

# **The conservation and fishery benefits of protecting large pike (*Esox lucius* L.) by harvest regulation in recreational fishing**

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## Interim Report

IR-10-022

### **The conservation and fishery benefits of protecting large pike (*Esox lucius* L.) by harvest regulations in recreational fishing**

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**The conservation and fishery benefits of protecting large pike (*Esox lucius* L.) by harvest regulations in recreational fishing**

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# **The conservation and fishery benefits of protecting large pike (*Esox lucius* L.) by harvest regulations in recreational fishing**

## **ABSTRACT**

Traditional fisheries management theory supports aggressive exploitation of old and large fish to maximize a stock's biomass production and yield. Here we present an age-structured fish population model with multidimensional density-dependence to test the hypotheses that protection of large, fecund individuals is beneficial for the population and selected fisheries variables and that effects of maternal size on early survival rate change the resilience and fisheries productivity of a pike population (*Esox lucius* L.) exploited by recreational angling. We find that, compared to the traditional regulatory approach of management by small minimum-length limits (so that culling of large fish is encouraged), preservation of large and old individuals through harvestable-slot length limits promises considerable benefits for fisheries quality, without compromising the long-term conservation of the population. We also find that ignoring maternal effects on early survival of offspring might overestimate the equilibrium spawning stock abundance by up to 17% and the predicted harvest by up to 11%, potentially putting pike populations at risk from overharvest if size-dependent maternal effects are ignored in fisheries models. If the findings from our simulation study hold for empirical systems, they suggest altered harvest regulations in many of consumptive pike recreational fisheries are needed to protect large individuals to a greater extent than currently pursued.

**Keywords:** angling; maternal effects; recreational fishing; recruitment; spawning potential ratio; size selectivity

## 1. Introduction

Fishing mortality has had, and continues to have, major impacts on wild fish populations (Worm et al., 2009). However, it is only recently that fishing mortality exerted by recreational fishing has been identified as contributing to fish stock declines (Post et al., 2002; Lewin et al., 2006). In both commercial and recreational fisheries, positively size-selective exploitation is common (Lewin et al., 2006). Therefore, naturally less abundant large and old fish within a stock tend to be removed at a higher rate than small and young individuals (e.g., Braña et al. 1992; Paul et al., 2003). Traditional fisheries theory encourages the resulting truncation of the size and age structure of the stock because the decline of virgin population abundance relaxes intraspecific food competition, resulting in higher per capita prey intake and increased production in terms of somatic body mass by on average small and young and thus fast growing individuals (Schaefer, 1957; Silliman and Gutsell, 1958; Schäperclaus, 1960). Therefore, demographic truncation of the age and size distribution of a stock can be beneficial from the perspective of maximizing fisheries yield (Silliman and Gutsell, 1958; Schäperclaus, 1960). However, this yield-based fisheries management objective has been called into question as a viable long-term approach to sustainable fisheries management (Larkin, 1977). It is particularly unsuitable as a universal objective for recreational angling fisheries, because many anglers value the body size of fish as memorable trophies or enjoy other body size-related determinants of angling quality (e.g., a challenging fight with a large fish) more than maximized harvest biomass (Arlinghaus, 2006). Moreover, conservation concerns have been raised that fishing-induced truncation of the age and size structure of a population will impact recruitment dynamics and may destabilize populations (Berkeley et al., 2004a; Hsieh et al., 2006; Anderson et al., 2008; Venturelli et al., 2009).

Several mechanisms acting in isolation or combination have been proposed that may explain the impact of demographic changes towards on average younger and smaller fish to affect recruitment dynamics in exploited fish stocks. Firstly, a large fraction of young fish amplifies a stock's nonlinear

dynamics and destabilizes its abundance (Anderson et al., 2008). Secondly, in many fish stocks individuals of different sizes and ages reproduce at different times and locations (Wright and Trippel, 2009). This spreads larval production in time and space providing a buffer against environmental stochasticity (Berkeley et al., 2004a). Thirdly, in many fish species the fecundity of a female increases exponentially with its body length and linearly with its body weight (Wotton, 1998). This is due to larger fish not only having a greater body volume for holding eggs, but also because they may devote a greater proportion of energy to egg production rather than somatic growth (Edeline et al., 2007). Therefore, strongly reducing the abundance of large fecund fish in a population might affect total egg abundance (Berkeley et al., 2004a; Birkeland and Dayton, 2005). Finally, the existence of age and size-dependent maternal effects on egg and larval survival is thought to influence recruitment dynamics in some marine and freshwater fish stocks (Berkeley et al., 2004a,b; Scott et al., 2006; Venturelli et al., 2009).

Maternal effects are non-genetic impacts that female phenotypes have on phenotypes of their offspring (Bernardo, 1996). An example of a size-dependent maternal effect is when the size of an offspring at hatching is a function of the female's size at reproduction. Size-dependent maternal effects on egg quality-traits (e.g., egg size, nutrient composition) and larval performance-traits (e.g., size, growth rate, resistance to starvation) have been documented in a variety of fish species (reviewed in Chambers and Leggett, 1996; Heath and Blouw, 1998; Marshall et al., 2008). It is known that small differences in the survival rate at young life stages can have major impacts on year-class strength in fish (Miller et al., 1988; Wright, 1990; Marshall et al., 2008). Thus, size-dependent maternal effects on early survival can affect recruitment, population variability, yield, and time to recovery from overexploitation (Murawski et al., 2001; Scott et al., 2006; Lucero, 2009; Venturelli et al., 2009). This outcome, however, seems to be species-dependent and influenced by the exact nature of the maternal effects on early life-history, and will also depend on a species' maturation schedule and reproductive

life span as well as fishery selectivity and exploitation patterns (O'Farrell and Botsford, 2006; Ottersen, 2008; Venturelli et al., 2009).

In response to concerns about the conservation issues associated with pronounced age and size truncation in exploited fish stocks, some authors have proposed to save large portions of old and large fish from exploitation for demographic (Berkeley et al. 2004a; Palumbi, 2004; Birkeland and Dayton 2005) or evolutionary reasons (Law, 2007). This might also be beneficial from a fishing-quality perspective (Trippel, 1993). However, few studies (for exceptions, see Berkeley, 2006 and Venturelli et al., in press) have systematically investigated the impact of various simple harvest regulations on fish populations and fishing quality in models with and without the existence of assumed age or size-dependent maternal effects on egg and offspring survival. This gap of knowledge currently precludes the derivation of robust management advice as to the appropriateness of different variants of common harvest regulations to jointly meet conservation and fishing quality objectives.

Here, we present a simulation model of a recreationally exploited freshwater fish population parameterized for the top freshwater piscivore, northern pike (*Esox lucius* L.) (hereafter termed pike). This fast growing and early maturing species is a popular, yet highly vulnerable (Pierce et al., 1995; Paukert et al., 2001), target of recreational fishing in the northern hemisphere. It constitutes an apex predator in most mesotrophic to slightly eutrophic lakes and slow-flowing rivers of the temperature regions (Raat, 1988; Craig, 1996). There exist a handful of case studies on the effects of simple harvest regulations, such as minimum-length limits or protected slot-length limits, on pike populations and their size structure (reviewed in Pierce, in press). However, no study has studied the conservation and fishery benefits of harvest regulations designed to protect large-sized pike from recreational fishing harvest, such as harvestable slot length limits, under the assumption that size-dependent maternal effects on early life history exist. In this study, we model a size-selectively exploited population of pike that is governed by multiple density-dependent processes to account for the compensatory po-



tential of pike stocks to fishing mortality, thus adding realism to model predictions. We contrasted model runs with and without empirically measured size-dependent maternal effects on early survival of offspring to investigate the importance of these effects for the long-term dynamics of exploited pike populations. We investigate the hypothesis that saving large and old fish through simple harvest regulations is beneficial for the conservation of the population as well as for fishing quality. While focused on the life-history of pike, our study has implications for other fish species size-selectively exploited by commercial or recreational fisheries as long as these life-histories share characteristics of pike such as fast growth, early maturation, positively size-dependent fecundity and strong density-dependent population control.

## 2. Methods

We developed an age-structured pike simulation model with multidimensional density-dependence on the vital rates of pike as well as density-dependent angling effort attracted to the fishery (Fig. 2). The model was modified from Arlinghaus et al. (2009) focusing on ecological dynamics exclusively and omitting any evolutionary perspective. The parameter set used (Table 1) represented a prototypical lake population of pike exploited by recreational fisheries. Constants determined by empirical studies were represented by Greek letters except for some popular notations (e.g., catchability  $q$ ). Recreational fishing patterns (e.g., size-selectivity, angling effort dynamics and resulting annual exploitation rates) resembled those typical for harvest-oriented (i.e., consumptive) anglers targeting top predatory fish such as pike (Arlinghaus et al., 2009). No study was available that reported all the needed information; thus, parameter values were collected from different sources (Arlinghaus et al., 2009). However, studies from the pike population in Lake Windermere (U.K.) were favored due to the availability of long-term data sets on pike demography (e.g., Edeline et al., 2007; Haugen et al. 2007). Below, in addition to describing model equations we will comment on parameter values deserving

special clarification for the purpose of the present analysis and not already described in Arlinghaus et al. (2009).

## 2.1 Population dynamics

We use a deterministic Leslie-matrix population model. Such models classify a population into distinct stages (here age classes) and project their abundances in discrete time (Caswell, 2001). Our model is designed for application to fish species with a single breeding season per year, such as pike (Raatt, 1988), so that annual time steps can be used. In Leslie matrix models (see Caswell, 2001 for details), changes in the age structure and density of the population are described by  $N(t+1) = KN(t)$  or

$$\begin{pmatrix} N_1(t+1) \\ N_2(t+1) \\ N_3(t+1) \\ \dots \\ N_{a_{\max}}(t+1) \end{pmatrix} = \begin{pmatrix} f_1 & f_2 & f_3 & \dots & f_{a_{\max}} \\ s_1 & 0 & 0 & \dots & 0 \\ 0 & s_2 & 0 & \dots & 0 \\ \dots & \dots & \dots & \dots & \dots \\ 0 & 0 & 0 & s_{a_{\max}-1} & 0 \end{pmatrix} \begin{pmatrix} N_1(t) \\ N_2(t) \\ N_3(t) \\ \dots \\ N_{a_{\max}}(t) \end{pmatrix}. \quad (1)$$

The matrix  $K$  is the population-projection matrix (Leslie matrix), and the vector  $N(t)$  represents the density of fish (i.e., the abundance of fish per area of the considered water body) in year  $t$  across all age classes  $a = 1, \dots, a_{\max}$ . Census time is chosen so that reproduction occurs at the beginning of each season (prebreeding census, Caswell, 2001).  $f_a$  is the fertility at age  $a$  (i.e., the number of recruits defined as age-1 fish produced per female of age  $a$ ),  $s_a$  is the survival probability of individuals from age  $a$  to age  $a+1$ , and  $a_{\max}$  is the maximum age (Table 1).

The vital rates  $f_a$  and  $s_a$  are functions of the total population density  $D$  (defined in the next section) and thus vary with time  $t$  until demographic equilibrium is reached (Arlinghaus et al., 2009). 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 fishing mortality as defined below.

## 159 2.2 Biological processes

160 Crucial biological processes that determine the life history of a fish species include growth, repro-  
161 duction, fecundity, and mortality (Wotton, 1998). In the present pike model, for simplicity, we assume  
162 an equal sex ratio and we do not model sex-specific vital rates in terms of growth and mortality. Pike  
163 growth is modeled according to the biphasic growth model by Lester et al. (2004) (Fig. 1a). They  
164 showed that the von Bertalanffy growth equation provides a good description of post-maturation  
165 somatic growth in temperate fish, whereas growth is almost linear until the age at which allocation of  
166 energy to reproduction begins (termed  $T$  by Lester et al., 2004). By explicitly considering allocation  
167 of surplus energy into somatic growth and reproduction (see Appendix B in Lester et al., 2004), length  
168 at age  $a$  is represented as

$$169 \begin{cases} L_a = \frac{3}{3 + g_{a-1}} (L_{a-1} + h) \\ L_1 = h(1 - t_1) \end{cases}, \quad (2)$$

170 where  $g_a$  is annual reproductive investment at age  $a$  (i.e., the surplus energy devoted to reproduc-  
171 tion), and  $h$  is the annual length increment of immature fish (Lester et al., 2004). As  $g_a = 0$  until the  
172 age of maturation, immature growth is linear with the annual increment  $h$ . In our model application to  
173 pike, and in contrast to Lester et al. (2004), maturation is determined by size (Raaf, 1988). Accordingly,  
174 a female pike starts her reproductive investment at age  $a$  if its body length  $L_a$  reaches the size of  
175 maturation  $L_M$  (Table 1). Then, the age at first spawning for the female is  $a + 1$ . Although Lester et al.  
176 (2004) assumed  $g_a$  to be constant after age of maturation, we assume it to be positively  
177 size-dependent in pike following Edeline et al. (2007) (Table 1).

