends on reproductive investment g , because g sets an upper
 308 limit on the production of eggs (Roff 1983; Lester et al. 2004). The age-specific
 309 fecundity, f_a , expressed in terms of hatched larvae, is 0 for $a \leq T$ and is defined for
 310 $a > T$ as

$$311 \quad f_a = \psi \frac{gW_a}{2\omega W_E} \exp(-\rho\tilde{D}), \quad (7)$$

312 where ψ is the survival until hatching, ω is the relative caloric density of eggs
 313 compared to soma, W_E is the average egg weight, and $\exp(-\rho\tilde{D})$ describes a decrease
 314 of fecundity with increasing fish population density \tilde{D} (Fig. S1c). The tilde indicates
 315 that f_a is influenced by \tilde{D} with a time lag of t_L years (Appendix A). $(gW_a)/(\omega W_E)$ is
 316 the maximum number of eggs produced by a female at $\tilde{D}=0$, which is divided by 2
 317 because only half of a particular age class are assumed to be females. Total hatched egg
 318 density (i.e., larval density) B of the population is the sum of age-specific fecundities
 319 across all age classes and trait values,

$$320 \quad B = \sum_{a=T+1}^{a_{\max}} \int f_a(x) N_a(x) dx. \quad (8)$$

321 Recruitment from egg hatching to age 1 is assumed to be density-dependent as a
 322 result of competition and cannibalism. Following an empirical relationship reported by
 323 Minns et al. (1996) for our species of interest (pike), the survival rate s_0 from egg
 324 hatching to age 1 is assumed to depend on the density of hatched larvae following a
 325 dome-shaped relationship with overcompensation (Fig. S1d),

$$326 \quad s_0 = s_{0,\max} \exp(-\kappa G(B)), \quad (9)$$

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

$$330 \quad G(B) = \frac{B^\mu}{B^\mu + B_{1/2}^\mu}, \quad (10)$$

331 where μ is an exponent determining the rapidity of the transition between $s_{0,\max}$ and
 332 $s_{0,\min}$ through changes in hatched larvae density, and $B_{1/2}$ is the density of hatched
 333 larvae at which $s_0 = s_{0,\max} \exp(-\kappa/2)$.

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

$$338 \quad M_a = \begin{cases} M_b & \text{for } a < T \\ M_b + \tau g & \text{for } a \geq T \end{cases}, \quad (11)$$

339 where τ is a constant (Fig. S1e). The rationale in including τg is an assumed trade-off
 340 between reproductive investment and survival that can result for example from an
 341 inverse relation between current reproductive effort and post-reproduction condition and
 342 survival (Hirshfield 1980; Wootton 1998). For the baseline mortality M_b , we use
 343 empirical relationships representing density-dependent and size-dependent mortalities
 344 (e.g., due to cannibalism) reported by Haugen et al. (2007) for our focal species, pike
 345 (Appendix A). It follows that s_a is given by

$$346 \quad s_a = \exp(-(M_a + F_a)). \quad (12)$$

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

350 **Angling processes**

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

$$355 \quad V_a = [1 - \exp(-\eta L_a)]^\theta, \quad (13)$$

356 where V_a is the vulnerability of fish of age a with length L_a , and η and θ describe the
357 shape of the relationship (Fig. S1f). The total density N_V of vulnerable fish in the
358 population is then given by summing across all age classes and trait values,

$$359 \quad N_V = \sum_{a=1}^{a_{\max}} \int V_a(x) N_a(x) dx. \quad (14)$$

360 A realistic expectation about angler behavior is a response of angling effort E to
361 the perceived quality of the fishery (Johnson and Carpenter 1994; Cox and Walters
362 2002). As the quality of fishing measured in terms of angler satisfaction is often catch-
363 dependent (Arlinghaus and Mehner 2005; Arlinghaus 2006), increasing numbers of
364 vulnerable fish are expected to increase the number of anglers spending effort on a
365 particular fishery (Cox et al. 2003). As empirical information on this effort dynamic is
366 not available for many fisheries, a generic sigmoid numerical response of angling effort
367 density A to fish availability, modified from Post et al. (2003), was chosen,

$$368 \quad A = u \left(p + \frac{N_V^\xi}{N_V^\xi + N_{V,1/2}^\xi} (1 - p) \right), \quad (15)$$

369 where u is the maximum effort density, p is the effort proportion of u that is always
 370 present, $N_{V,1/2}$ is the density of vulnerable fish that elicits one-half of the effort density,
 371 and ξ is an exponent that characterizes the steepness of the effort-response curve (Fig.
 372 S1g). Note that this model ignores regional angler dynamics, i.e., anglers here choose a
 373 particular water body depending only on the quality of its fishery (Post et al. 2003).

374 In most recreational fisheries, some variants of size-based harvest regulations are
 375 used to maintain recruitment, manipulate the size structure of the fish stocks, or
 376 distribute the harvest more equitably among anglers (Arlinghaus et al. 2002). Therefore,
 377 anglers may voluntarily or mandatorily release a certain proportion of fish (Arlinghaus
 378 et al. 2007). In our model, a minimum-size limit MSL is assumed, above which every
 379 caught fish is removed for consumption. This situation is characteristic for purely
 380 consumptive recreational fisheries in countries such as Germany, where catch-and-
 381 release fishing is often not tolerated (Arlinghaus 2007). However, the situation is
 382 different in many other fisheries in which large percentages of legally sized fish are
 383 released (Arlinghaus et al. 2007). In our model, catch-and-release fishing only applies to
 384 undersized fish. However, anglers may also illegally harvest undersized fish (Sullivan
 385 2002). Therefore, in our model three sources of fishing mortality are considered (Post et
 386 al. 2003): harvest mortality of fish exceeding the minimum-size limit, hooking mortality
 387 of fish caught undersized and then released, and non-compliance mortality from illegal
 388 harvest of undersized fish. On this basis, the density of dead fish D_a at age a is given
 389 by

$$390 \quad D_a = \begin{cases} V_a N_a [1 - \exp(-qA)] & \text{for } L_a \geq MSL \\ V_a N_a [1 - \exp(-qAU)] & \text{for } L_a < MSL \end{cases}, \quad (16)$$

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

$$392 \quad U = \phi + Q - \phi Q, \quad (17)$$

393 where ϕ is the proportion of fish below the minimum-size limit that experience hooking
 394 mortality from catch-and-release fishing, and Q is the proportion of fish below the
 395 minimum-size limit that are harvested illegally. The non-compliance mortality Q was
 396 treated as a dynamic variable following Sullivan (2002), who found that in walleye
 397 (*Sander vitreum*) angling it was inversely related to the angling catch rate C_r of
 398 undersized fish,

$$399 \quad Q' = \varepsilon (C_r / C_u)^\zeta, \quad (18)$$

400 where ε and ζ are empirically derived constants defining the relationship and C_u is a
 401 unit-standardizing constant. As the prime indicates, we assume that the catch rate of
 402 undersized fish influences the non-compliance mortality by anglers in the following
 403 year. Note that the parameter ζ is negative, so that the non-compliance mortality
 404 declines as the catch rate C_r of undersized fish increases (Fig. S1h). The catch rate C_r
 405 of undersized fish,

$$406 \quad C_r = A^{-1} \sum_{a=1}^{a_{\max}} \int c_a(x) dx, \quad (19)$$

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

$$408 \quad c_a = \begin{cases} 0 & \text{for } L_a \geq MSL \\ D_a / U & \text{for } L_a < MSL \end{cases}, \quad (20)$$

409 where A is angling effort density and U is the proportion of fish below the minimum-
410 size limit that experience either hooking mortality or non-compliance mortality. The
411 instantaneous angling mortality F_a at age a is then

$$412 \quad F_a = -\ln(1 - D_a/N_a). \quad (21)$$

413 **Outline of analysis**

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

419 The analysis then proceeded in three steps:

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

- 431 • Second, the minimum-size limit was varied for different angling intensities to
432 investigate the potential of simple standard harvest regulations to counteract
433 angling-induced selection on reproductive investment.
- 434 • Lastly, we conducted a series of analyses to estimate the robustness of our model
435 to examine how the results are affected by some of the most critical underlying
436 assumptions. We first examined how incorporation of density dependence in
437 relative fecundity, somatic growth, and natural mortality affected predicted
438 selection differentials. We then examined how selection differentials changed
439 over time rather than only examining the situation at demographic equilibrium.
440 We also relaxed the assumption of deterministic population dynamics by
441 incorporating stochasticity in recruitment and examining the resultant impact on
442 the predicted selection differentials. Finally, the sensitivity of results to
443 individual parameters was assessed by varying parameters by 5% and
444 calculating the resultant percentage of change in the predicted selection
445 differentials.