178 For conversions from length to weight, an empirical allometric relationship

$$179 W_a = \alpha_1 (L_a / L_u)^{\alpha_2} \quad (3)$$

180 is used, where  $W_a$  is somatic weight at age  $a$ ,  $L_u$  is a unit-standardizing constant, and  $\alpha_1$  and  $\alpha_2$  are  
 181 empirical parameters defining the relationship for pike (Willis, 1989). The growth model by Lester et  
 182 al. (2004) is based on the assumption that the exponent of the length-to-weight relationship is 3, and  
 183 the corresponding value in Willis (1989) for typical pike populations is 3.059. For species or popula-  
 184 tions whose exponent of the length-weight-relationships differs substantially from 3, the generalized  
 185 bi-phasic growth model by Quince et al. (2008) rather than the special case reported by Lester et al.  
 186 (2004) may be more appropriate. Because the empirical exponent in Willis (1989) is fairly close to 3,  
 187 we chose the simpler growth model by Lester et al. (2004) and assume an exponent of 3 (Table 1). Fish  
 188 density  $D$  is then simply the sum of biomasses across all age classes,

$$189 \quad D = \sum_{a=1}^{a_{\max}} W_a N_a . \quad (4)$$

190 Growth in fish is often density-dependent due to increased competition for food with increasing  
 191 density (Lorenzen and Enberg, 2002). This crucial population dynamical mechanism is included into  
 192 the model by fitting empirical data from pike of Lake Windermere to a competition equation to provide  
 193 a relation of the average immature annual length increment  $h$  as a function of population density  $D$   
 194 (Arlinghaus et al., 2009),

$$195 \quad h = \frac{h_{\max}}{1 + \beta_1 (D / D_u)^{\beta_2}} , \quad (5)$$

196 where  $\beta_1$  and  $\beta_2$  define the shape of this relationship,  $D_u$  is a unit-standardizing constant, and  $h_{\max}$  is  
 197 the maximum immature annual length increment at  $D = 0$  (Fig 1b, Table 1). According to equation (2),  
 198 density-dependence in  $h$  also influences post-maturation growth.

199 The age-specific fertility  $f_a$  is defined as

$$200 \quad f_a = s_0 \psi k_a , \quad (6)$$

201 where  $k_a$  is age-specific fecundity (defined as the number of spawned eggs per female),  $\psi$  is the  
 202 hatching rate, and  $s_0$  is the survival rate from egg hatch to age 1. We assume fecundity to diminish  
 203 with population density, as elevated food competition with increasing pike density in a given year  
 204 reduces surplus energy and energy invested in gonad development in subsequent years (Craig and  
 205 Kipling, 1983; Haugen et al., 2006). Maximum fecundity at  $D=0$  depends on reproductive invest-  
 206 ment  $g_a$ , because  $g_a$  sets an upper limit on the production of eggs (Lester et al., 2004). Note that in  
 207 broadcast spawning fish with lack of pronounced spawning migrations or parental care, such as pike,  
 208 in females  $g_a$  may be approximated by the energy density of gonads prior to spawning (Shuter et al.,  
 209 2005) because gonads constitute the bulk of reproductive investments in female pike (Diana, 1996).  
 210 Under this simplifying assumption, which underestimates the true energy investment into reproduction  
 211 resulting for example from energetic costs of pike spawning activity (Lucas, 1992), the age-specific  
 212 fecundity  $k_a$ , expressed in terms of spawned eggs, is defined as

$$213 \quad k_a = \frac{J_a}{2I_a} \exp(-\rho D), \quad (7)$$

214 where  $I_a$  and  $J_a$  are the egg weight and the gonad weight of females at age  $a$  and density  $D=0$ ,  
 215 respectively, and  $\exp(-\rho D)$  describes a decrease of fecundity with increasing pike population den-  
 216 sity  $D$  as per Craig and Kipling (1983) (Fig. 1c, Table 1).  $J_a / I_a$  is the maximum number of eggs  
 217 produced by a female at  $D=0$ . The fecundity  $k_a$  is multiplied by  $\frac{1}{2}$  because only half of the indi-  
 218 viduals of each age class  $N_a$  are assumed to be females. We consider the gonad weight  $J_a$  to be  
 219 allometrically related to female length in pike following Edeline et al. (2007),

$$220 \quad J_a = \gamma_1 (L_a / L_u)^{\gamma_2}, \quad (8)$$

221 where  $\gamma_1$  and  $\gamma_2$  are empirically derived parameters, and  $L_u$  is a unit-standardizing constant (Table 1).

222 Annual reproductive investment  $g_a$  is calculated as

223 
$$g_a = \omega \frac{J_a}{W_a}, \quad (9)$$

224 where  $\omega$  is the relative caloric density of eggs compared to soma. The weight of eggs  $I_a$  is assumed  
225 to linearly depend on the size of female pike as,

226 
$$I_a = \delta_1 L_a + \delta_2, \quad (10)$$

227 where  $\delta_1$  and  $\delta_2$  are empirically derived parameters from data in Lindroth (1946) ( $R^2 = 0.44$ ,  $P <$   
228  $0.001$ , Table 1).

229 Recruitment from egg hatch to age 1 in pike is assumed to be density-dependent with over-  
230 compensation as a result of cannibalism (Edeline et al., 2008, Fig. 1e). Following Minns et al. (1996),  
231 the survival rate  $s_0$  from egg hatch to age 1 is assumed to depend on the density of hatched pike larvae  
232 according to a Ricker-type, dome-shaped relationship,

233 
$$s_0 = s_{0,\max} \exp(-\kappa G(B)), \quad (11a)$$

234 where  $s_{0,\max}$  is the maximum survival rate,  $\kappa$  is a constant that specifies the minimum survival rate  
235  $s_{0,\min} = s_{0,\max} \exp(-\kappa)$  as a fraction of  $s_{0,\max}$ , and  $B$  is the hatched egg density (i.e., larval density).

236 The function  $G(B)$  determines the relationship between the density of hatched larvae and their sur-  
237 vival,

238 
$$G(B) = \frac{B^\mu}{B^\mu + B_{1/2}^\mu}, \quad (11b)$$

239 where  $\mu$  is an exponent determining the rapidity of the transition between  $s_{0,\max}$  and  $s_{0,\min}$  through  
 240 changes in hatched larvae density, and  $B_{1/2}$  is the density of hatched larvae at which  
 241  $s_0 = s_{0,\max} \exp(-\kappa/2)$ . (11c)

242 The larval density  $B$  is the sum of age-specific larval production across all age classes,  
 243  $B = \sum_{a=1}^{a_{\max}} \psi k_a N_a$ . (11d)

244 Annual survival rates  $s_a$  at age are calculated by combining age-specific instantaneous natural  
 245 mortality rates  $M_a$  with instantaneous fishing mortality rates  $F_a$ ,  
 246  $s_a = \exp(-(M_a + F_a))$ . (12)

247 The natural mortality rates  $M_a$  are determined according to an empirical model for predicting the  
 248 age-specific half-year survival probability  $s_{1/2,a}$  of pike as reported by Haugen et al. (2007),

$$249 \quad s_{1/2,a} = \frac{\exp(\tau_0 + \tau_X X + \tau_Y Y + \tau_L L_a)}{1 + \exp(\tau_0 + \tau_X X + \tau_Y Y + \tau_L L_a)}, \quad (13a)$$

250 where  $X$  and  $Y$  are densities of “small” (i.e., age-2) and “large” pike (i.e., older than age-2), respec-  
 251 tively, and  $L_a$  denotes the length of fish at age  $a$ , and  $\tau_0$ ,  $\tau_X$ ,  $\tau_Y$ , and  $\tau_L$  are empirically determined  
 252 coefficients (Table 1). The half-year survival rates were translated into instantaneous mortality rates  
 253 (Arlinghaus et al., 2009) using

$$254 \quad M_a = -\log s_{1/2,a}^2. \quad (13b)$$

255 To describe size-dependent maternal effects on early life-history of pike and enable us to  
 256 quantify the impact of these mechanisms for recruitment dynamics and fishery variables, we use two  
 257 choices for the impact of a female’s size-at-age on the early survival probability of her offspring (Fig.  
 258 1d),

$$259 \quad r_a = 1 \text{ (constant, i.e., lack of a size-dependent maternal effect),} \quad (14a)$$

260 or

261  $r_a = -\lambda_1 \exp(-\lambda_2 L_a) + \lambda_3$  (asymptotic increase of size-dependent maternal effect), (14b)

262 where  $r_a$  is the relative early survival probability of pike offspring during the first month after  
263 hatching. Note that because age and size are strongly correlated in most fish, including pike,  
264 size-dependent maternal effects on offspring survival will also be age-dependent. The baseline as-  
265 sumption of a constant relationship between size of females and early survival of their offspring (eq-  
266 uation 14a) represents the traditional assumption in fisheries models that the survival probability of  
267 offspring is independent of the female's size (e.g., Wright and Shoesmith, 1988). The second as-  
268 sumption of an asymptotic increase in relative early survival with the female's size (equation 14b) is  
269 based on recent experimental evidence about the differential relative survival of pike larvae spawned  
270 by five female pike ranging in total length between 33.5 and 99 cm. Equal numbers of larvae from each  
271 female were stocked into common garden ponds and offspring survival was measured over a period of  
272 one month after stocking (stocking May, 5, 2008; complete retrieval of survivors by draining of ponds,  
273 June, 12, 2008, Arlinghaus, Faller, Wolter & Bekkevold, unpublished data). Surviving offspring in the  
274 otherwise fishless ponds (so as to expose age 0 pike to strong intraspecific competition and intracohort  
275 cannibalism) were assigned to each of the five females using ten microsatellite loci, and relative sur-  
276 vival rates of offspring as a function of female size was determined (Arlinghaus, Faller, Wolter &  
277 Bekkevold, unpublished data). Data were used to fit an asymptotic size-dependent maternal effect on  
278 early survival using equation 14b, and values for the parameters ( $\lambda_1$ ,  $\lambda_2$ , and  $\lambda_3$ ) were determined so  
279 as to provide the best fit to the data ( $R^2 = 0.85$ , Fig. 1d, Table 1). We coupled this relative survival  
280 function of offspring originating from a particular size (and hence age) class to the general stock re-  
281 cruitment function with overcompensation (equation 11a). Thereby, an initial relative survival ad-  
282 vantage is maintained until recruitment to age-1, but not afterwards due to the lack of empirical evi-  
283 dence for size-dependent maternal effects on offspring traits being maintained after the first year of life



284 in pike. Accordingly, equation (11a) was modified as

$$285 \quad s_{0,a} = \frac{r_a}{\sum_{a=1}^{a_{\max}} r_a k_a N_a / \sum_{a=1}^{a_{\max}} k_a N_a} s_{0,\max} \exp(-\kappa G(B)). \quad (11a')$$

286 The factor on the right side of equation  $\frac{r_a}{\sum_{a=1}^{a_{\max}} r_a k_a N_a / \sum_{a=1}^{a_{\max}} k_a N_a}$  represents whether the survival  
 287 probability of offspring from a female of age  $a$  during the first month is larger or smaller than the  
 288 population average  $\sum_{a=1}^{a_{\max}} r_a k_a N_a / \sum_{a=1}^{a_{\max}} k_a N_a$ . It therefore represents an age-specific early survival  
 289 weight multiplied with the population's first year survival probability from equation (11a).

## 290 **2.3 Recreational angling processes**

291 The vulnerability of individual age classes to recreational fishing is represented by a sigmoid rela-  
 292 tionship with length and scaled from 0 (completely invulnerable) to 1 (completely vulnerable),

$$293 \quad V_a = (1 - \exp(-\eta L_a))^\theta, \quad (15)$$

294 where  $V_a$  is the vulnerability of fish of age  $a$  with length  $L_a$ , and  $\eta$  and  $\theta$  describe the shape of the  
 295 relationship (Paul et al., 2003, Table 1). The total density  $N_v$  of vulnerable fish is then given by

$$296 \quad N_v = \sum_{a=1}^{a_{\max}} V_a N_a. \quad (16)$$

297 A realistic expectation about angler behavior is a response of angling effort  $E$  to the quality of  
 298 the fishery (Post et al., 2003). As the quality of fishing measured in terms of angler satisfaction is often  
 299 catch-dependent (Arlinghaus, 2006; Arlinghaus et al., 2008), increasing numbers of vulnerable fish are  
 300 expected to increase the number of anglers spending effort on a particular fishery (Post et al., 2003). As  
 301 empirical information on this effort dynamic is currently not available for pike fisheries, a general  
 302 sigmoid numerical response of angling effort to fish availability, modified from Post et al. (2003), was  
 303 chosen (Fig. 1f),

$$E = u \left( p + \frac{N_V^\xi}{N_{V,1/2}^\xi + N_V^\xi} (1 - p) \right), \quad (17)$$

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

In most recreational fisheries, some variants of length-based harvest regulations are used to maintain recruitment, manipulate the size structure of the fish stock, or distribute the harvest more equitably among anglers (Noble and Jones, 1999). Therefore, anglers will mandatorily release a certain proportion of fish protected by the regulation (Arlinghaus et al., 2007). In our model, a minimum-length limit (MinL-L) is assumed, above which every caught fish is removed for consumption. This situation is characteristic for purely consumptive recreational fisheries such as Germany, where voluntary catch-and-release fishing is usually not tolerated (Arlinghaus, 2007) and MinL-L are set so as to protect immature pike. However, the situation is different in many other pike fisheries in which large percentages of legally sized fish are released (Pierce et al., 1995; Pierce, in press). To save large fish in addition to small immature individuals, we also modeled a combination of a MinL-L and a maximum-length limit (MaxL-L). This regulation is known in the fisheries literature as inverse, reverse or harvestable-slot length limit (Noble and Jones, 1999), hereafter termed harvestable-slot length limit (HSL-L). This means that fish smaller than the MinL-L and larger than the MaxL-L must be released mandatorily. Anglers may also illegally harvest fish protected by harvest regulations (Sullivan, 2002). Therefore, in our model three sources of fishing mortality are assumed (Post et al., 2003): harvest mortality of legal fish, hooking mortality of protected fish sizes that are released, and

326 non-compliance mortality from illegal harvest of protected fish. On this basis, the number of dead fish  
 327  $d_a$  at age  $a$  is given by (Arlinghaus et al., 2009)

$$328 \quad d_a = \begin{cases} V_a N_a [1 - \exp(-qE)], & \text{if } \text{MinL-L} \leq L_a \leq \text{MaxL-L} \\ V_a N_a [1 - \exp(-UqE)], & \text{if } L_a < \text{MinL-L} \text{ or } L_a > \text{MaxL-L} \end{cases}, \quad (18)$$

329 where  $q$  is a constant catchability coefficient,  $E$  is angling effort density, and

$$330 \quad U = \phi + Q - \phi Q, \quad (19)$$

331 where  $\phi$  is the proportion of protected fish that experience hooking mortality from catch-and-release,  
 332 and  $Q$  is the proportion of protected fish that are harvested illegally (Table 1). The non-compliance  
 333 mortality  $Q$  was treated as a dynamic variable following Sullivan (2002), who found that in walleye  
 334 (*Sander vitreum*) angling it was inversely related to angling catch rate of protected fish,  $C_r$ , as

$$335 \quad Q(t+1) = \varepsilon (C_r(t)/C_u)^{-\zeta}, \quad (20a)$$

336 where  $\varepsilon$  and  $\zeta$  are empirically derived constants, and  $C_u$  is a unit-standardizing constant (Table 1).