446 **Results**

447 Pike populations size-selectively exploited by anglers equilibrate after about 20 years at
448 much reduced abundance density as compared with the unexploited case (Fig. 2). This
449 corresponds to a biomass density between 4.5 and 9.9 kg ha⁻¹ compared to 15.8 kg ha⁻¹
450 in the unexploited case. Increasing angling effort results in monotonically increasing
451 annual angling exploitation rates of up to 66.5% of fish larger than the minimum-size
452 limit and of up to 22.4% for fish aged 1 or older (Table 1). Note that in Table 1 A (total

453 angling effort per area at demographic equilibrium) differs from u (maximum angling
454 effort per area) owing to the density dependence of angling effort. The resulting
455 demographic equilibrium represents the ecological environment that determines the
456 selection differentials on reproductive investment exerted by size-selective recreational
457 fishing.

458 At demographic equilibrium, size-selective angling induces positive selection
459 differentials on annual reproductive investment for wide ranges of average reproductive
460 investment values (Fig. 3a). Selection differentials increase with angling intensity and
461 the associated higher annual exploitation rates (Fig. 3a; Table 1). Positive selection
462 differentials would cause the mean phenotype to increase, whereas negative selection
463 differentials would cause it to decrease. The phenotype at which such directional
464 selection ceases (and only stabilizing selection remains) is the evolutionarily stable
465 strategy (ESS). It occurs where the curve of selection differentials intersects with the
466 horizontal axis (Fig. 3a). These intersections thus describe the expected endpoints of
467 angling-induced evolution for different angling intensities. Accordingly, intensive
468 recreational angling selects for increased annual reproductive investment, with
469 evolutionary endpoints ranging from $g = 0.10$ in the absence of angling to $g = 0.23$ at
470 $u = 150 \text{ h ha}^{-1} \text{ yr}^{-1}$ (Fig. 3a) and up to $g = 0.44$ under extreme exploitation (Fig. 3b).

471 Note that at particular conditions the selection differential exhibits jumps, for
472 example, at a mean reproductive investment of 0.14 and 0.17 for $u = 125 \text{ h ha}^{-1} \text{ yr}^{-1}$ and
473 $u = 150 \text{ h ha}^{-1} \text{ yr}^{-1}$, respectively (Fig. 3a). This can be understood by appreciating the
474 complex interplay among the size variation caused by polymorphism in g , size-
475 dependent angling, and density-dependent growth. For example, when the population
476 mean g takes a particular value, a component of a particular age class comprising fish

477 with high g values can remain below the minimum-size limit, resulting in positive
478 selection differentials. However, this situation is limited to a small range of the
479 population's mean g . As the population mean of g increases, a greater component of
480 the considered age class stays smaller than the minimum-size limit. This in turn results
481 in an increase of the population biomass, which further reduces the size of some
482 phenotypes due to density-dependent growth. Eventually, all individuals of one
483 particular age class may remain smaller than the minimum-size limit, causing the
484 selection differential to decrease. As shown in Fig. 3a, however, these irregular patterns
485 for particular situations do not change the general result of stabilizing selection on
486 reproductive investment in response to varying levels of angling intensity.

487 To address the second objective of our study (i.e., to investigate the potential for
488 standard harvest regulations to counteract recreational fishing-induced selection), we
489 analyzed the effects of changing harvest regulations on the selection differentials acting
490 on annual reproductive investment (Fig. 4). Increasing minimum-size limits decrease
491 the strength of angling-induced evolution. Although minimum-size limits generally
492 reduce selection pressures, some irregular patterns with increases in selection
493 differentials are visible in Fig. 4, for example, at a maximum angling effort level of
494 $u = 50 \text{ h ha}^{-1} \text{ yr}^{-1}$ and a minimum-size limit of 70 cm. The increase in the selection
495 differential at this parameter combination is caused by part of an age class being saved
496 from harvest as described before, which does not change the general observation that
497 increasing minimum-size limits reduce selection pressures. These findings are strongly
498 dependent on levels of angling effort. Increasing minimum-size limits at high angling
499 effort leads to more drastic reductions in the selection differentials than it does at low
500 angling effort. It is important to note that even under extremely high minimum-size

501 limits (corresponding to total catch-and-release fishing) there are always positive
502 selection differentials on annual reproductive investment, so that recreational fishing-
503 induced selection cannot be avoided by standard harvest regulations alone.

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

513 The situation is different for density-dependent growth. In simulations without
514 density-dependent growth, the predicted selection differentials and evolutionary
515 endpoints are larger or smaller than in simulations with density-dependent growth. The
516 direction of change depends on whether the density-independent immature growth rate
517 is higher or lower than the one in the density-dependent case at equilibrium. What is
518 particularly noticeable is that jumps in the selection differentials are more prominent
519 under density-independent growth than under density-dependent growth. Large
520 selection differentials occur when there is a large fitness advantage for part of an age
521 class to stay below the minimum-size limit by increasing reproductive investment and
522 thus reducing growth. Under density-dependent growth, ecological feedback resulting
523 from increased population density in response to some fish escaping harvest reduces
524 growth further, eventually saving an entire age class from harvest. This reduces

525 selection differentials on reproductive investment. Such feedback mechanisms do not
526 occur under density-independent growth, which explains the more pronounced increases
527 in selection pressures in Fig. 5. Our model is thus sensitive to assumptions about
528 density-dependent growth. Ignoring density dependence in growth may thus result in
529 erroneous predictions about the strength of selection and the predicted evolutionary
530 endpoints.

531 Support for our deterministic approach to estimate selection differentials in
532 response to size-selective recreational fishing was obtained when stochasticity in
533 recruitment was introduced to the model and the resulting dynamics in selection
534 differentials were examined. As shown in Fig. 6, stochastic recruitment results in
535 largely constant selection differentials, except for short-term irregularities that are not
536 correlated with population abundance (Pearson product-moment correlation coefficient
537 $r = -0.09$, with $p = 0.35$). The largely constant selection pressures provide support for
538 the simplifying assumption of deterministic population dynamics.

539 Finally, we examined the model's sensitivity to individual parameters. For most
540 parameters, model predictions were robust to changes in parameter values (Fig. 7). 5%
541 changes in each of the parameters resulted in changes in the predicted standardized
542 selection differential of less than 5% in all parameters except β , τ , and μ . β is the
543 exponent in the length-weight regression, μ is the exponent in the stock-recruitment
544 relationship determining density-dependent larval survival, and τ is a parameter
545 determining the relationship between reproductive investment and natural mortality,
546 which represents the immediate cost of reproduction. Changes of these parameters thus
547 influence fecundity and/or mortality, and in turn fitness and selection differentials.
548 Among the parameters characterizing the angling fishery, q (catchability) and p

549 (proportion of maximum angling effort always present) were found to be particularly
550 sensitive for prediction of selection pressures. This calls for more accurate
551 determination of these parameters if our model is to be applied to real fisheries.

552 **Discussion**

553 The primary purpose of this study was to demonstrate how an age-structured fish
554 population model incorporating density dependence as a crucial aspect of population
555 dynamics can be used to estimate selection differentials caused by size-selective
556 recreational angling. We illustrated our model's applicability with a hypothetical size-
557 selective angling fishery for pike, investigating reproductive investment as the adaptive
558 trait under selection. We showed that angling mortality exerts a positive directional
559 selection pressure on annual reproductive investment and analyzed how the strength and
560 direction of standardized selection strength depends on the pattern of exploitation, the
561 level of angling mortality, and the mean trait value. The selection differential is positive
562 and largest in a population with low average reproductive investment and rises with
563 increased angling mortality and decreased minimum-size limit. Model predictions are
564 sensitive to assumptions about density dependence in growth, a common process in
565 most fish stocks (Lorenzen and Enberg 2002). This justifies the methodological choice
566 of including multiple eco-evolutionary feedbacks for estimating ecology-driven fitness
567 functions. Inclusion of multidimensional density dependence renders the problem
568 intractable through fitness optimization principles. Therefore, a numerical approach to
569 estimate fishing-induced selection is needed and justified. It is important to note that our
570 model estimates initial selection strength and not subsequent evolutionary rates.
571 Determining evolutionary rates would depend on the calculation of selection responses,

572 which are the product of selection differentials and heritabilities (Hilborn and Minte-
573 Vera 2008).