337 The catch rate  $C_r$  of protected fish was calculated following Arlinghaus et al. (2009) on the basis of  
 338 the number of illegal catch  $c_a$  at age  $a$  as

$$339 \quad C_r = E^{-1} \sum_{a=1}^{a_{\max}} c_a, \quad (20b)$$

340 where

$$341 \quad c_a = \begin{cases} 0, & \text{if } \text{MinL-L} \leq L_a \leq \text{MaxL-L} \\ V_a N_a U^{-1} [1 - \exp(-UqE)], & \text{if } L_a < \text{MinL-L} \text{ or } L_a > \text{MaxL-L} \end{cases}. \quad (20c)$$

342 The instantaneous angling mortality  $F_a$  at age  $a$  is then simply

$$343 \quad F_a = -\ln(1 - d_a / N_a). \quad (21)$$

## 2.4 Outline of analysis

Our study objective was to elucidate the population-level and fishery benefits of saving large and old fish through simple harvest regulations in simulations with and without consideration of age/size-dependent maternal effects on egg quality. Accordingly, we initially modeled the relative effects of implementation of an increasingly more restrictive HSL-L compared to a default harvest regulation of a MinL-L of 45 cm for two scenarios of maternal effects on early survival of offspring (constant and asymptotic increase, Fig. 1d). This was accomplished by modifying the MaxL-L (i.e., the upper bound of the HSL-L) from a maximum of 100 cm to a minimum value of 50 cm, while keeping the lower bound of the HSL-L constant at 45 cm. This default value of a MinL-L was chosen as it represents a standard harvest regulation for pike (Paukert et al., 2001) and is particularly common in jurisdictions where pike stocks are managed for angler harvest.

HSL-Ls are rarely implemented in pike management (Paukert et al., 2001). This regulation is therefore uncommon and may therefore be perceived with caution by the angling public (Page and Radomski, 2006). To compare the effect of a HSL-L relative to a simpler and more common MinL-L, we also investigated how output variables (population size and structure, catch and harvest) differed between model runs comparing increasingly stricter MinL-L (from 45 to 100 cm) with increasingly stricter HSL-L relative to a default MinL-L of 45 cm. We also included a total catch-and-release fishing scenario for comparative purposes. We simulated increasingly more intensive angling fisheries by varying the maximum angling effort level per area represented by the parameter  $u$  and for visualization purposes decided to present the results for a low maximum angling effort scenario ( $u = 50$  annual angling-h  $\text{ha}^{-1} \text{yr}^{-1}$ ) and a high, yet realistic (Kempinger and Carline, 1978), maximum angling effort scenario ( $u = 250$  annual angling-h  $\text{ha}^{-1} \text{yr}^{-1}$ ). This allowed us to test the impact of saving increasingly larger fractions of old and large fish using a HSL-L regulation relative to MinL-L regulations as well as analyzing the impact of maternal effects on early survival of offspring on conservation

368 and fishery variables for several typical angling regulations in pike management. Note that the para-  
369 meter  $u$  represents a maximum potential angling effort level, which at equilibrium will not be equiv-  
370 alent to the realized angling effort due to the strong density-dependence in angling effort (Arlinghaus  
371 et al., 2009).

372         Output variables at long-term equilibrium (note that in every simulation equilibrium conditions  
373 were reached) were thought to be indicative of the long-term average benefits (or penalties) expected  
374 under different regulations; they included variables of the stock status and of fishery quality. Stock  
375 status was represented by pike abundance density for pike aged-1 and older and the spawning potential  
376 ratio (SPR) based on viable egg abundance (i.e., the ratio of viable eggs in the exploited equilibrium  
377 relative to the unexploited case). SPR is a common stock assessment tool to evaluate the degree to  
378 which fishing has reduced the potential population reproductive output (Goodyear, 1993). Recruitment  
379 overfishing is thought to occur when  $SPR \leq 0.35$  (Mace, 1994). To represent age truncation, we cal-  
380 culated the average age of spawners. In terms of fishery metrics, harvest (yield) and catches of large  
381 (i.e., from an angler's perspective so-called memorable) pike were evaluated. The length of memora-  
382 ble pike of 86 cm total length was taken from Anderson and Neumann (1996). We also calculated the  
383 harvesting efficiency, i.e. the ratio of harvest to total deaths due to fishing. This is a way to ethically  
384 evaluate conservation goals, as low harvesting efficiency values indicate that the majority of losses of  
385 individual pike are due to post release mortality rather than harvest (Pine et al., 2008). Sensitivity of  
386 results to parameter values was assessed by varying parameters independently by 10 % and calculating  
387 the resultant percentage of change for two response variables, absolute harvest and SPR. We further  
388 contrasted SPR values between the two maternal effect scenarios to investigate the robustness of the  
389 size-dependent maternal effect simulation results. We chose a moderate fishing mortality and a HSL-L  
390 of 45 to 70 cm for all sensitivity analyses. In all simulations, variation among individuals within an age

class was introduced by assuming that the density-dependent annual juvenile growth increment  $h$  is normally distributed around the population mean with a 5% coefficient of variation.

### 3. Results

#### 3.1 Impacts of angling mortality on the pike population

Size-selective recreational fishing effort substantially affected the fish stock as indicated by reduced equilibrium pike population densities (Fig. 3) and spawning potential ratio (SPR) values with increasing effort levels (Fig. 4, top panels). The unexploited equilibrium pike abundance density was 25 pike aged 1 and older  $\text{ha}^{-1}$ , declining strongly and collapsing at a realized effort level of about 130 annual angling-h  $\text{ha}^{-1}$  in the absence of harvest regulations (Fig. 3). The population-level effects of recreational angling were particularly pronounced at relaxed harvest regulations (i.e., low MinL-L or wide HSL-L, see Fig. 3 and left area in the top panels in Fig. 4). For example, the pike abundance density for fish aged 1 and older was reduced by 50% or more (i.e.,  $< 12.5$  pike  $\text{ha}^{-1}$ ) relative to the unexploited case at low MinL-L and reasonably wide upper bounds for the HSL-L regulation ( $\geq 80$  cm) when the realized angling effort levels exceeded about 100 annual angling-h  $\text{ha}^{-1}$ . Highest population densities of pike aged 1 and older were maintained under total catch-and-release policies, but population sizes at equilibrium were smaller than in the unexploited case due to hooking mortality (Fig. 3). Note that realized angling effort values in Fig. 3 correspond to regulation-specific maximum angling effort levels  $u$ . Due to density-dependent effort (Fig. 2 f) realized effort was generally lower than the maximum effort levels at equilibrium (Fig. 3). For example, at a MinL-L of 45 cm maximum effort levels of  $250 \text{ h ha}^{-1} \text{ yr}^{-1}$  resulted in a realized angling effort of only about  $125 \text{ h ha}^{-1} \text{ yr}^{-1}$  due to changes in the availability of pike due to harvesting, which reduced the attractiveness of the fishery, and hence realized angling effort. Note that in Figures 4-6 only two extreme forms for the maximum

414 annual angling effort per ha are displayed for illustrative purposes.

415         The equilibrium SPR of pike was greatest under total catch-and-release fisheries and did not  
416 fall below critical levels (0.35) at low maximum angling effort ( $u = 50$  angling-h  $ha^{-1}$   $yr^{-1}$ ) for all levels  
417 of harvest regulations (Fig. 4 top panels). However, when angling effort was high (maximum annual  
418 angling effort  $u = 250$  angling-h  $ha^{-1}$   $yr^{-1}$ ), the SPR dropped below 0.35 at wide HSL-Ls with an upper  
419 HSL-L bound of  $\geq 80$  cm and for low MinL-Ls of  $< 50$  cm. Also, at high maximum angling effort  
420 density the SPR under total catch-and-release regulations was up to 12% lower than at low maximum  
421 angling effort resulting from hooking mortality. Incorporation of size-dependent maternal effects on  
422 early survival of offspring (broken lines in top panels in Fig. 4) consistently influenced the predicted  
423 equilibrium SPR shifting it to lower values when existence of maternal effects on early survival was  
424 assumed. SPR may be overestimated by as much as 17 % when maternal effects on early survival are  
425 ignored when they are in fact present.

426         Exploitation under HSL-Ls and MinL-L regulations resulted in substantial age truncation of  
427 the pike population as indicated by the decreasing average age of spawners at both angling intensity  
428 levels and for all types of regulations (Fig. 4 bottom panels). Thus, truncation of the age and size  
429 structure of the pike population is inevitable whenever anglers start cropping the stock (see also Sup-  
430plementary Table 1). As to be expected, the decrease in the average age of spawners was most pro-  
431nounced at the highest maximum fishing effort level and for strongly relaxed harvest regulations.  
432 While the average age of spawners was always three years or older across all harvest regulations at low  
433 maximum angling effort levels, it dropped to values below three years on average at high maximum  
434 angling effort densities for MinL-L regulations of  $< 80$  cm and upper bounds for HSL-L of  $> 50$  cm  
435 (Fig. 4). Generally, HSL-L regulations resulted in a lower average age of spawners compared to  
436 MinL-L regulations, while total catch-and-release policies were the most efficient regulations at pre-  
437serving a more natural age structure (Fig. 4, bottom panels). At the same time, however, only HSL-L

were effective in preserving old and large fish in a stock at high angling effort levels. For example, while pike aged 7 years or older were extirpated at a maximum angling effort level of 250 angling-ha<sup>-1</sup> yr<sup>-1</sup> with MinL-Ls < 80 cm, they were preserved in the stock under HSL-L regulations with an upper bound of 80 cm or less, albeit at low relative abundances (Supplementary Table 1). In contrast to the results in terms of SPR, the age truncation effect of recreational harvesting was largely unaffected by size-dependent maternal effects on early survival (Fig. 4 bottom panels).

### **3.2 Impacts of angling mortality on fisheries quality**

Divergent patterns in equilibrium angler harvest in terms of numbers of pike harvested per ha and year were observed when comparing HSL-Ls and MinL-L relative to a baseline regulation of a small MinL-L of 45 cm (Fig. 5 top panels). At low maximum angling effort and a MinL-L of 45 cm, equilibrium harvest was about 3 pike ha<sup>-1</sup> yr<sup>-1</sup> falling to 2 fish ha<sup>-1</sup> yr<sup>-1</sup> at high maximum angling effort due to reduced pike abundance (Fig. 3). The protection of increasingly larger fish sizes through increasing MinL-L generally decreased harvest abundance across both maximum angling effort levels (Fig. 5 top panels). In contrast, at low maximum angling effort upper bounds of HSL-Ls of  $\geq 80$  cm resulted in harvest levels that were similar to a MinL-L of 45 cm, and only upper bounds of < 80 cm reduced equilibrium harvest abundance at low maximum angling effort relative to a MinL-L of 45 cm. At high maximum angling effort levels all HSL-L regulations except of highly restrictive upper bounds of  $\leq 50$  cm elevated harvest levels compared to a MinL-L of 45 cm. Equilibrium harvest was generally larger under HSL-L regulations compared to MinL-L regulations, with upper bounds for HSL-L between 60 and 80 cm providing largest harvest under high maximum angling effort. This indicated that saving large and old pike from harvest through HSL-Ls increased (up to 34% for constant, and 46% for asymptotic size-dependent maternal effects scenarios) rather than decreased harvest levels relative to the baseline situation of a small MinL-L of 45 cm at high effort levels. In contrast, at these high angling effort levels only a MinL-L of 50 cm resulted in an elevated harvest abundance level relative the



standard MinL-L of 45 cm, and larger MinL-L than 60 cm greatly reduced harvest abundance levels. Assumptions about size-dependent maternal effects on early survival of offspring changed predicted harvest levels only moderately, and only did so in the case of less restrictive harvest regulations (Fig. 5 top panels). Overall, predictions about equilibrium harvest levels with size-dependent maternal effects on early survival were up to 10 % lower than model runs without maternal effects on early survival of offspring.

Harvest regulations also substantially affected the average size of pike harvested by anglers at equilibrium. HSL-Ls resulted in a fairly consistent average harvest size of pike between 50 and 60 cm (total length) irrespective of its upper bound (Fig. 5 middle panels). In contrast, increasing MinL-L regulations promoted a sharp increase in the average harvested size of pike for both simulated maximum angling effort levels. Existence of size-dependent maternal effects on early survival did not affect the predicted average size of the harvested fish for either type of harvest regulation (Fig. 5 middle panels).

Increasingly stricter harvest regulations were predicted to substantially affect the relative catch (not to be confused with harvest) of large, memorable fish  $\geq 86$  cm total length (Fig. 5 bottom panels). Generally, catches of large fish were low with values  $< 1$  memorable pike  $\text{ha}^{-1} \text{yr}^{-1}$  at low maximum angling effort for all types of regulations. Highest catches of trophy fish were realized by total catch-and-release regulations. Both restrictive HSL-Ls (upper bound  $< 80$  cm) and large MinL-L  $> 70$  cm resulted in large increases in the catches of rare, memorable fish, by a factor of 1.9 – 4.8 at low angling intensities and by a factor of 15 – 130 at high maximum angling effort relative to the baseline condition of a MinL-L of 45 cm. Generally, HSL-Ls were more effective in maintaining high catch rates of large fish at both angling effort levels. Sharp increases in the catch of large pike were found at HSL-L regulations with an upper bound  $< 80$  cm at high angling effort. Similar increases were expressed only at highly restrictive MinL-L of  $> 70$  cm when angling is intense. Predicted increases in

catches of large memorable fish did not depend on size-dependent maternal effects on early survival of offspring at high angling effort density.

In terms of harvesting efficiency (i.e., the fraction harvested relative to all death resulting from fishing), HSL-Ls performed better in meeting high index levels than MinL-L. Except at an upper bound of 50 cm at high effort, index levels for HSL-Ls usually were  $> 0.5$  and were often close to 1 (Fig. 6). In contrast, MinL-Ls drastically reduced harvesting efficiency values falling close to zero at high MinL-Ls. This indicates that HSL-Ls result in less “cryptic” mortality through catch-and-release-induced hooking mortality compared to MinL-L regulations when upper bounds of HSL-L are at least 60 cm. Similar to the fishery variables examined above, assumptions about size-dependent maternal effects on early survival of offspring did not affect harvesting efficiency index (Fig. 6).

### 3.3 Model sensitivity

The sensitivity of the pike population model was investigated by analyzing changes in the absolute harvest to modification of input parameter values (Table 2). As to be expected, the absolute harvest was sensitive to changes in one parameter ( $\mu$ ) specifying the stock-recruitment relationship, and maximum immature growth rate ( $h_{\max}$ ). A 10% change of these parameters resulted in a change larger than 10% in the absolute harvest. SPR was fairly insensitive to changes in parameter values. With the exception of one parameter specifying life-time growth ( $h_{\max}$ ), a 10% change of most parameters caused only a few percent changes in the equilibrium SPR (Table 2). However, both absolute harvest and SPR were sensitive to changes in both the exponent of the length-weight regression  $\alpha_2$  and the exponent of the length-gonad weight regression  $\gamma_2$  (Table 2).

To verify the robustness of our results about the importance of the size-dependent maternal effect on early survival, SPR values under the assumption of an asymptotic relationship of early sur-

vival with pike size were compared with a simulation run with a no size-dependent maternal effects on early survival (Table 2). This relative SPR response variable (SPR with asymptotic maternal effect / SPR with constant maternal effect) was largely insensitive to changes of individual parameters by  $\pm 10\%$  (Table 2), indicating the robustness of the maternal effects results reported in this study.

#### 4. Discussion

Many fisheries managers interested in managing stocks for maximized harvest tend to set a minimum-length limit (MinL-L) in a way to allow at least one successful reproduction per individual and facilitating aggressive exploitation for harvest afterwards (Schäperclaus, 1960). In pike, this objective is usually achieved by setting the MinL-L to 45 - 50 cm because most pike individuals start to reproduce at much smaller sizes (Raatt, 1988). However, our model results suggest that intensive recreational exploitation of pike with low MinL-Ls can lead to recruitment overfishing and will also strongly change the size structure of pike stocks resulting in the loss of large fish in addition to an increase in the relative frequency of small and young size classes. This prediction agrees with various empirical studies in exploited pike populations (e.g., Pierce et al., 1995; Jolley et al., 2008; Pierce, in press). By contrast, our model suggests that a pike population can be effectively preserved, and SPR values  $\geq 0.35$  achieved, by increasing MinL-L regulations to values  $> 50$  cm. Increasing the MinL-L also benefits the size-structure of pike stocks. For example, in a long-term study on the effectiveness of various harvest regulations for maintaining size structure in pike stocks Pierce (in press) found that MinL-Ls of 76.2 cm strongly increased the abundance of pike  $\geq 50.8$  and  $\geq 61$  cm total length across various lake fisheries. However, such high MinL-Ls were not successful at increasing the abundance of pike above 76.2 cm total length relative to reference lakes without MinL-L regulations, and only maximum-length limits of 76.2 cm were able to conserve such large fish sizes in recreationally exploited stocks (Pierce, in press).

533           According to our model implementing harvestable-slot length limit (HSL-L) regulations with a  
534 lower bound of 45 cm and upper bounds  $\leq 80$  cm were as effective as appropriately designed MinL-L  
535 at avoiding recruitment overfishing in pike by keeping SPR values  $\geq 0.35$ . In addition and in line with  
536 empirical findings by Pierce (in press) in terms of maximum-length limits HSL-L regulations with an  
537 upper bound above which pike must be released also preserved large pike in the stock, albeit at low  
538 abundances. Thus, if the goal of harvest regulations in pike stocks is to maintain large fish in the stock  
539 and manage size structure, HSL-L (this study) or maximum-length limits (Pierce, in press) seem to  
540 constitute superior regulations to low or moderate MinL-L. However, if the goal of management in-  
541 tervention is to conserve the spawning stock of the pike population or its general biomass, our model  
542 did not suggest any substantial advantage of protection of large pike by implementation of HSL-L over  
543 the standard management by MinL-L regulations. In fact, MinL-L regulations of appropriate choice  
544 (i.e.,  $> 50$  cm) were predicted to be as or more effective as moderately wide HSL-Ls (e.g.,  $45 - \leq 80$   
545 cm) in protecting both abundance density of pike aged 1 and older, the spawning stock in terms of SPR  
546 values and maintaining a comparatively high average age of spawners. Thus, our model results suggest  
547 that distinct levels of protection offered to very large pike (implemented through HSL-L regulations) is  
548 not a necessary condition to conserve pike population abundance and spawning stock biomass in the  
549 face of recreational fishing exploitation. However, if the goal is also to conserve large pike in the stock,  
550 HSL-Ls are superior to MinL-Ls, and similar benefits can be expected from maximum-length limits  
551 (Pierce, in press). It is important to note that maintenance of large size classes of pike in a stock does  
552 not constrain the abundance and development of smaller size classes via increased cannibalism, as one  
553 might expect in this strongly cannibalistic species (Pierce, in press). This is possibly related to the fact  
554 that pike form spatially size-structured populations (Nilsson, 2006), and large fish tend to be found in  
555 less structured and more open water (Chapman and Mackay, 1984), thereby possibly decoupling the  
556 more vegetation bound smaller size classes (Grimm and Klinge, 1996) from large sized pike and their

557 predation pressure.

558         The outlook is different in terms of the relative benefits for fisheries quality offered by ap-  
559 propriately chosen HSL-L by preserving large pike in the stock . In fact, our model indicated that  
560 HSL-Ls of 45 –  $\leq$  80 cm outperformed MinL-L regulations for most of the chosen response metrics of  
561 fisheries quality. This is particularly so when the intention of the regulation is to increase the quality of  
562 the fishery in terms of provisioning of exceptionally large fish in the catch, while maintaining harvest  
563 levels of intermediate “kitchen-sized” pike high and unwanted hooking mortality low. Because  
564 HSL-Ls were found relatively more effective than MinL-L at maintaining large fish in the stock, these  
565 trophy fish accordingly occurred in the catch at a higher rate, particularly when fishing effort was high.  
566 Moreover, in terms of harvested pike numbers at high angling intensities, HSL-Ls with a wide range of  
567 upper limits resulted in conservation and even in increases in harvest relative to the default regulation  
568 of a MinL-L of 45 cm. By contrast, in our model increasing the MinL-L to values larger than 60 cm  
569 substantially reduced pike numbers harvested by anglers. This is in line with recent empirical findings  
570 (Pierce, in press). The reason for these differential reactions is the ability of large fecund pike protected  
571 by HSL-Ls, but not by MinL-L, to buffer intensive exploitation due to their overwhelmingly high  
572 larvae production potential maintaining recruitment despite absolute population size reductions. When  
573 HSL-L are used as management tools, the fast growth rates of pike allow them to grow after puberty  
574 and initial reproduction into the harvestable slot quickly, where they are harvested at intermediate sizes,  
575 after which they enter the safe zone to serve as large fecund spawner fish for future generations.

576         A further advantage of HSL-L over MinL-L in terms of fisheries variables related to the by far  
577 greater fraction of “wasted” fish under MinL-L regulations due to unwanted catch-and-release mor-  
578 tality compared to most HSL-L regulations with upper bounds  $> 60$  cm. This results from the generally  
579 greater abundance of small pike that are vulnerable to the angling gear but must be released under  
580 MinL-L regulations, thereby suffering from unintended catch-and-release mortality. This greater

degree of undesired bycatch mortality associated with MinL-Ls is of concern from an ethical perspective (Pine et al., 2008). This suggests that implementation of most types of HSL-L regulations in pike management may be ethically more advisable than high MinL-Ls.

We found that some model predictions as to the benefits of HSL-Ls and MinL-Ls for pike conservation and fishing quality were affected by the presence of size, and thus age, dependent maternal effects on early survival rate of pike. Ignoring such maternal effects on early life-history in pike was predicted to lead to overestimation of the equilibrium spawning stock and of harvest abundance by as much as 17% and 10%, respectively. This is in agreement with previous studies on the importance of maternal effects on early life-history traits for recruitment dynamics and fishery resiliency in various marine (Scott et al., 2006; Berkeley, 2006; Carr and Kaufman, 2009; Lucero, 2009; Venturelli et al., 2009) and freshwater fish stocks (Venturelli et al., in press). In pike, we found maternal effects on early survival rates to be relevant for SPR, and to a lesser degree for harvest abundance, but these maternal influences appeared largely irrelevant for other response metrics such as the average age of spawners, average harvest size or the harvesting efficiency. We also found that maternal effects on early survival of pike mattered more substantially at high than at low fishing effort levels. The differential importance of size-dependent maternal effects on early life-history traits for population and fisheries variables and their dependency on the degree of fishing mortality is in agreement with other modeling studies on marine fish by Lucero (2009) and O'Farrell and Botsford (2006). It results from the greater age and size truncation associated with high fishing mortality such that size or age dependent maternal effects matter more under these situations because the relative reproductive value of the otherwise less abundant large fish becomes more prominent. Note, however, that the beneficial effects of saving large pike from harvesting for fisheries quality in our model holds irrespective of the prevalence of size-dependent maternal effects on offspring survival. The reason relates to disproportionately greater fecundity of large individuals compared to small pike that maintains recruitment and

605 subsequently fishing quality (harvest, catch of large fish) despite the largely inevitable declines in  
606 population abundance that result from intensive harvesting under all forms of harvest regulations,  
607 unless they become overly strict.

608         In our model we included an empirically measured asymptotic size-dependent maternal effect  
609 on early pike survival, which translated into a relative survival advantage to age 1 of offspring from  
610 larger females. The mechanistic reason for this effect in pike is related to inferior egg quality of  
611 first-time spawners and lower size-at-hatching (Hubenova et al., 2007), which translates into greater  
612 mortality of offspring from first-time spawners relative to offspring from larger repeat spawners  
613 through competitive disability or intracohort cannibalism (Skov et al., 2003). The size-dependent  
614 maternal effect we included in our model assumed the lack of any form of reproductive senescence in  
615 pike, which agrees with recent findings by Pagel (2009). One might still argue that we underestimate  
616 the importance of size-dependent maternal effects on offspring traits for pike recruitment because the  
617 maternal effect mechanism we incorporated in our model was constrained to the relative survival  
618 advantage of pike offspring from larger-sized females during the first month of life (Arlinghaus, Faller,  
619 Wolter & Bekkevold, unpublished data, Fig. 2d) translated into differential first year survival. Thereby,  
620 we did not account for potential survival advantages of differently sized larvae resulting from posi-  
621 tively size-dependent intracohort competitive abilities and cannibalism (Skov et al., 2003) after age 1  
622 later in life. Acknowledging the fundamental importance of body size for survival in pike (Haugen et  
623 al., 2006), one could indeed assume that offspring originating from large females might experience a  
624 survival advantage throughout their lifetime by having a persistent size advantage to offspring from  
625 small pike. However, there is no empirical support for this hypothesis in pike justifying our conserv-  
626 ative assumption about size-dependent maternal effects on offspring survival in the present study. The  
627 possibility of other size-dependent mechanisms of maternal effects in pike, however, cannot be ruled  
628 out and should be investigated further. Our model is open to additions of important population dy-

namical processes if empirical evidence on alternative mechanisms of maternal effects or other biological or fishery processes accumulates for pike.

To add realism, we incorporated various processes of density-dependent compensation to fishing mortality (e.g., growth, fecundity, recruitment), which were not included in previous pike harvesting models (e.g., Dunning et al., 1982). We also included all known size-dependent relationships on reproductive parameters from the recent pike literature, such as length-dependent gonad weight (Edeline et al., 2007) and the positive relationship between size of females and egg sizes. Yet, our model may suffer from omission of important processes, which might also influence population dynamics of pike. In particular, we did not explicitly model size-dependent spawning timing in pike and its possible relation to temperature, food abundance and subsequent growth and survival of offspring. Yet, it is known from some inland water bodies that large-sized pike might spawn first in the season (Svårdson, 1949; Pagel, 2009), and equally common are protracted spawning seasons lasting 6-8 weeks (Farrell et al., 2006; Pagel, 2009). Thus, size-dependent maternal effects on offspring phenotypes and spawning timing can be confounded in pike, potentially inhibiting the expression of maternal effects on offspring traits such as growth if early spawning coincides with low temperature and low food availability. Indeed, Pagel (2009) reported a lack of a relationship between relative reproductive success and size of female pike during a single spawning season in a natural lake, and he also reported an inverse relationship between size of females and spawning timing. If these relationships also hold for other years and ecosystems, our model does not fully represent pike population dynamics and will need to be modified in the future. This is because even if size-dependent maternal effects on offspring traits do not materialize in nature in our model fecundity was assumed to increase disproportionately with size of female pike. This in turn implicitly fuelled a greater contribution to future generation by a large spawning fish compared to a small female. However, the study by Pagel (2009) suggests that a size-dependent “fecundity-effect” on relative reproductive success must not



necessarily be expected under natural conditions. Although this uncertainty remains, our model results predicting substantial fisheries benefits stemming from the protection of large pike through HSL-Ls suggest that various size-dependent maternal “influences” on reproduction (Venturelli et al., 2009) may play an important role in preservation of reproductive potential of a pike population, ultimately determining its resiliency to fishing-induced age and size truncation.