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

590 Increased reproductive investment as an evolutionary response to angling results
591 from the life-history trade-off between investing surplus energy into either current or
592 future reproduction. One of the costs associated with investment into current
593 reproduction is decelerated somatic growth, which reduces future reproductive output
594 (Roff 1983; Lester et al. 2004). However, in an environment in which larger or older
595 fish face high mortalities, as when anglers heavily crop a stock of pike in a size-

596 selective manner, betting on future reproduction by investing surplus energy into growth
597 may not pay off. Instead, individual fitness can be raised by investment into current
598 reproduction, through gonads and/or spawning and mating behavior. Reduced somatic
599 growth due to such investment may even further reduce exposure to size-selective
600 angling. Indeed, theoretical studies have shown that increased annual reproductive
601 investment is expected under conditions of elevated adult mortality (Law 1979; Roff
602 1992), and empirical evidence in various fish species (Reznick et al. 1990; Rijnsdorp
603 1993b; Hutchings 1993b; Rochet et al. 2000; Yoneda and Wright 2004; Rijnsdorp et al.
604 2005; Thomas et al. 2009), including pike (Diana and Mackay 1979; Diana 1983;
605 Edeline et al. 2007), has supported this. Such adaptive changes increase the fitness of
606 individual fish in the exploited stock, but – in the long run – may be harmful to the
607 population as a whole, because these changes can be maladaptive with regard to natural
608 selection pressures (Conover et al. 2005). They may also reduce the socio-economic
609 value of the fishery, because the size of harvested fish may shrink (Jørgensen et al.
610 2007).

611 Our results indicate that saving a greater proportion of adult fish through
612 increased minimum-size limits can greatly reduce the selective pressures exerted by
613 anglers. This is good news for the fisheries manager and is in agreement with other
614 research on fishing-induced evolution pointing to the possibility of counteracting
615 fishing-induced adaptive changes through appropriate harvest regulations (Conover and
616 Munch 2002; Ernande et al. 2004; Baskett et al. 2005) or gear choices (Jørgensen et al.
617 2009). However, it is also important to realize that selection differentials were positive
618 even when the minimum-size limit was high, thus mimicking a total regulatory catch-
619 and-release fishery. The reason why some selective pressures persist even under such

620 very restrictive harvest regulations is that unwanted hooking mortality (Arlinghaus et al.
621 2007; Coggins et al. 2007) and/or illegal harvest (Sullivan 2002) will still take place.
622 Both of these common types of “cryptic” (Coggins et al. 2007) angling mortalities were
623 incorporated into our model of a recreational fishery, resulting in positive directional
624 selection on reproductive investment being predicted even for a total catch-and-release
625 pike fishery.

626 How strong are the selection pressures induced by a recreational angling fishery
627 relative to natural selection pressures? Hereford et al. (2004) and Stinchcombe (2005)
628 suggested that the mean-and-variance-standardized selection differential $S_{\text{std}} = S\bar{x} / \sigma_p^2$
629 is an appropriate measure of the strength of selection on adaptive traits, as this
630 dimensionless measure is insensitive to changes in a trait’s variability. This measure,
631 S_{std} , has also an intuitive interpretation in terms of elasticity: changing the considered
632 trait value by a fraction f of the mean trait value causes fitness to increase by $S_{\text{std}}f$
633 (Hereford et al. 2004). For annual angling exploitation rates of legally sized pike of up
634 to 67%, we estimated mean-and-variance-standardized selection differentials of up to
635 0.60 per generation (Table 1). This means that doubling annual reproductive investment
636 would increase fitness by up to 60%. Hereford et al. (2004) conducted a meta-analysis
637 of available mean-and-variance-standardized selection differentials and reported a
638 median value of 0.48 for univariate traits. The strength of angling-induced selection on
639 annual reproductive investment reported here is thus comparable in magnitude to
640 natural selection pressures, neither being unusually low or unusually high. This
641 observation seems to disagree with a recent meta-analysis on phenotypic changes by
642 Darimont et al. (2009), who reported that human predators in general exerted
643 significantly greater phenotypic changes compared with both natural and non-

644 exploitative anthropogenic environmental changes. However, direct comparison of our
645 model with the findings by Darimont et al. (2009) is difficult for two reasons. First, the
646 meta-analysis by Darimont et al. (2009) includes many other traits in addition to
647 reproductive investment. The selection responses of those different traits to fishing will
648 very likely differ considerably, limiting the usefulness of grand averages across traits.
649 Second, Darimont et al. (2009) compared rates of long-term phenotypic changes in the
650 wild, which are jointly determined by evolutionary and/or ecological processes, while
651 we estimated initial selection strength on reproductive investment and did not analyze
652 the expected resultant long-term phenotypic changes.

653 Our analysis suggests that angling-induced selection on reproductive investment
654 in pike is moderately strong and positive, but we confined our analysis to this trait only.
655 Other studies on fisheries-induced evolution of life-history traits suggest that, in
656 addition to reproductive investment, other traits such as age and size at maturation can
657 evolve. In iteroparous species, evolution towards maturation at younger age and
658 smaller size in response to size-selective harvesting is likely and has been documented
659 repeatedly for various species (reviewed in Dieckmann and Heino 2007; Jørgensen et al.
660 2007; Hard et al. 2008). The room for evolution of age at maturation is limited for an
661 early maturing fish such as pike. However, Diana (1983) reported that in pike
662 populations exploited by anglers pike tended to mature earlier than in unexploited
663 reference lakes, but no attempt was made to control for the impact of relaxed density
664 dependence in high-exploitation lakes on age at maturation. Our model can and should
665 be extended in further studies to investigate selection on other traits, such as age and
666 size at maturation.

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

682 Second, many models of life-history evolution assume, like we did, that the main
683 trade-off in energy allocation is that between gonadic and somatic growth (Roff 1983;
684 Law and Grey 1989; Rowell 1993; see Heino and Kaitala 1999 for a review). Our model
685 incorporates an additional trade-off, between reproduction and survival, which may
686 arise, e.g., from intraspecific interactions on a spawning site or poor condition after
687 reproduction (Wootton 1998). Although this trade-off cannot be readily quantified for
688 pike populations, we considered its incorporation crucial since it is expected to imply
689 selection pressures naturally counteracting those originating from angling (Edeline et al.
690 2007). As expected, we found that this trade-off affects the dependence of the

691 evolutionarily stable strategy for annual reproductive investment on angling mortality
692 predicted by our model (Fig. 3).

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

702 Fourth, we used an empirical dome-shaped stock-recruitment function that
703 resembles a Ricker-type stock-recruitment relationship (Minns et al. 1996). Empirically
704 estimated parameter values for this function in pike were associated with large standard
705 errors (Minns et al. 1996). This uncertainty is an issue if our model is to be applied to
706 predicting selection differentials for a real fishery, since we found that the selection
707 differentials estimated with our model were sensitive to the exponent μ determining
708 density-dependent larval survival in the stock-recruitment relationship. There is thus a
709 need for improved long-term monitoring to reduce the uncertainty in parameter
710 estimates for stock-recruitment relationships in pike (and other fish species). Similarly,
711 when our model is applied to a particular fishery there is a need for a thorough
712 assessment of the exponent β in the length-weight regression, as this parameter exerts a
713 large influence on the predicted strength of selection. Fortunately, this is one of the
714 biological parameters that is most accurately estimated for a given population,

715 considering the high regression coefficients reported in the literature (0.95-0.99, Willis
716 1989).

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

727 To conclude, this study is the first attempt to estimate selection differentials on
728 life-history traits caused by recreational angling based on an ecologically realistic model
729 incorporating density-dependent effects resulting in density- and frequency-dependent
730 selection. Compared with traditional optimization models used for studying fishing-
731 induced selection (see examples in Stokes et al. 1993), the fitness function in our
732 approach is dynamically determined by the ecological environment through density-
733 dependent growth, survival, fecundity, angling effort, and non-compliance mortality.
734 Our model thus captures key ecological and fisheries-related mechanisms that
735 optimization models by definition cannot incorporate. Once some crucial biological and
736 fishery-related processes have been quantified from field data or compiled from the
737 literature, our approach is applicable to evaluate the vulnerability of a particular
738 recreational fishery to fishing-induced evolution. In the absence of long-term data to

739 quantify density dependence in recreationally exploited fish stocks, our model could be
740 further simplified by the omission of density-dependent mortality or fecundity, as our
741 analysis has shown that this would still yield valid approximations of the selection
742 differentials for reproductive investment induced by angling. Our approach may also be
743 valuable as an educational tool for managers, as a quantitative approach to evolutionary
744 impact assessment, and as an antidote to the belief that anglers are neither persistent nor
745 efficient enough to act as an evolutionary force.

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763

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- 1093

1094 **Table 1.** Relationships between the maximum annual angling effort per area (u ; unit h
1095 $\text{ha}^{-1} \text{yr}^{-1}$) and the resultant annual angling effort per area (A ; unit $\text{h ha}^{-1} \text{yr}^{-1}$), annual
1096 exploitation rate, and standardized selection differentials (per year and per generation)
1097 for annual reproductive investment in a size-selectively exploited pike population at
1098 demographic equilibrium. Default values are given in Table A1. The average value of
1099 annual reproductive investment g was the default value 0.1 at which the standardized
1100 selection differential S_{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_{std}	
		for pike older than 1 yr	for 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

1101

1102 **Figure captions**

1103 **Fig. 1.** Calculation of the selection differential S as the difference in trait means before
1104 and after selection. This is the last step in the general approach introduced in this
1105 article for estimating fishing-induced selection differentials from an age-structured
1106 life-history model. After compilation of life-history information and the
1107 specification of density dependences, the four steps involved are a) determination
1108 of the demographic equilibrium and thereby of the ecological environment in
1109 which fitness is considered, b) calculation of trait-specific fitness for the given
1110 ecological environment, c) transformation of the trait distribution before selection
1111 (continuous curve) into the trait distribution after selection (dotted curve) by
1112 weighting the former by trait-specific fitness (dashed curve) and normalizing the
1113 resultant distribution, d) calculation of the selection differential.

1114 **Fig. 2.** Population dynamics of pike at age 1 yr and older exploited at different
1115 intensities by anglers. Curves show the equilibration of abundance density over
1116 time for different levels of maximum angling effort per area and year (u ; unit h
1117 $\text{ha}^{-1} \text{yr}^{-1}$), with thicker curves corresponding to higher efforts. The corresponding
1118 annual exploitation rates at equilibrium are shown in Table 1 and default
1119 parameter values are listed in Table A1.

1120 **Fig. 3.** (a) Dependence of the standardized selection differential for annual reproductive
1121 investment g on the mean of g in a pike population size-selectively exploited by
1122 anglers at varying intensities (Table 1). Positive (negative) selection pressures are
1123 expected to increase (decrease) annual reproductive investment. Filled circles

1124 along the horizontal axis indicate the evolutionarily stable strategies at which
1125 selection pressures vanish. These vary with the maximum angling effort per area
1126 (u ; unit $\text{h ha}^{-1} \text{ yr}^{-1}$), with thicker curves corresponding to higher efforts. (b)
1127 Dependence of the evolutionarily stable strategy for g on the maximum angling
1128 effort per area. Default parameter values are listed in Table A1.

1129 **Fig. 4.** Influence of different minimum-size limits on the standardized selection
1130 differential for annual reproductive investment in a pike population size-
1131 selectively exploited by anglers. These vary with the maximum angling effort per
1132 area (u ; unit $\text{h ha}^{-1} \text{ yr}^{-1}$), with thicker curves corresponding to higher efforts. In
1133 the figure, the average value of annual reproductive investment g was the default
1134 value 0.1 at which the selection differential on g vanishes in the absence of
1135 angling pressure.

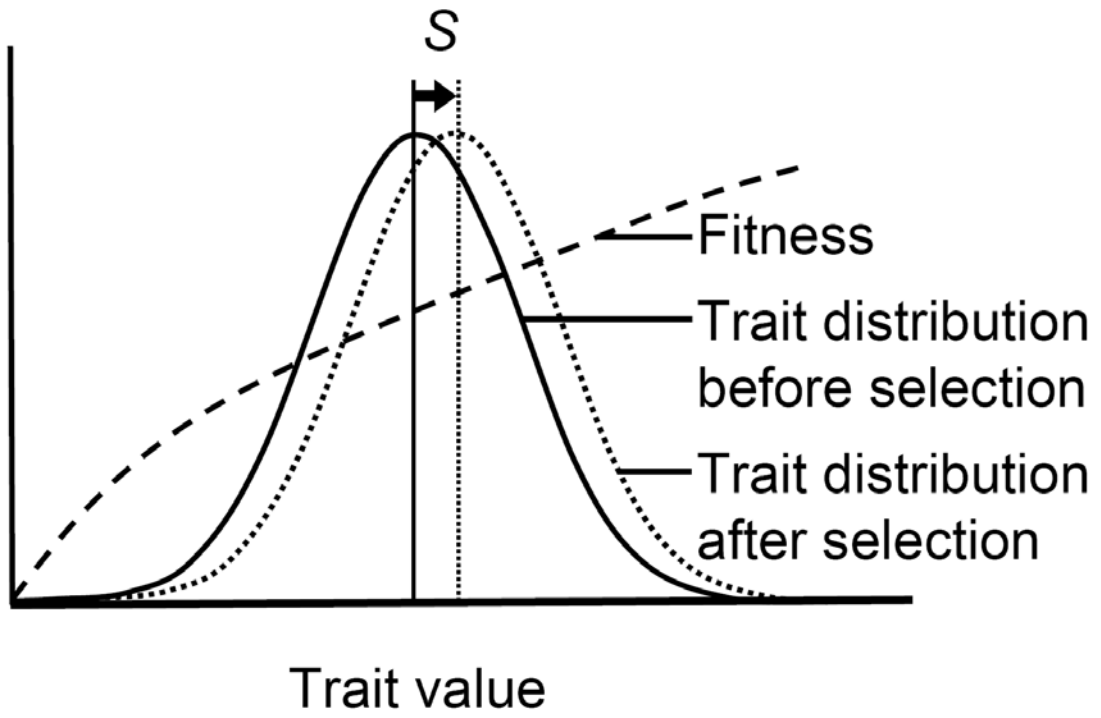
1136 **Fig. 5.** Influence of removed density dependence of either somatic growth (equation 6),
1137 relative fecundity (equation 7), or natural mortality (equation 11 and equation A1)
1138 relative to the baseline case with density dependence. Average values from
1139 empirical studies (Craig and Kipling 1983, Kipling 1983a) were used in density-
1140 independent cases, assuming (a) $h = 18.0$ cm and (b) $h = 16.0$ cm in equation (6),
1141 $\exp(-\rho D) = 0.79$ in equation (7), or $M_b = 0.23$ in equation (11). As in Fig. 3, the
1142 influence of the mean annual reproductive investment g in the resident condition
1143 on the standardized selection differential in a pike population size-selectively
1144 exploited by anglers was examined. The maximum angling effort per area was set
1145 at $u = 100 \text{ h ha}^{-1} \text{ yr}^{-1}$.

1146 **Fig. 6.** Influence of stochastic variations in the stock-recruitment relationship on (a)
1147 abundances of pike aged 1 yr and older and (b) standardized selection differentials.
1148 We assumed multiplicative lognormally distributed fluctuations around the
1149 deterministic recruitment in equation (8), $B = \exp(\nu) \sum_{a=T+1}^{a_{\max}} \int f_a(X) N_a(X) dX$,
1150 where ν is drawn randomly from a normal distribution with mean 0 and standard
1151 deviation $\sigma_\nu = 0.5$. The maximum angling effort per area was set at $u = 100$ h
1152 $\text{ha}^{-1} \text{yr}^{-1}$.

1153 **Fig. 7.** Sensitivity analysis of standardized selection differentials with respect to
1154 parameters that determine the dynamics of a pike population size-selectively
1155 exploited by anglers. Black (white) bars depict the relative change in standardized
1156 selection differentials when the corresponding parameter is increased (decreased)
1157 by 5%. For easier reference, the dashed vertical lines indicate the $\pm 5\%$ range for
1158 the relative change in standardized selection differentials. Default parameter
1159 values are listed in Table A1.