Our model predictions were found to be reasonably robust against variation of most parameters, however, some sensitive parameters were also identified. In particular, our model predictions were sensitive to one parameter determining the stock-recruitment function in pike. We used a Ricker-type stock-recruitment function reported by Minns et al. (1996) for pike, but the parameter values for this function were associated with large standard errors. Although a Ricker stock-recruitment function is a valid representation of pike recruitment (Edeline et al., 2008), this parameter uncertainty is an issue if our model is to be applied to make detailed predictions. Moreover, the sensitivity of model predictions to parameters specifying the stock-recruitment function suggests that all biological mechanisms affecting the recruitment of pike to age 1 as a function of a given size and composition of the spawning stock, such as all maternal influences on offspring survival (Venturelli et al., in press) or changes in vegetation structure increasing the carrying capacity of ecosystems for young-of-the-year pike (Grimm and Klinge, 1996), are important to develop sophisticated predictive models of pike population development for a given fishery. Similarly, when our model is applied to a particular fishery there is a need for a thorough assessment of the exponent  $\alpha_2$  in the length-weight regression, as this parameter exerted a large influence on the model predictions. Moreover, our growth model followed the bi-phasic growth model by Lester et al. (2004), which assumes that the exponent of the length-weight relationship ( $\alpha_2$ ) is 3. Therefore, changes to the model structure might be needed if our model is applied to a specific pike population where  $\alpha_2$  substantially differs from 3. Fortunately, for a given population this parameter can be accurately estimated as indicated by the high  $R^2$  reported in the li-

677 terature (0.95-0.99, Willis, 1989). This reduces the problem of parameter sensitivity for  $\alpha_2$  if our  
678 model is to be applied to a real fishery. It nevertheless is worthwhile to estimate the density depen-  
679 dence of  $\alpha_2$  further and include this process in extensions of our model. Finally, further empirical  
680 studies are needed to obtain more precise estimates for  $\gamma_2$ , being the exponent of the length-gonad  
681 weight regression. So far, only one study (Edeline et al., 2007) has been published reporting this re-  
682 lationship, and further research for other populations is needed before our model can be considered of  
683 general applicability for pike.

684         We used a deterministic model with no environmental stochasticity in the present paper, which  
685 is an oversimplified representation of pike population dynamics, despite is generally less variable  
686 between-year population size compared to other species with less pronounced cannibalism (Mills and  
687 Mann, 1985; Persson et al., 2004). However, even if stochastic recruitment or other biological varia-  
688 bility exists in nature this pattern does not change the major conclusions of our study because we  
689 investigated long-term average stock developments. In fact, keeping the model deterministic allowed  
690 relating model outcomes to variation of the parameters of interest (harvest regulations or maternal  
691 effects). Therefore and because we accounted for various pathways of density-dependent ecological  
692 feedback on vital rates as well as angling effort and illegal harvest (Sullivan, 2002), we argue that our  
693 approach is useful and our model results robust. In real fisheries, meaningful evaluation of  
694 length-based harvest restrictions will require long-term annual sampling efforts designed to monitor  
695 the fate of multiple year-classes of similar magnitudes during both pre-regulation and post-regulation  
696 periods (Pierce, in press). Before such research becomes available for pike, our model results in par-  
697 ticular with regard to HSL-L regulations should be viewed as scientifically supported hypotheses to  
698 inspire empirical work and help interpret empirical findings.

699         We examined a range of angling intensities and a range of harvest regulations in the present  
700 modelling study but we want to stress that angling intensity levels were in agreement with values

found in typical pike fisheries. A recent review showed that anglers can remove up to 80% of a target population within a single angling season (Lewin et al., 2006), and annual exploitation rates for pike with a moderate annual angling effort of 150 angling-h  $\text{ha}^{-1} \text{yr}^{-1}$  ranged between 47 and 74% in consumptive fisheries (Arlinghaus et al., 2009), but are lower in fisheries where anglers voluntarily release pike (Pierce et al., 1995). The maximum potential angling effort levels used in our model reached 250 angling-h  $\text{ha}^{-1} \text{yr}^{-1}$  but these values as well as the size-dependent vulnerability curves used were in accord with field studies on pike (Kempinger and Carline, 1978; Pierce et al., 1995; Margenau et al., 2003). We thus used realistic fishing intensities that can be expected in many pike fisheries world-wide (Arlinghaus et al., 2009).

## 5. Conclusions and Implications

Our study results in terms of population and fishery benefits of protecting large pike from recreational exploitation emphasize the superiority of a moderately wide HSL-Ls of 45 –  $\leq$  80 cm over a low MinL-L of 45 cm for managing pike effectively maintaining the population and large fish in the stock while benefiting the fishery. If both population-level and fishery benefits are jointly considered, such HSL-Ls were also found to be superior to high MinL-L of 60 cm or larger, particularly if exploitation is intense. This conclusion is in line with earlier research in freshwater salmonids (Clark et al., 1980; Jensen, 1981), but shall not be uncritically transferred to other life-histories that differ strongly from pike biology. However, in fast growing, early maturing species such as pike or walleye (Venturelli et al., in press), preservation of large fish in the stock through HSL-L, maximum-length limits (Pierce, in press), or even total catch-and-release where ethically and socially possible (see Arlinghaus, 2007), may represent a safeguard by which the high risk of mortality during the early life stages in response to a suite of unpredictable environmental factors is averaged out by repeated spawning over the lifetime of individual fish. It also reduces the importance of first-time spawners providing the bulk of egg

production as these fish typically have reduced egg quality (Hubenova et al., 2007). Preserving an extended age structure, in turn, increases the stability of the stock (Anderson et al., 2008). It has been speculated before that if the goal is to preserve large fish in a stock highly restrictive regulations are needed in fisheries for esocid species (Dunning et al., 1982; Simonson and Hewett, 1999), and our modeling results and recent findings by Pierce (in press) support this proposition. We conclude that preservation of old and large fecund pike in an exploited stock through variants of harvested slot length limits may offer benefits for conservation and increase fishing quality, in particular when angler value the catch of large-sized pike and ethical arguments are present for limiting “cryptic” hooking mortality associated with high minimum-length limits. However, non-compliance with regulations seems to be common in pike fisheries (Pierce and Tomcko, 1998). To encourage rule compliance with unfamiliar regulations, such as harvestable slot length limits, effective enforcement of regulations is needed along with good communication of the underlying objectives of the novel regulation (Page and Radomski, 2006; Walker et al., 2007).

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## 750 REFERENCES

- 751 Anderson, C.N.K., Hsieh, C., Sandin, S.A., Hewitt, R., Hollowed, A., Beddington, J., May, R.M.,  
 752 Sugihara, G., 2008. Why fishing magnifies fluctuations in fish abundance. *Nature* 452, 835-839.
- 753 Anderson, R.O., Neumann, R.M., 1996. Length, weight, and associated structural indices. In: Murphy,  
 754 B.R., Willis, D.W. (Eds.), *Fisheries Techniques* (2<sup>nd</sup> ed.). American Fisheries Society, Bethesda,  
 755 Maryland, pp. 447-482.
- 756 Arlinghaus, R., 2006. On the apparently striking disconnect between motivation and satisfaction in  
 757 recreational fishing: the case of catch orientation of German anglers. *North American Journal of*  
 758 *Fisheries Management* 26, 592-605.
- 759 Arlinghaus, R., 2007. Voluntary catch-and-release can generate conflict within the recreational an-  
 760 gling community: a qualitative case study of specialised carp (*Cyprinus carpio*) angling in  
 761 Germany. *Fisheries Management and Ecology* 14, 161-171.
- 762 Arlinghaus, R., Cooke, S.J., Lyman, J., Policansky, D., Schwab, A. Suski, C., Sutton, S.G., Thorstad,  
 763 E.B., 2007. Understanding the complexity of catch-and-release in recreational fishing: an inte-  
 764 grative synthesis of global knowledge from historical, ethical, social, and biological perspectives.  
 765 *Reviews in Fisheries Science* 15, 75-167.
- 766 Arlinghaus, R., Bork, M., Fladung, E., 2008. Understanding the heterogeneity of recreational anglers  
 767 across an urban-rural gradient in a metropolitan area (Berlin, Germany), with implications for  
 768 fisheries management. *Fisheries Research* 92, 53-62.
- 769 Arlinghaus, R., Matsumura, S., Dieckmann, U., 2009. Quantifying selection differentials caused by  
 770 recreational fishing: development of modeling framework and application to reproductive in-  
 771 vestment in pike (*Esox lucius*). *Evolutionary Applications* 2, 335-355.

772 Berkeley, S.A., 2006. Pacific rockfish management: are we circling the wagons around the wrong  
773 paradigm? *Bulletin of Marine Science* 78, 655-668.

774 Berkeley, S.A., Hixon, M.A., Larson, R.J., Love, M.S., 2004a. Fisheries sustainability via protection  
775 of age structure and spatial distribution of fish populations. *Fisheries* 29(8), 24-32.

776 Berkeley, S.A., Chapman, C., Sogard, S.M., 2004b. Maternal age as a determinant of larval growth  
777 and survival in a marine fish, *Sebastes melanops*. *Ecology* 85, 1258-1264.

778 Bernardo, J., 1996. Maternal effects in animal ecology. *American Zoologist* 36, 83-105.

779 Birkeland, C., Dayton, P.K., 2005. The importance in fishery management of leaving the big ones.  
780 *Trends in Ecology and Evolution* 20, 356-358

781 Carr, J.P., Kaufman, L., 2009. Estimating the importance of maternal age, size, and spawning expe-  
782 rience to recruitment of Atlantic cod (*Gadus morhua*). *Biological Conservation* 142, 477-487.

783 Caswell, H., 2001. *Matrix population models* (2nd edition). Sinauer Associates, Sunderland, U.S.A.

784 Chambers, R.C., Leggett, W.C., 1996. Maternal influences on variation in egg sizes in temperate  
785 marine fishers. *American Zoologist* 36, 180-196.

786 Chapman, L.J., Mackay, W.C., 1984. Direct observation of habitat utilization by northern pike. *Copeia*  
787 1984, 255-258.

788 Clark, R.D. Jr., Alexander, G.R., Growling, H., 1980. Mathematical description of trout-stream fish-  
789 eries. *Transactions of the American Fisheries Society* 109, 587-602.

790 Craig, J.F., (Ed.) 1996. *Pike: Biology and Exploitation*. Chapman & Hall, London, UK.

791 Craig, J.F., Kipling, C., 1983. Reproduction effort versus the environment; case histories of Win-  
792 dermere perch (*Perca fluviatilis* L.) and pike (*Esox lucius* L.). *Journal of Fish Biology* 22,  
793 713-727.

794 Diana, J.S., 1996. Energetics. In: Craig, J.F. (Ed.), *Pike: Biology and Exploitation*. Chapman & Hall,  
795 London, UK, pp. 103-124.

796 Dunning, D.J., Ross, Q., Gladden, J., 1982. Evaluation of minimum size limits for St. Lawrence river  
797 northern pike. *North American Journal of Fisheries Management* 2, 171-175.

798 Edeline, E., Carlson, S.M., Stige, L.C., Winfield, I.J., Fletcher, J.A. et al., 2007. Trait changes in a  
799 harvested population are driven by dynamic tug-of-war between natural and harvest selection.  
800 *Proceedings of the National Academy of Sciences U.S.A.* 104, 15799-15804.

801 Edeline, E., Ari, T.B., Vøllestad, L.A., Winfield, I.J., Fletcher, J.A., James, J.B., Stenseth, N.C., 2008.  
802 Antagonistic selection from predators and pathogens alters food-web structure. *Proceedings of*  
803 *the National Academy of Sciences U.S.A.* 105, 19792-19796.

804 Braña A., Nicieza, G., Toledo, M.M., 1992. Effects of angling on population structure of brown trout,  
805 *Salmo trutta* L., in mountain streams of Northern Spain. *Hydrobiologia* 237, 61-66.

806 Farrell, J.M., Mead, J.V., Murry, B.A., 2006. Protracted spawning of St. Lawrence river northern pike  
807 (*Esox lucius*): simulated effects on survival, growth, and production. *Ecology of Freshwater*  
808 *Fish* 15, 169-179.

809 Franklin, D.R., Smith Jr., L.L., 1963. Early life history of the northern pike (*Esox lucius* L.) with  
810 special reference to the factors influencing the numerical strength of year classes. *Transactions*  
811 *of the American Fisheries Society* 92, 91-110.

812 Grimm, M.P., Klinge, M., 1996. Pike and some aspects of its dependence on vegetation. In: Craig, J.F.  
813 (Ed.), Pike: Biology and Exploitation. Chapman & Hall, London, UK, pp. 125-156.

814 Goodyear, C.P., 1993. Spawning stock biomass per recruit in fisheries management: foundation and  
815 current use. Canadian Special Publication Fisheries and Aquatic Sciences 120, 67-81

816 Haugen, T.O., Winfield, I.J., Vøllestad, L.A., Fletcher, J.M., James, J.B., Stenseth, N.C., 2006. The  
817 ideal free pike: 50 years of fitness-maximizing dispersal in Windermere. Proceedings of the  
818 Royal Society B 273, 2917-2924.

819 Haugen, T.O., Winfield, I.J., Vøllestad, L.A., Fletcher, J.M., James, J.B., Stenseth, N.C., 2007. Den-  
820 sity dependence and density independence in the demography and dispersal of pike over four  
821 decades. Ecological Monographs 77, 483-502.