1160

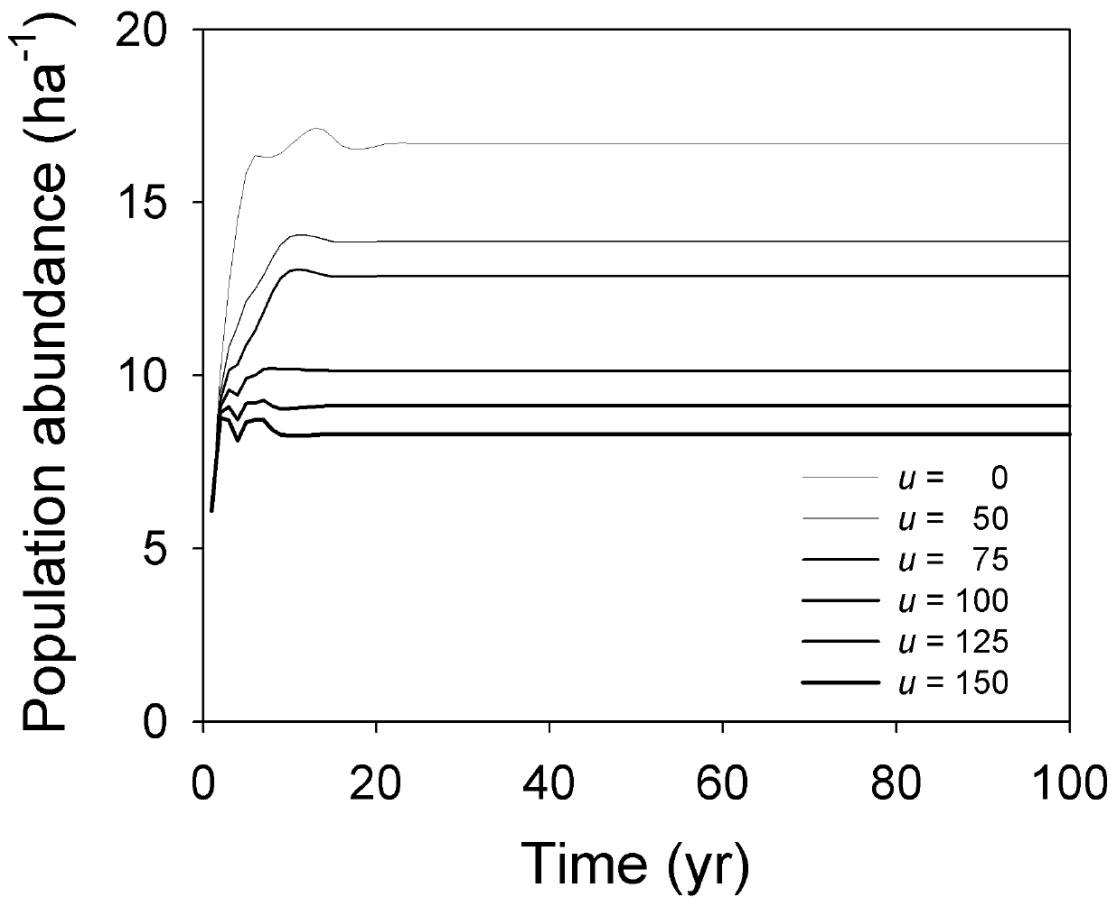
1161 **Fig. 1**



1162

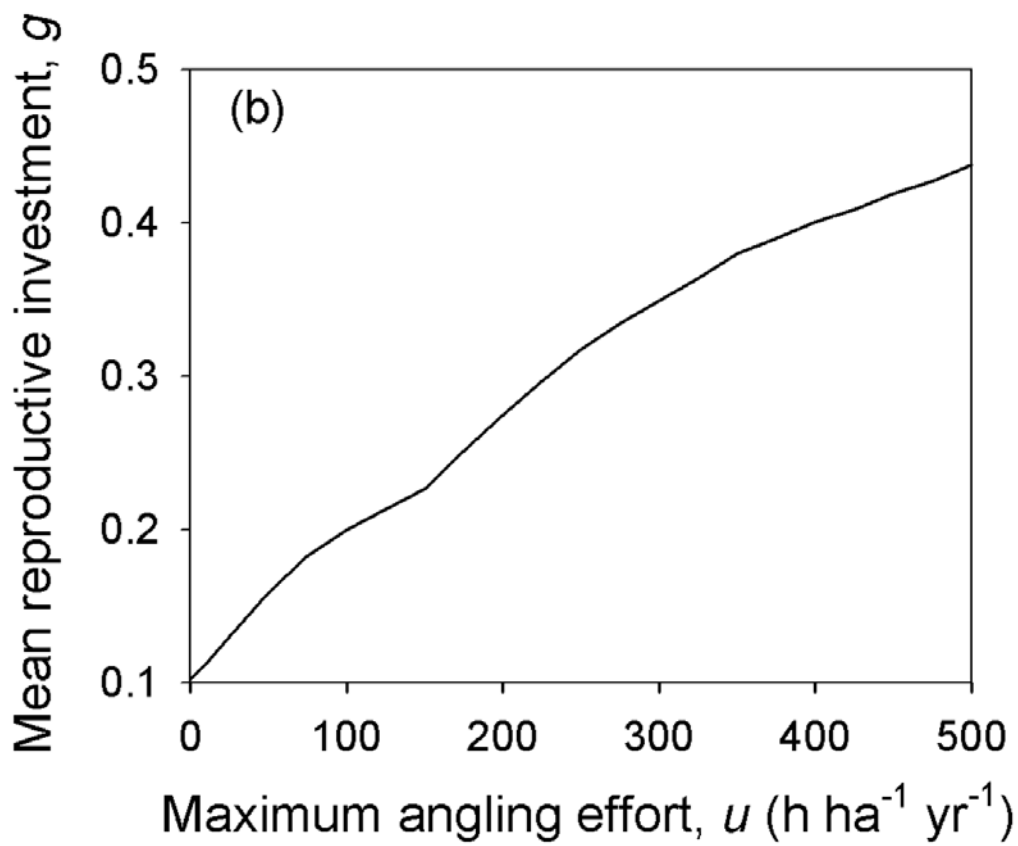
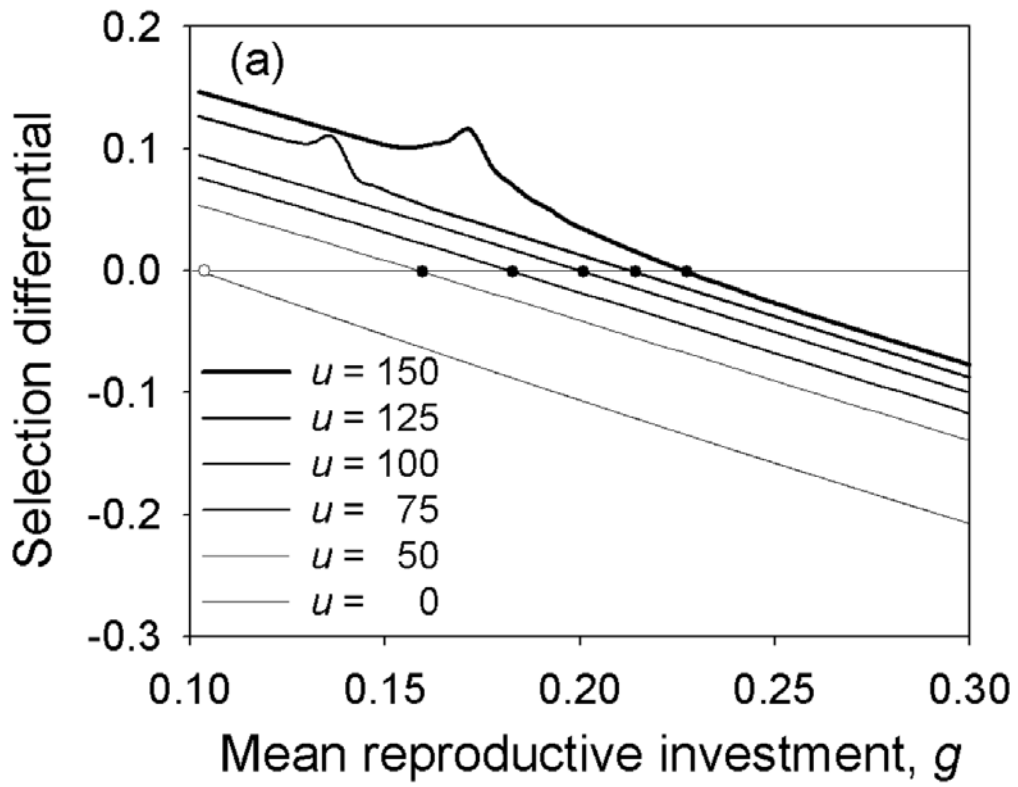
1163