822 Heath, D.D., Blouw, D.M., 1998. Are maternal effects in fish adaptive or merely physiological side  
823 effects? In: Mousseau, T.A., Fox, C.W. (Eds.) Maternal effects as adaptations. Oxford Univer-  
824 sity Press, pp. 178-201.

825 Hsieh, C., Reiss, C.S., Hunter, J.R., Beddington, J.R., May, R.M., Sugihara, G., 2006. Fishing elevates  
826 variability in the abundance of exploited species. Nature 443, 859-862.

827 Hubenova, T., Zaikov, A., Vasileva, P., 2007. Investigation on fecundity, follicles and free embryo  
828 size of pond-reared pike (*Esox lucius*) of different age and size. Aquaculture International 15,  
829 235-240.

830 Isermann, D.A., 2007. Evaluating walleye length limits in the face of population variability: case  
831 studies from Western Minnesota. North American Journal of Fisheries Management 27,  
832 551-568.

833 Jensen, A.L., 1980. Optimum size limits for trout fisheries. Canadian Journal of Fisheries and Aquatic  
834 Sciences 38, 657-661.



835 Jolley, J.C., Willis, D.W., DeBates, T.J., Graham, D.D., 2008. The effects of mechanically reducing  
836 northern pike density on the sport fish community of West Long Lake, Nebraska, USA. *Fisheries*  
837 *Management and Ecology* 15, 251-258.

838 Kempinger, J.J., Carline, R.F., 1978. Dynamics of the northern pike population and changes that  
839 occurred with a minimum size limit in Escanaba Lake, Wisconsin. *American Fisheries Society*  
840 *Special Publications* 11, 382-389.

841 Larkin, P. A., 1977. An epitaph for the concept of maximum sustained yield. – *Transactions of the*  
842 *American Fisheries Society* 106, 1-11.

843 Law, R., 2007. Fisheries-induced evolution: present status and future directions. *Marine Ecology*  
844 *Progress Series* 335, 271-277.

845 Lester, N.P., Shuter, B.J., Abrams, P.A., 2004. Interpreting the von Bertalanffy model of somatic  
846 growth in fishes: the cost of reproduction. *Proceedings of the Royal Society B* 271, 1625-1631.

847 Lewin, W.-C., Arlinghaus, R., Mehner, T., 2006. Documented and potential biological impacts of  
848 recreational fishing: insights for management and conservation. *Reviews in Fisheries Science* 14,  
849 305-367.

850 Lindroth, A., 1946. Zur Biologie der Befruchtung und Entwicklung beim Hecht. *Mitteilungen der*  
851 *Anstalt der Binnenfischerei in Drottningholm* 24, 1-173.

852 Lukas, M.C., 1992. Spawning activity of male and female pike, *Esox lucius* L., determined by acoustic  
853 tracking. *Canadian Journal of Zoology* 70, 191-196.

854 Lorenzen, K., Enberg, K., 2002. Density-dependent growth as a key mechanism in the regulation of  
855 fish populations: evidence from among-population comparisons. *Proceedings of the Royal So-*  
856 *ciety B* 269, 49-54.

857 Lucero, Y., 2009. A multivariate stock-recruitment function for cohorts with sympatric subclasses:  
 858 application to maternal effects in rockfish (genus *Sebastes*). *Canadian Journal of Fisheries and*  
 859 *Aquatic Sciences* 66, 557-564.

860 Mace, P.M., 1994. Relationships between common biological reference points used as thresholds and  
 861 targets of fisheries management strategies. *Canadian Journal of Fisheries and Aquatic Sciences* 51,  
 862 110-122.

863 Marshall, D.J., Allen, R.M., Crean, A.J., 2008. The ecological and evolutionary importance of ma-  
 864 ternal effects in the sea. *Oceanography and Marine Biology: An Annual Review* 46, 203-205.

865 Margenau, T.L., Gilbert, S.J., Hatzenbeler, G.R., 2003. Angler catch and harvest of northern pike in  
 866 northern Wisconsin lakes. *North American Journal of Fisheries Management* 23, 307-312.

867 Miller, T.J., Crowder, L.B., Rice, J.A., Marschall, E.A., 1988. Larval size and recruitment mechanisms  
 868 in fishes: toward a conceptual framework. *Canadian Journal of Fisheries and Aquatic Sciences*,  
 869 45, 1657–1670.

870 Mills, C.A., Mann, R.H.K., 1985. Environmentally-induced fluctuations in year-class strength and  
 871 their implications for management. *Journal of Fish Biology* 27 (Suppl.A), 209-226.

872 Minns, C.K., Randall, R.G., Moore, J.E., Cairns, V.W., 1996. A model simulating the impact of habitat  
 873 supply limits on northern pike (*Esox lucius*) in Hamilton Harbour, Lake Ontario. *Canadian*  
 874 *Journal of Fisheries and Aquatic Sciences* 53(Suppl. 1), 20-34.

875 Murawski, S.A., Rago, P.J., Trippel, E.A., 2001. Impacts of demographic variation in spawning  
 876 characteristics on reference points for fishery management. *ICES Journal of Marine Science* 58,  
 877 1002-1014.

878 Nilsson, P.A., 2006. Avoid your neighbours: size-determined spatial distribution patterns among  
879 northern pike individuals. *Oikos* 113, 251-258.

880 Noble, R.L., Jones, T.W., 1999. Managing fisheries with regulations. In: Kohler, C.C., Hubert, W.A.  
881 (Eds.) *Inland fisheries management in North America* (2<sup>nd</sup> ed.). American Fisheries Society,  
882 Bethesda, Maryland, pp. 455-480.

883 O'Farrell, M.R., Botsford, L.W., 2006. The fisheries management implications of mater-  
884 nal-age-dependent larval survival. *Canadian Journal of Fisheries and Aquatic Sciences* 63,  
885 2249-2258.

886 Ottersen, G., 2008. Pronounced long-term juvenation in the spawning stock of Arcto-Norwegian cod  
887 (*Gadus morhua*) and possible consequences for recruitment. *Canadian Journal of Fisheries and*  
888 *Aquatic Sciences* 65, 523-534.

889 Page, K.S., Radomski, P., 2006. Compliance with sport fishery regulations in Minnesota as related to  
890 regulation awareness. *Fisheries* 31, 166-178.

891 Pagel, T., 2009. Determinants of individual reproductive success in a natural pike (*Esox lucius* L.)  
892 population: a DNA-based parentage assignment approach. Master Thesis, Humboldt-University  
893 of Berlin (available at [http://www.adaptfish.rem.sfu.ca/Theses/Thesis\\_MSc\\_Pagel.pdf](http://www.adaptfish.rem.sfu.ca/Theses/Thesis_MSc_Pagel.pdf))

894 Paukert, C.P., Klammer, J.A., Pierce, R.B., Simonson, T.D., 2001. An overview of northern pike  
895 regulations in North America. *Fisheries* 26, 6-13.

896 Paul, A.J., Post, J.R., Stelfox, J.D., 2003. Can anglers influence the abundance of native and nonnative  
897 salmonids in a stream from the Canadian Rocky Mountains? *North American Journal of Fi-*  
898 *sheries Management* 23,109-119.

899 Persson, L., de Roos, A.M., Bertolo, A., 2004. Predicting shifts in dynamics of cannibalistic field  
 900 populations using individual-based models. *Proceedings of the Royal Society London B* 271,  
 901 2489-2493.

902 Pierce, R.B., in press. Long term evaluations of length limit regulations for northern pike in Minnesota.  
 903 *North American Journal of Fisheries Management* 30, 000-000.

904 Pierce, R.B., Tomcko, C.M., 1998. Angler noncompliance with slot length limits for northern pike in  
 905 five Minnesota lakes. *North American Journal of Fisheries Management* 18, 720-724.

906 Pierce, R.B., Tomcko, C.M., Schupp, D.H., 1995. Exploitation of northern pike in seven small  
 907 North-Central Minnesota lakes. *North American Journal of Fisheries Management* 15, 601-609.

908 Pine III, W.E., Martell, S.J.D., Jensen, O.P., Walters, C.J., Kitchell, J.F., 2008. Catch-and-release and  
 909 size limit regulations for blue, white, and striped marlin: the role of postrelease survival in ef-  
 910 fective policy design. *Canadian Journal of Fisheries and Aquatic Sciences* 65, 975-988.

911 Post, J. R., Sullivan, M., Cox, S., Lester, N. P., Walters, C. J., Parkinson, E. A., Paul, A. J., Jackson, L.,  
 912 Shuter, B. J., 2002. Canada's recreational fisheries: the invisible collapse? *Fisheries* 27(1), 6-15.

913 Post, J.R., Mushens, C., Paul, A., Sullivan, M., 2003. Assessment of alternative harvest regulations for  
 914 sustaining recreational fisheries: model development and application to bull trout. *North*  
 915 *American Journal of Fisheries Management* 23, 22-34.

916 Quince, C., Abrams, P.A., Shuter, B.J., Lester, N.P., 2008. Biphase growth in fish II: empirical as-  
 917 sessment. *Journal of Theoretical Biology* 254, 207-214.

918 Raat, A.J.P., 1988. Synopsis of biological data on the northern pike (*Esox lucius* Linnaeus, 1758).  
 919 *FAO Fisheries Synopsis* 30, Review 2. FAO, Rome, Italy.

920 Schaefer, M.B., 1957. A study of the dynamics of the fishery for yellowfin tuna in the Eastern Tropical  
 921 Pacific Ocean. *Inter-American Tropical Tuna Commission Bulletin* 2, 247-285.

- 922 Schäperclaus, W. (1960): Fischereiwirtschaftslehre (Seen- und Flusswirtschaft). In: Wundsch, H.H.  
 923 (Ed.) Fischereikunde: Eine Einführung für die Praxis (2. Aufl.). Neumann Verlag, Radebeul  
 924 und Berlin, pp. 154-194.
- 925 Scott, B.E, Marteinsdottir, G., Begg, G.A., Wright, P.J., Kjesbu, O.S., 2006. Effects of population  
 926 size/age structure, condition and temporal dynamics of spawning on reproductive output in  
 927 Atlantic cod (*Gadus morhua*). *Ecological Modelling* 191, 383-415.
- 928 Shuter, B.J., Lester, N.P., LaRose, J., Purchase, C.F., Vascotto, K., Morgan, G., Collins, N.C., Abrams,  
 929 P.A., 2005. Optimal life histories and food web position: linkages among somatic growth, re-  
 930 productive investment and mortality. *Canadian Journal of Fisheries and Aquatic Sciences* 62,  
 931 738-746.
- 932 Silliman, R.P., Gutsell, J.S., 1958. Experimental exploitation of fish populations. *Fishery Bulletin* 58,  
 933 215-241.
- 934 Simonson, T.D., Hewett, S.W., 1999. Trends in Wisconsin's muskellunge fishery. *North American*  
 935 *Journal of Fisheries Management* 19, 291-299.
- 936 Skov, C., Jacobsen, L., Berg, S., 2003. Post-stocking survival of 0+ year pike in ponds as a function of  
 937 water transparency, habitat complexity, prey availability and size heterogeneity. *Journal of*  
 938 *Fish Biology* 62, 311-322.
- 939 Sullivan, M. G. 2002. Illegal angling harvest of walleyes protected by length limits in Alberta. *North*  
 940 *American Journal of Fisheries Management* 22, 1053-1063.
- 941 Trippel, E.A., 1993. Relations of fecundity, maturation, and body size of lake trout, and implications  
 942 for management of Northwestern Ontario lakes. *North American Journal of Fisheries Man-*  
 943 *agement* 13, 64-72.

944 Venturelli, P.A., Shuter, B.J., Murphy, C.A., 2009. Evidence for harvest-induced maternal influences  
 945 on the reproductive rates of fish populations. *Proceedings of the Royal Society London B* 276,  
 946 919-924.

947 Venturelli P. A., Murphy, C.A., Shuter, B.J., Johnston, T.A., deGroot, P.J., Boag, P.T., Casselman, J.  
 948 M., Montgomerie, R., Weigand, M. D., Legget, W. C., in press. Maternal influences on popu-  
 949 lation dynamics: evidence from an exploited freshwater fish. *Ecology*.

950 Willis, D.W., 1989. Proposed standard length-weight equation for northern pike. *North American*  
 951 *Journal of Fisheries Management* 9, 203-208.

952 Wootton, R J., 1998. *Ecology of teleost fishes* (2<sup>nd</sup> ed.). Chapman & Hall, London, U.K.

953 Worm B., Hilborn, R., Baum, J.K., Branch, T.A., Collie, J.S., Costello, C., Fogarty, M.J., Fulton, E.A.,  
 954 Hutchings, J.A., Jennings, S., Jensen, O.P., Lotze, H.K., Mace, P.A., McClanahan, T.R., Minto,  
 955 C., Palumbi, S.R., Parma, A.M., Ricard, D., Rosenberg, A.A., Watson, R., Zeller, D., 2009.  
 956 Rebuilding global fisheries. *Science* 325, 578-585.

957 Wright, R.M., Shoesmith, E.A., 1988. The reproductive success of pike (*Esox lucius*): aspects of  
 958 fecundity, egg density and survival. *Journal of Fish Biology* 33, 623-636.

959 Wright, R.M., 1990. The population biology of pike, *Esox lucius* L., in two gravel pit lakes, with  
 960 special reference to early life history. *Journal of Fish Biology* 36, 215-229.

961 Wright, P.J., Trippel, E.A., 2009. Fishery-induced demographic changes in the timing of spawning:  
 962 consequences for reproductive success. *Fish and Fisheries* 10, 283-304.

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964

965 **Table 1.** Life-history parameters for a pike population exploited by recreational fisheries. Parameters  
966 and symbols are arranged according to biological and recreational angling processes. – indicates ratio  
967 scales or dimensionless parameters fitted to empirical data.