1164 **Fig. 2**



1165

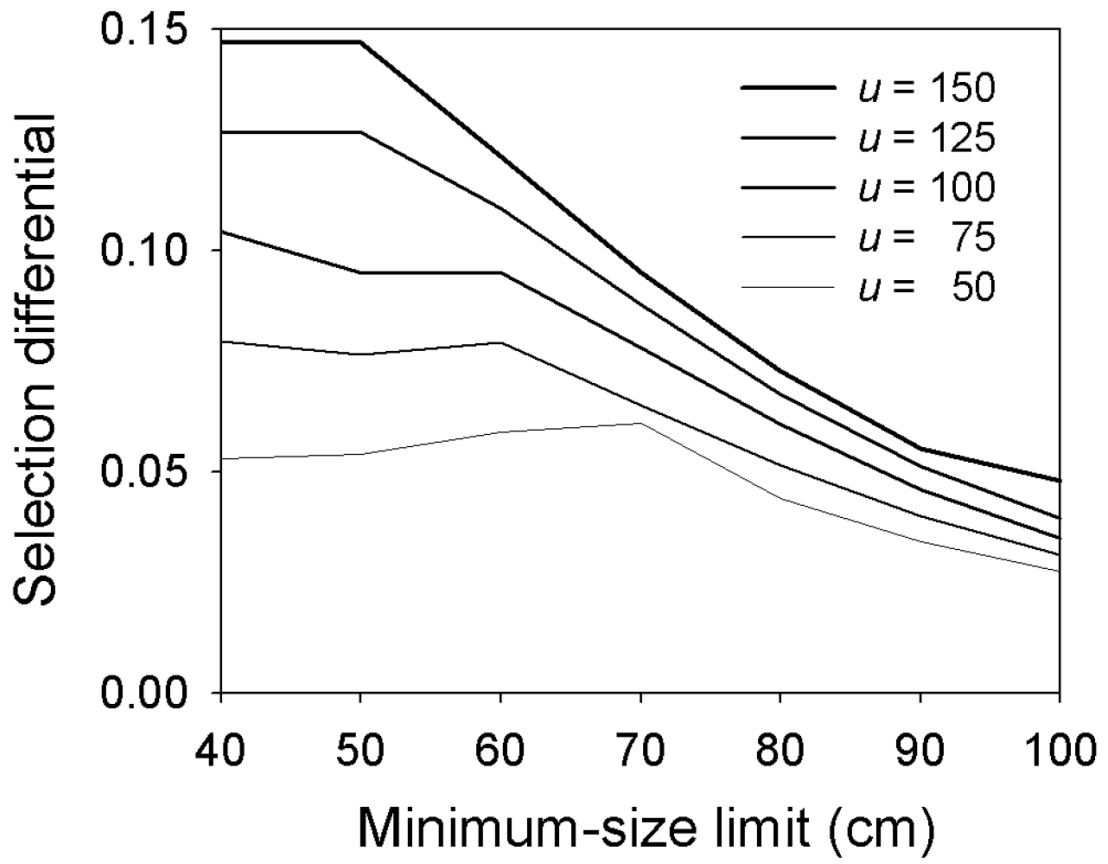
1166 Fig. 3



1167

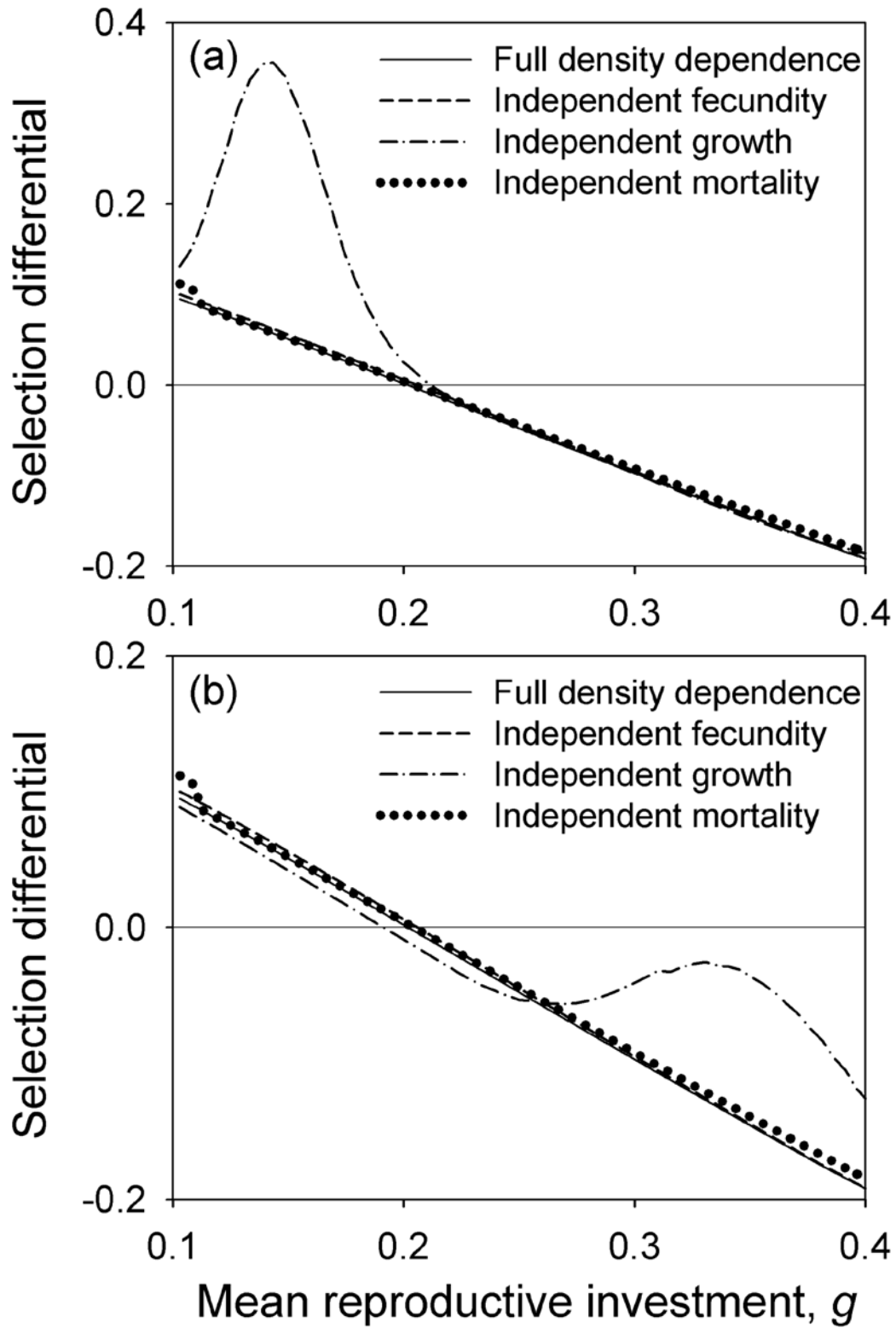
1168

1169 **Fig. 4**



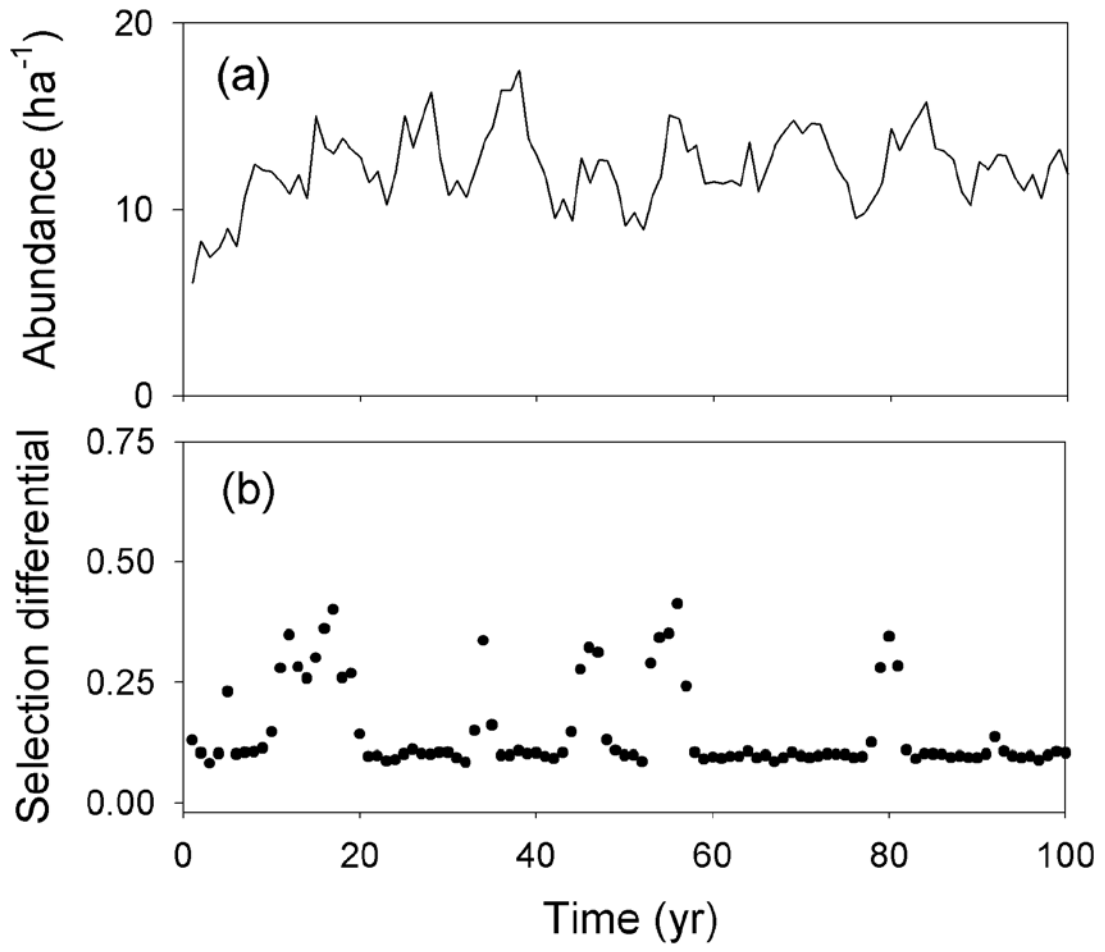
1170
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1172 Fig. 5



1173
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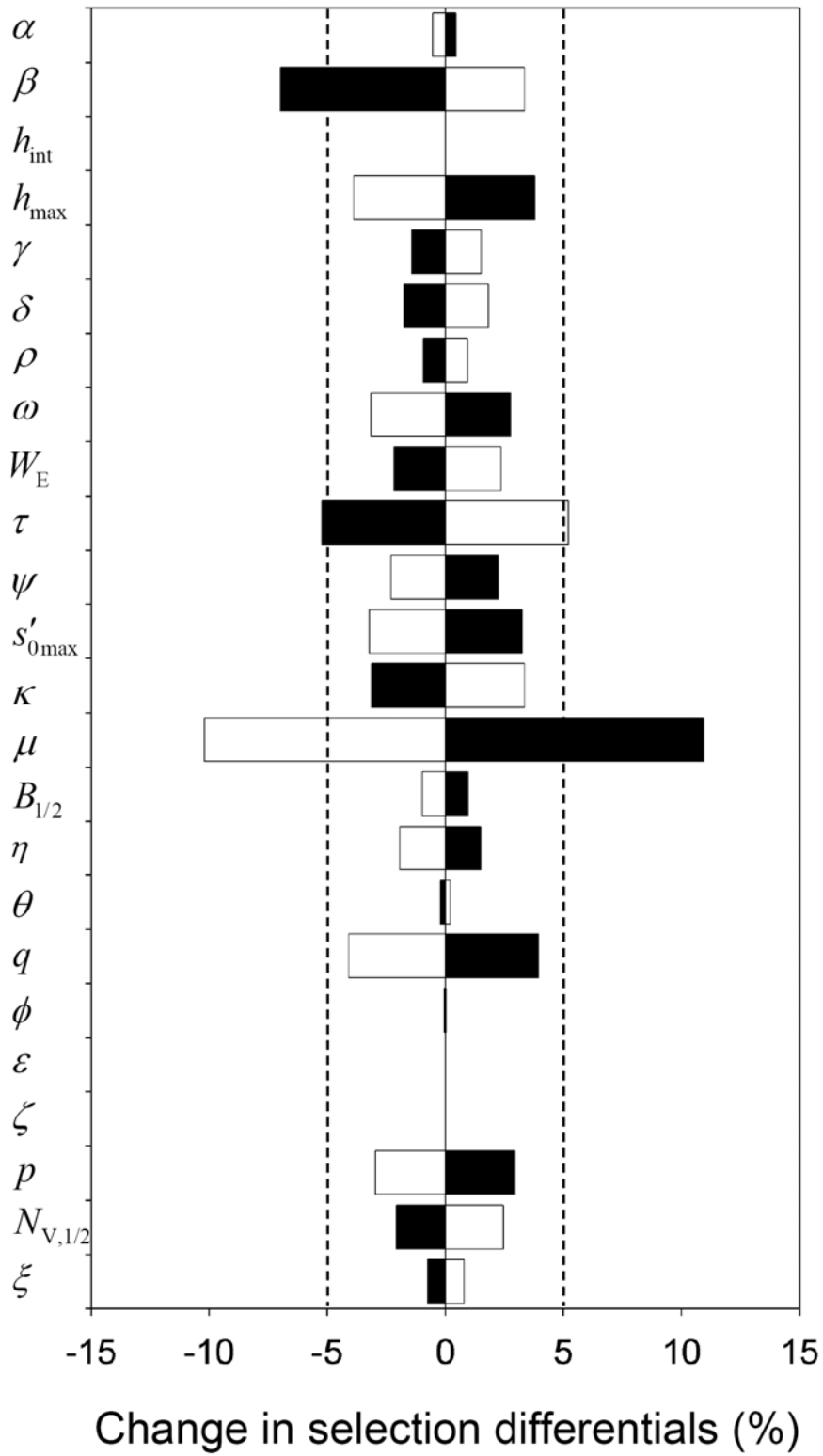
1175 **Fig. 6**



1176

1177

1178 **Fig. 7**



1179

1180

1181 **Appendix A: Parameterization of the model for pike (*Esox***
1182 ***lucius* L.)**

1183 The parameter set used in our analysis (Table A1) was developed to represent a
1184 hypothetical lake population of northern pike. Constants determined by empirical
1185 studies were represented by Greek letters, except when following popular notations (e.g.
1186 catchability q). Recreational fishing patterns (e.g., annual exploitation rates, size-
1187 selectivity, angling-effort dynamic) resembled those typical for consumptive anglers
1188 targeting top predatory fish such as pike (reviewed in Lewin et al. 2006). The parameter
1189 set is a compilation of literature data. No study was available that reported all the
1190 needed information in a single source; thus, parameter values were collected from
1191 different sources. Studies from the pike population in Lake Windermere (U.K.) were
1192 favored, due to the availability of long-term data sets on population demography from
1193 this lake (Haugen et al. 2007). It was assumed that the modeled fishery reflected
1194 common effects on the population dynamics of pike exerted by the presence and actions