Symbol		Equat	Value	Unit	Source	Population**
		ion				
<b>Biological processes</b>						
$a_{\max}$	maximum age		11	yr	Raat (1988)	G
$h$	annual juvenile growth increment	2	16.725 (initial value in year $t$ $= 1$ )	cm	Own calculations	(W)
$t_1$	(growth trajectory)	2	-0.423		Own calculations	(W)
$L_M$	length at maturation (onset of reproduc- tive investment)		20	cm	Raat (1988)	G
$\alpha_1$	(length-weight rela- tionship)*	3	$4.8 \times 10^{-6}$	kg	Willis (1989)	A
$\alpha_2$	(length-weight rela- tionship)	3	3	–	See text	O
$L_u$	–	3	1	cm	unit	–
$h_{\max}$	maximum annual juvenile growth increment	5	27.094	cm	Own calculations	(W)
$\beta_1$	(density-dependent	5	0.18190	–	Own calculations	(W)

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	growth)					
$\beta_2$	(density-dependent growth)	5	0.56783	–	Own calculations	(W)
$D_u$	–	5	1	kg ha <sup>-1</sup>	unit	–
$\psi$	(hatching rate, constant)	6	0.735	–	Franklin and Smith (1963)	A
$\rho$	(density-dependent relative fecundity)	7	0.04818	ha kg <sup>-1</sup>	Craig and Kipling (1983)	W
$\gamma_1$	(relationship between female length and gonad weight)	8	$1.01 \times 10^{-5}$	g	Own calculations	(W)
$\gamma_2$	(relationship between female length and gonad weight)	8	4.01	–	Edeline et al. (2007)	W
$\omega$	relative caloric density of eggs compared to soma	9	1.22	–	Diana (1983)	A
$\delta_1$	(relationship between female length and egg size)	10	$2.95 \times 10^{-5}$	g cm <sup>-1</sup>	Lindroth (1946)	E
$\delta_2$	(relationship between female length and egg size)	10	$5.15 \times 10^{-3}$	g	Lindroth (1946)	E

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$s_{0\max}$	(first-year mortality)	11	$4.76 \times 10^{-4}$	–	$\exp(f_a)$ in Minns et al. (1996)	A
$\kappa$	(first-year mortality)	11	31.73	–	$-f_b$ in Minns et al. (1996)	A
$\mu$	(first-year mortality)	11	0.31	–	$f_c$ in Minns et al. (1996)	A
$B_{1/2}$	(first-year mortality)	11	$1.68362 \times 10^9$	lar- vae $\text{ha}^{-1}$	$f_d^{1/f_c}$ in Minns et al. (1996)	A
$\tau_0$	(natural mortality)	13	2.37 (small pike), 1.555 (large pike)	–	Haugen et al. (2007)	(W)
$\tau_x$	(natural mortality)	13	-0.02 (small pike), 0.40 (large pike)	–	Haugen et al. (2007)	(W)
$\tau_y$	(natural mortality)	13	-0.29 (small pike), -0.88 (large pike)	–	Haugen et al. (2007)	(W)
$\tau_L$	(natural mortality)	13	0.25 (small pike),	–	Haugen et al. (2007)	(W)

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			0.00 (large pike)			
$\lambda_1$	(early survival)	14	0.9191	–	See text	O
$\lambda_2$	(early survival)	14	4.1	$\text{cm}^{-1}$	See text	O
$\lambda_3$	(early survival)	14	0.059	–	See text	O
<b>Angling processes</b>						
$\eta$	(vulnerability)	15	0.25	$\text{cm}^{-1}$	See text	O
$\theta$	(vulnerability)	15	1300	–	See text	O
u	maximum angling effort	17	varied up to 250	$\text{h ha}^{-1}$ $\text{yr}^{-1}$	See text	G
p	proportion of an- gling effort always present	17	0.5	–	See text	O
$N_{v,1/2}$	(numerical response of angling effort to fish availability)	17	10	fish $\text{ha}^{-1}$	See text	O
$\xi$	(numerical response of angling effort to fish availability)	17	5	–	See text	O
q	catchability	18, 20	0.01431	$\text{ha h}^{-1}$	Own value	O
$\phi$	hooking mortality	19	0.094	–	Munoeke and Childress (1994)	A

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$\varepsilon$	(non-compliance mortality)	20	1.25	–	Sullivan (2002)	X
$\zeta$	(non-compliance mortality)	20	-0.84	–	Sullivan (2002)	X
$C_u$	–	20	1	fish $h^{-1}$	unit standardizing factor	–

968 \* When symbol names are parenthesized, the symbols are parameters in a certain relationship. For  
969 example, (length-weight relationship) means that the symbol represents a parameter in the  
970 length-weight relationship.

971 \*\* W: Windermere, U.K., E: Europe other than Windermere, A: North America, G: global database,  
972 X: taken from other species than pike, O: own calculation. Location symbols in parentheses represent  
973 own calculation based on data from a particular location. For example, (W) means that we calculated  
974 the parameter value from original data at Windermere.

975

976

977 **Table 2.** Sensitivity analysis of three variables [absolute harvest in terms of numbers of pike,  
978 spawning potential ratio (SPR), and SPR with asymptotic early survival relative to constant early  
979 survival with female size]. Parameter order and values follow Table 1. We chose an intermediate  
980 maximum angling effort ( $u = 150 \text{ h ha}^{-1} \text{ yr}^{-1}$ ), a harvest regulation of a harvestable-slot length limit of  
981  $45 - 70 \text{ cm}$ , and an asymptotic increase of early survival probability of offspring with their mother's  
982 size for the analysis of the first two variables. We also tested the constant maternal effect scenario for  
983 the first two variables and found qualitatively the same results. Percent changes for the first three  
984 variables when the default value of each parameter is altered by  $\pm 10\%$  are shown. Changes in response  
985 variables  $\geq |10\%|$  (i.e., sensitive/elastic changes) are highlighted in bold.

Parameters	Absolute harvest		SPR		SPR compared to constant early sur- vival <sup>1</sup>	
	+10%	-10%	+10%	-10%	+10%	-10%
$t_1$	0.4	-1.1	0.5	-0.4	0.3	-0.3
$L_M$	-0.6	0.0	1.5	-0.5	0.0	0.6
$\alpha_1$	-2.7	2.0	4.2	-4.2	-0.1	0.3
$\alpha_2$	<b>-44.4</b>	0.4	<b>63.3</b>	<b>-59.3</b>	1.0	2.0
$h_{\max}$	<b>10.7</b>	<b>-12.3</b>	<b>13.5</b>	<b>-12.3</b>	1.5	-1.1
$\beta_1$	-4.2	3.8	-3.4	5.0	0.2	0.5
$\beta_2$	-4.8	4.4	-2.3	4.5	-0.1	0.5
$\psi$	5.1	-6.3	-0.8	1.3	-0.3	0.5
$\rho$	-2.5	1.6	5.0	-4.2	0.6	0.4
$\gamma_1$	3.2	-4.1	-2.6	3.2	0.1	0.2
$\gamma_2$	<b>55.3</b>	<b>-65.9</b>	<b>-11.1</b>	<b>25.3</b>	-8.0	2.9
$\omega$	-2.3	1.6	-1.7	2.2	0.1	0.1
$\delta_1$	-2.0	1.6	0.8	-0.5	0.7	0.0
$\delta_2$	-4.2	3.8	0.9	-0.6	0.4	-0.2
$s'_{0\max}$	7.9	-8.7	-1.0	1.5	0.1	0.5
$\kappa$	-9.3	9.1	1.9	-1.0	1.0	-0.2
$\mu$	<b>27.3</b>	<b>-31.7</b>	-3.2	5.5	-1.4	1.6
$B_{1/2}$	1.9	-3.3	0.0	0.8	0.3	0.3

$\tau_0$ (small pike)	6.4	-8.0	0.1	0.3	-0.1	0.3
$\tau_0$ (large pike)	1.6	-2.5	-0.1	0.7	-0.1	0.4
$\tau_x$ (small pike)	-0.1	-0.3	0.1	0.1	0.1	0.1
$\tau_x$ (large pike)	-1.2	0.4	0.1	0.2	0.2	0.0
$\tau_y$ (small pike)	1.1	-1.6	-0.3	0.6	-0.1	0.4
$\tau_y$ (large pike)	1.5	-1.9	1.0	-0.8	0.2	0.5
$\tau_L$ (small pike)	-1.8	1.3	0.5	-0.2	0.4	0.0
$\tau_L$ (large pike)	0.0	0.0	0.0	0.0	0.0	0.0
$\lambda_1$	-1.1	0.0	0.3	0.8	0.3	0.8
$\lambda_2$	1.4	-2.7	0.8	-0.1	0.8	-0.1
$\lambda_3$	5.7	-6.9	-0.5	1.0	-0.5	1.0
$\eta$	-3.4	2.2	-2.9	2.4	0.1	0.1
$\theta$	0.0	-0.8	0.4	-0.1	0.1	0.1
$p$	-0.9	-0.3	-1.0	1.9	0.1	0.8
$N_{v,1/2}$	0.5	-1.6	2.7	-2.7	0.2	0.0
$\xi$	0.0	-0.4	0.1	0.2	0.1	0.3
$q$	-1.7	0.8	-3.0	3.7	0.0	0.4
$\phi$	-2.1	1.4	-0.4	0.8	0.1	0.1
$\varepsilon$	-0.2	-0.6	0.1	0.6	0.4	0.9
$\zeta$	-0.6	-0.4	0.6	0.6	0.9	0.9

<sup>1</sup> SPR relative to the case when the constant size-dependent early survival is assumed.

## 988 **Figure captions**

989 Fig. 1. Overview about population dynamical and fisheries biological assumptions used in the pike  
990 model. Plots (a) and (b) represent assumptions of density-dependence in growth, plots (c) and (e)  
991 represent assumptions of fecundity and stock-recruitment, plot (d) shows the two scenarios of maternal  
992 effects on first month survival (dots represent empirical values), and plot (f) represents assumptions  
993 about density dependent angling effort. In plot (a), the solid and dashed line represent the cases of no  
994 fishing ( $u = 0$ ) and medium fishing intensity ( $u = 150$ ) for illustrative purposes, respectively ( $u =$   
995 maximum angling effort in annual angling-h  $\text{ha}^{-1} \text{yr}^{-1}$ ).

996  
997 Fig. 2. Flow diagram summarizing relationships between biological and fishery processes in the pike  
998 model. Equation numbers are shown in parentheses. Density-dependent processes are in italics. GSI =  
999 gonadasomatic index.

1000

1001 Fig. 3. Population density of pike aged 1 and older ( $\# \text{ha}^{-1}$ ) at equilibrium as a function of realized  
1002 annual angling effort  $\text{ha}^{-1} \text{yr}^{-1}$  for various minimum-length limit regulations (MinL-L, left panel) and  
1003 harvestable-slot limit regulations (HSL-L, right panel). The lower bound of the harvestable-slot length  
1004 limits in the right panels is 45 cm. To highlight the difference between realized and maximum annual  
1005 angling effort, for a particular regulation type and realized effort levels dots indicate a corresponding  
1006 low maximum potential effort density  $u = 50$  annual angling-h  $\text{ha}^{-1}$  and open squares indicate a cor-  
1007 responding high maximum potential angling effort density  $u = 250$  annual angling-h  $\text{ha}^{-1}$ . These two  
1008 scenarios were used in Figs. 4 to 7. NR = no regulation case, total C&R = total catch-and-release  
1009 fishing.

1010

1011 Fig. 4. Spawning potential ratio (SPR) (top panels) and average age of spawners (bottom panels) in

1012 response to two levels of maximum angling effort (low and high by varying the parameter  $u = \text{max-}$   
1013  $\text{imum angling effort in annual angling-h ha}^{-1} \text{ yr}^{-1}$ ) at minimum-length limit regulations (left panels)  
1014 and harvestable-slot limit regulations (right panels). The lower bound of the harvestable-slot length  
1015 limits in the right panels is 45 cm. In each panel results of two scenarios of age-dependent maternal  
1016 effects on early survival are depicted. C&R = total catch-and-release angling. The horizontal line in  
1017 top panels indicates a theoretical reference point for recruitment overfishing that should not be sur-  
1018 passed for precautionary reasons.