1195 of pike anglers. The aim of this study was not to provide a precise and accurate
1196 description of a particular pike population and a particular angling fishery. Instead, the
1197 present study mainly aimed at elucidating the general modeling approach and its utility
1198 for estimating selection pressures acting on adaptive life-history traits. This objective
1199 justifies the more general compilation of pike parameters and demographic processes.
1200 Table A1 reports parameter values and references. Below, we comment on those
1201 parameter values that deserve special clarification.

1202 To determine the parameter value for h , time series data published in Kipling
1203 (1983a) on early growth of female pike until age-at-maturation from 1939 to 1978 in

1204 Lake Windermere (U.K.) were used (her Table 1). Pre-maturation growth is supposed to
1205 be linear with the slope of the age-length regression being given by h (Lester et al.
1206 2004). Kipling (1983a) did not report length-based growth-rate data from age 0 yr to
1207 age 1 yr. We thus calculated average length data from age 1 yr to age 2 yr in the
1208 published time series. Density-dependent early pike growth rate h was determined by
1209 combining data in Kipling (1983a) with data in Kipling (1983b, her Table 3) on total
1210 density of pike aged 2-18 in Lake Windermere for the years 1944-1978 and fitting this
1211 data to equation (6) to determine the parameter values h_{\max} , γ , and δ by minimizing
1212 the sum of squares of the residuals ($r^2 = 0.279$, $F = 12.37$, $p < 0.01$).

1213 To estimate density-dependent relative fecundity, the parameters in the original
1214 function by Craig and Kipling (1983) for pike in Lake Windermere were recalculated
1215 from their Fig. 1 to derive a function relating fecundity to fish biomass density D two
1216 years before spawning ($t_L = 2$). The baseline for recalculation was an area of littoral
1217 pike habitat of 550 ha in Lake Windermere according to Raat (1988). Relative caloric
1218 equivalents of gonads relative to soma were calculated as means of the values published
1219 in Table 2 in Diana (1983) taking March as the reference month. Mean egg weight was
1220 calculated taking the mean egg diameter value (2.3 mm) from Frost and Kipling (1967)
1221 assuming a spherical shape and a specific density of 1.0 g cm^{-3} . For the age at which
1222 energy is first diverted to reproduction, we used $T = 1$, so that fish start spawning at
1223 age 2. In our model, the length of fish of age 2 yr was usually larger than 40 cm (the
1224 smallest length was 36 cm in the unexploited case). These values agree well with
1225 common literature reports on the age and size at first spawning in female pike (Raat
1226 1988).

1227 Cannibalism and associated density-dependent recruitment is a well-known
 1228 process in pike populations (Raat 1988; Haugen et al. 2007). Empirical relationships
 1229 relating density-dependent first-year survival of pike to the density of hatched eggs were
 1230 taken from Minns et al. (1996) and converted into a more common representation of a
 1231 dome-shaped stock-recruitment function. The baseline instantaneous natural mortality
 1232 rate M_b of older pike was determined according to an empirical model for predicting
 1233 the half-year survival probability $s_{1/2}$ for “small” and “large” Lake Windermere pike as
 1234 reported by Haugen et al. (2007),

$$1235 \quad s_{1/2} = \frac{\exp(\beta_0 + \beta_x X + \beta_y Y + \beta_L L)}{1 + \exp(\beta_0 + \beta_x X + \beta_y Y + \beta_L L)}, \quad (\text{A1})$$

1236 where X and Y are densities of “small” (age 2 yr) and “large” pike (older than 2 yr),
 1237 respectively, and L denotes the length of fish, and β_0 , β_x , β_y , and β_L are empirically
 1238 determined coefficients. Values of β_0 , β_x , β_y , and β_L for “small” and “large” pike
 1239 were calculated from Table 3 in Haugen et al. (2007), assuming no specific basin of the
 1240 study lake and no sex structure. Since Haugen et al. (2007) did not report survival rate
 1241 of age-1 pike, we applied the survival rate estimated for small pike (i.e., age-2) also to
 1242 age-1 individuals. The half-year survival rates were translated into instantaneous
 1243 mortality rates,

$$1244 \quad M_b = -\log s_{1/2}^2. \quad (\text{A2})$$

1245 It is reasonable to assume a potential trade-off between reproductive investment
 1246 and post-reproduction survival in pike. No empirical data were available to parameterize
 1247 this trade-off (Wootton 1998). We determined τ so that the total instantaneous natural

1248 mortality rate M ranges between 0.3 yr^{-1} and 0.5 yr^{-1} , which is typical for many pike
1249 populations (Raat 1988).

1250 Anglers generally exploit fish stocks size-selectively (Lewin et al. 2006). For
1251 describing size-selectivity in pike fisheries, the parameters η and θ were set to reflect
1252 empirical data on length-specific vulnerability of pike in angling fisheries (Pierce et al.
1253 1995; Pierce and Cook 2000). Accordingly, pike smaller than 20 cm in total length were
1254 invulnerable and pike larger than 50 cm were assumed to be fully vulnerable.
1255 Catchability q in pike is density-independent (Pierce and Tomcko 2003). The value of
1256 q in the present model was determined from a field study on pike recreational angling
1257 conducted by Arlinghaus et al. (unpublished data) that also utilized natural baits to
1258 capture pike. The value found in this study ranged among the highest values for q
1259 reported by Pierce and Tomcko (2003). However, Pierce and Tomcko (2003) only used
1260 artificial lures. Catchability of pike is typically higher for natural baits, which are
1261 commonly used in many pike fisheries (Beukema 1970; Arlinghaus et al. 2008). This
1262 justifies our choice for the catchability parameter. Hooking mortality rate ϕ was
1263 estimated conservatively based on the maximum value published in Munoeke and
1264 Childress (1994) for esocids. Non-compliance rate was treated as a dynamic variable
1265 depending on the catch rate of undersized fish following Sullivan (2002). He found that
1266 Q was inversely related to the anglers' catch rate of undersized walleye (*Sander*
1267 *vitreum*). No investigations were available for pike. Therefore, the same functional
1268 relationship was assumed for pike fisheries as anecdotal evidence suggests similar
1269 relationships in many fisheries.

1270 Anglers respond dynamically to changing catch qualities (Post et al. 2003).
1271 Without quantitative information available to model the effort-response curve in pike
1272 fisheries, the coefficients in the modified model of Post et al. (2003) were chosen to
1273 correspond with published work on absolute annual angling effort density u in typical
1274 pike fisheries (Kempinger and Carline 1978; Pierce et al. 1995; Margenau et al. 2003).
1275 Accordingly, the maximum value for u was set at $150 \text{ h ha}^{-1} \text{ yr}^{-1}$. The sigmoid effort-
1276 response curve describes a relatively steep rise in effort with increased fish abundance
1277 (resulting from the positive effects of elevated catch rates on angler satisfaction,
1278 Arlinghaus 2006) and a flattening at high effort rates (resulting from the negative effect
1279 of crowding on angling experience). Exploitation of pike was modeled under different
1280 minimum-size limits MSL , a standard harvest regulation in pike fisheries world-wide.
1281

1282 **Table A1.** Life-history parameters for a pike (*Esox lucius* L.) population size-
 1283 selectively exploited by anglers. Parameters for biological processes and for angling
 1284 processes are presented in groups. Parameters with units indicated by “-” are
 1285 dimensionless. Unit standardizing constants were included to remove units in
 1286 empirically estimated relationships.

Symbol	Value	Unit	Source
Biological processes			
a_{\max}	12	yr	Raat (1988)
Length-weight relationship			
α	4.8×10^{-6}	kg	Willis (1989)
β	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	yr	Raat (1988)
h_{\max}	27.094	cm	Own calculations
γ	0.18190	-	Own calculations
δ	0.56783	-	Own calculations

D_u	1	kg ha ⁻¹	Standard unit
Fecundity			
g	Default mean 0.10 and standard deviation 0.015	-	See text
ρ	0.04818	ha kg ⁻¹	Craig and Kipling (1983)
t_L	2	yr	Craig and Kipling (1983)
ω	1.22	-	Diana (1983)
W_E	6.37×10^{-6}	kg	Own calculations
Hatching rate			
ψ	0.735	-	Franklin and Smith (1963)
Natural mortality			
τ	1.0	-	Own calculations
β_0	2.37 (small pike), 1.555 (large pike)	-	Haugen et al. (2007)
β_x	-0.02 (small pike), 0.40 (large pike)	-	Haugen et al. (2007)
β_y	-0.29 (small pike), -0.88 (large pike)	-	Haugen et al. (2007)

β_L	0.25 (small pike), 0.00 (large pike)	-	Haugen et al. (2007)
$s_{0,\max}$	4.76×10^{-4}	-	$\exp(f_a)$ in Minns et al. (1996)
κ	31.73	-	$-f_b$ in Minns et al. (1996)
μ	0.31	-	f_c in Minns et al. (1996)
$B_{1/2}$	1.68362×10^9	ha ⁻¹	f_d^{1/f_c} in Minns et al. (1996)
Angling processes			
η	0.25	cm ⁻¹	See text
θ	1300	-	See text
Catchability			
q	0.01431	ha h ⁻¹	Own empirical value
Other fishing mortalities			
ϕ	0.094	-	Munoeke and Childress (1994)
Q	0 (initial value in year $t = 1$)	-	Own calculations
ε	1.25	-	Sullivan (2002)
ζ	-0.84	-	Sullivan (2002)

Angling effort

u	varied up to 150 (default 100, if not varied)	h ha^{-1} yr^{-1}	See text
p	0.5	-	See text
$N_{V,1/2}$	10	ha^{-1}	See text
ξ	5	-	See text
C_u	1	h^{-1}	Standard unit
MSL	varied (default 50, if not varied)	cm	See text

1287