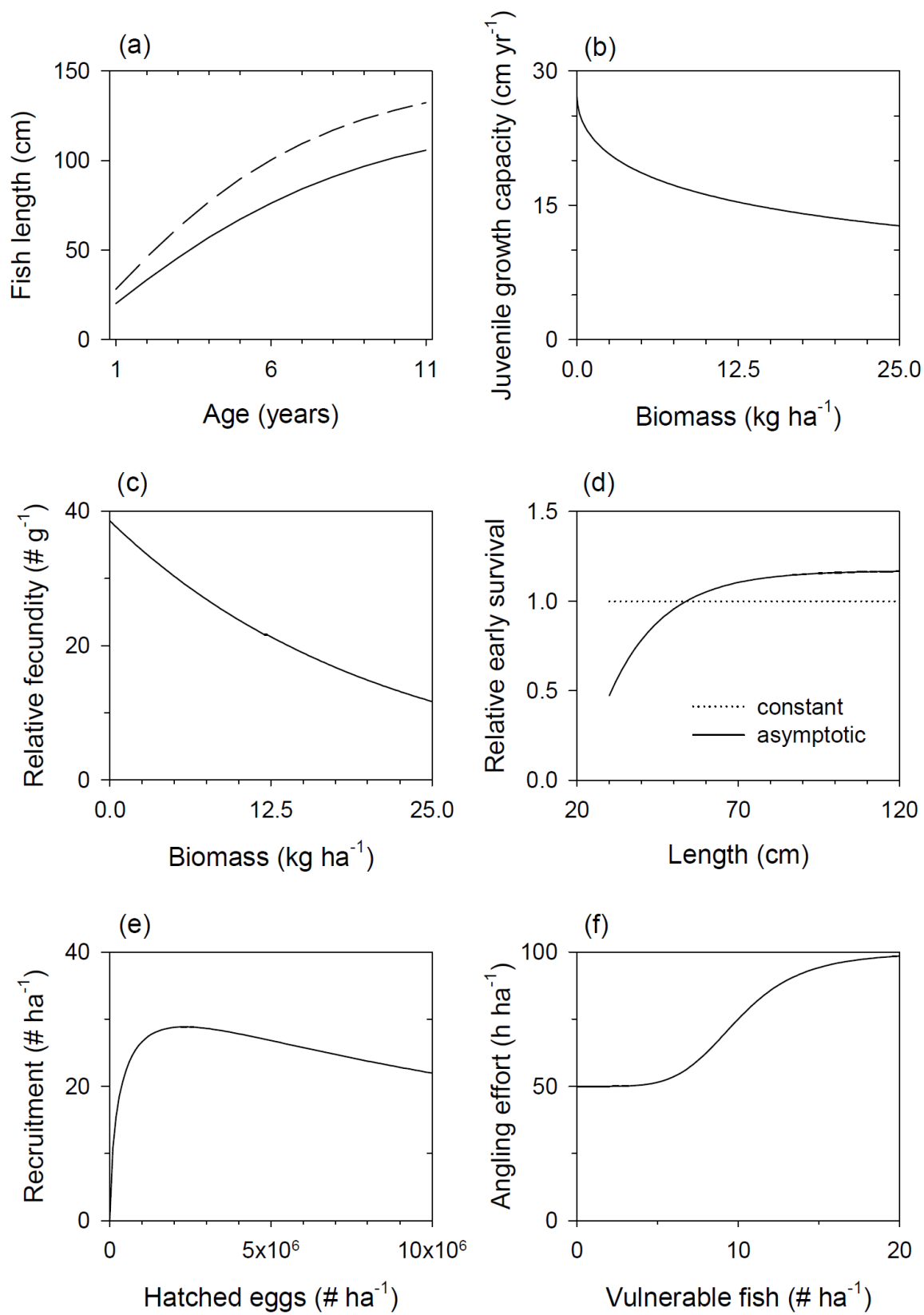
1019

1020 Fig. 5. Equilibrium harvest of pike (in terms of numbers, top panels), equilibrium average size of  
1021 harvested pike (total length in cm, middle panels) and equilibrium catch of large fish  $\geq 86$  cm total  
1022 length in response to two levels of maximum angling effort (low and high by varying the parameter  
1023  $u = \text{maximum angling effort in annual angling-h ha}^{-1} \text{ yr}^{-1}$ ) at minimum-length limit regulations (left  
1024 panels) and harvestable-slot limit regulations (right panels). The lower bound of the harvestable-slot  
1025 length limits in the right panels is 45 cm. In each panel results of two scenarios of age-dependent  
1026 maternal effects on early survival are depicted. C&R = total catch-and-release angling.

1027

1028 Fig. 6. Harvesting efficiency (total harvest in numbers relative to total deaths) at equilibrium in re-  
1029 sponse to two levels of maximum angling effort (low and high by varying the parameter  $u = \text{maximum}$   
1030  $\text{angling effort in annual angling-h ha}^{-1} \text{ yr}^{-1}$ ) at minimum-length limit regulations (left panel) and har-  
1031 vestable-slot limit regulations (right panel). The lower bound of the harvestable-slot length limits in  
1032 the right panels is 45 cm. In each panel results of two scenarios of age-dependent maternal effects on  
1033 early survival are depicted.

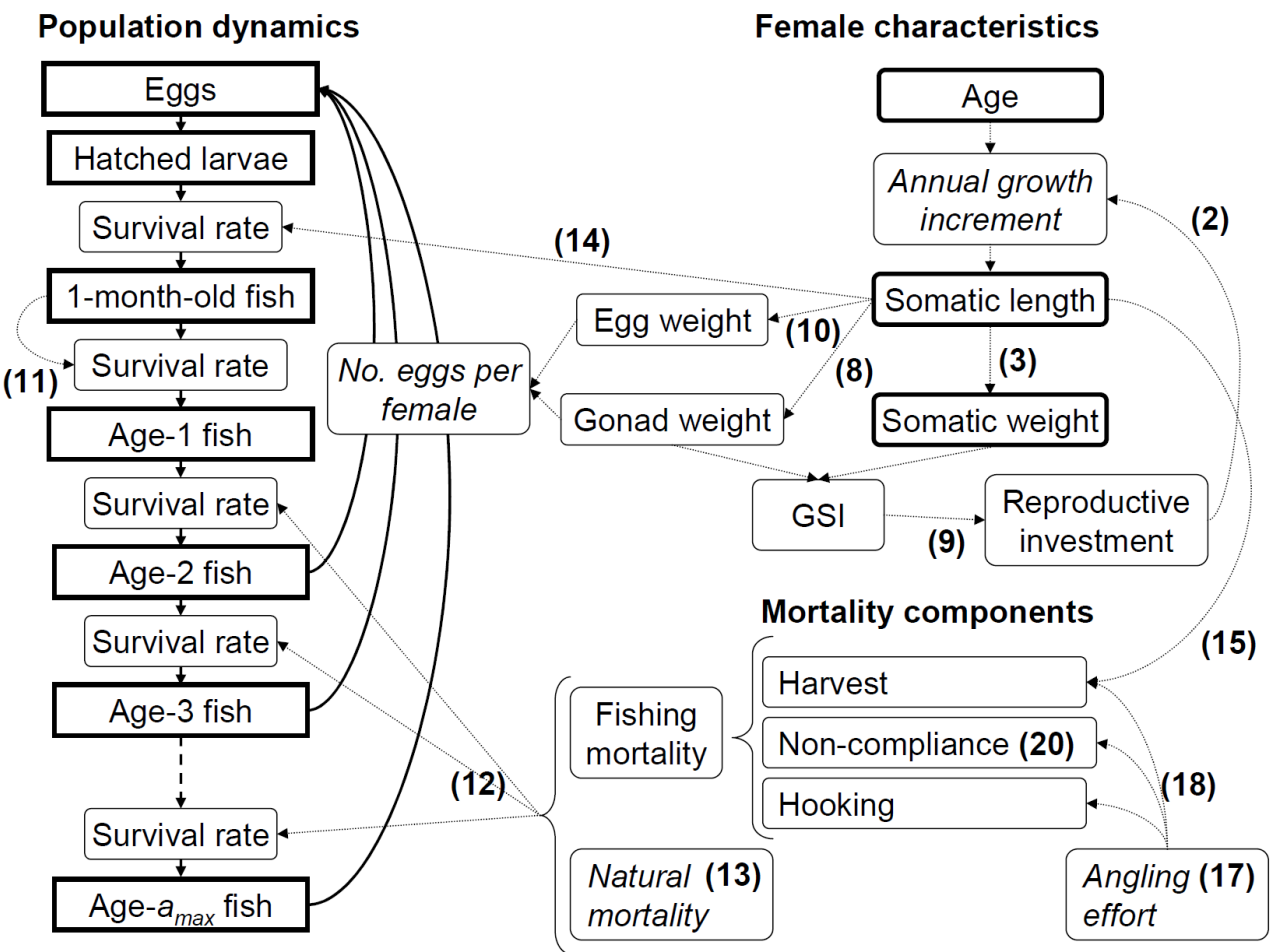
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1038 Fig. 2

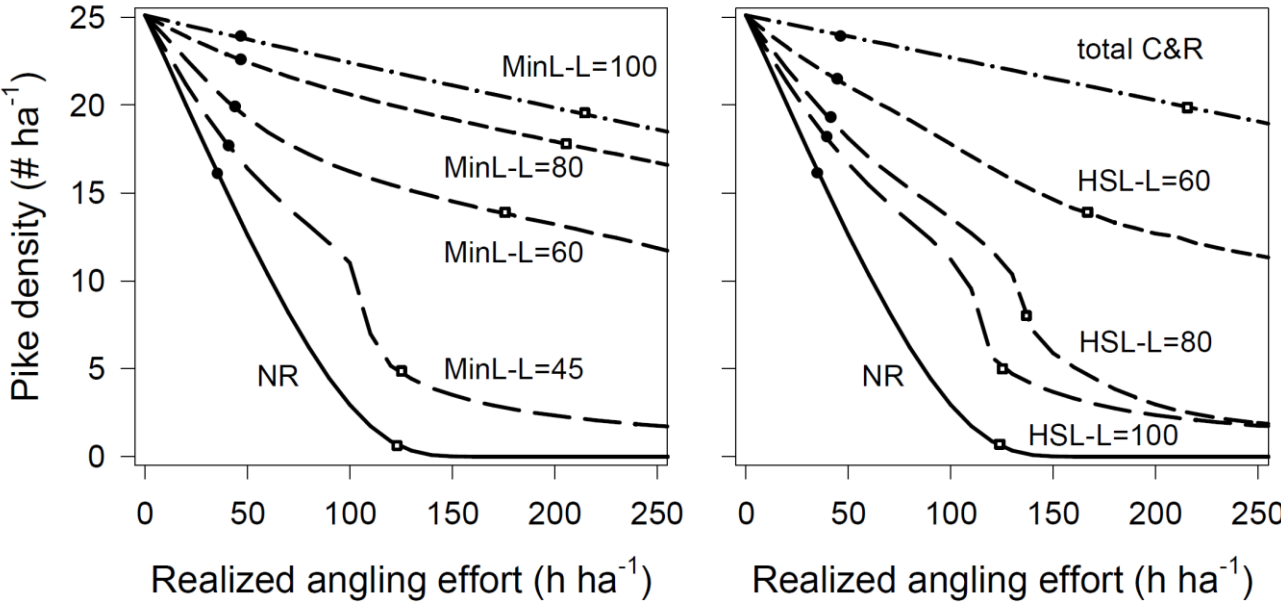
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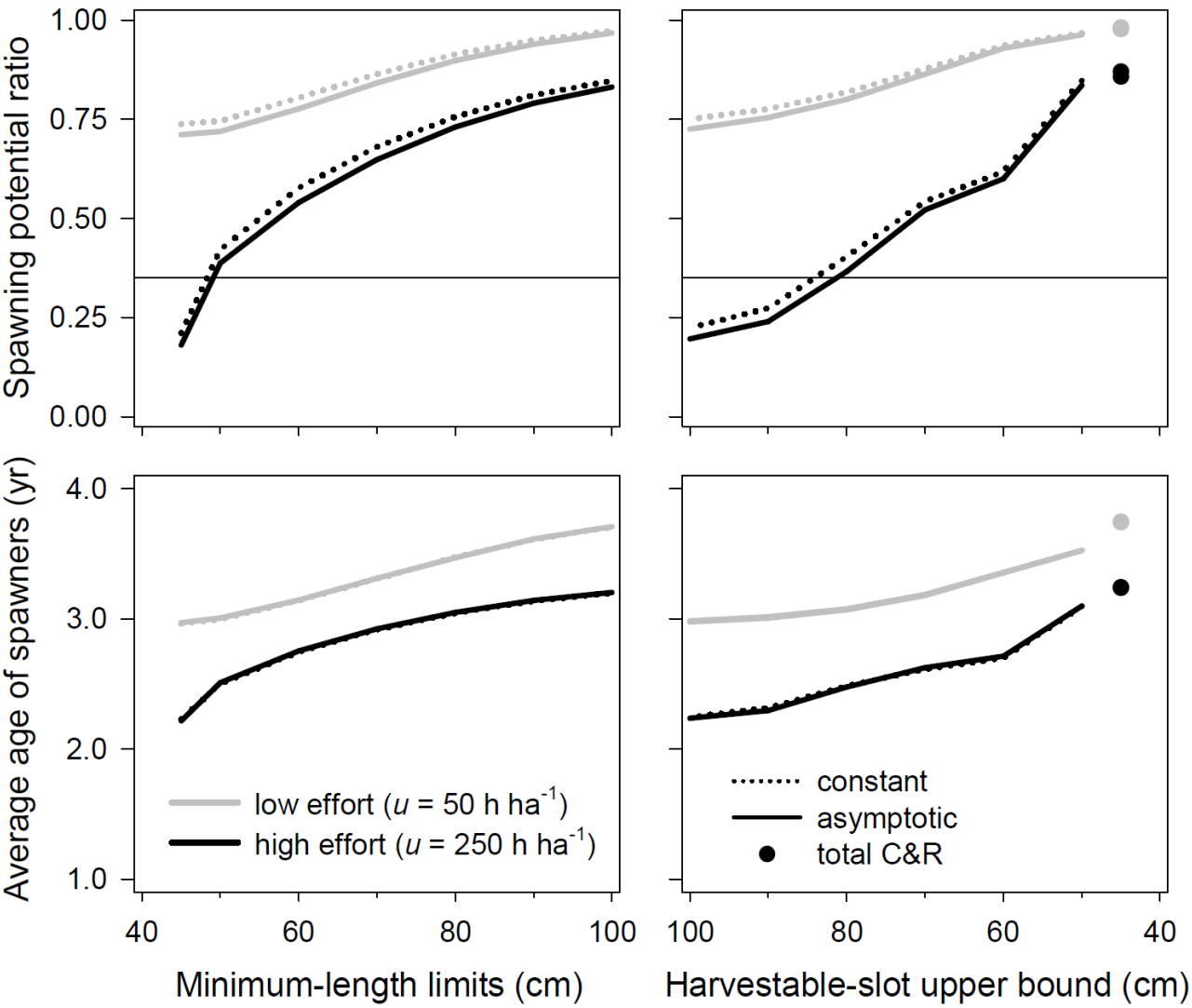
1042 Fig. 3



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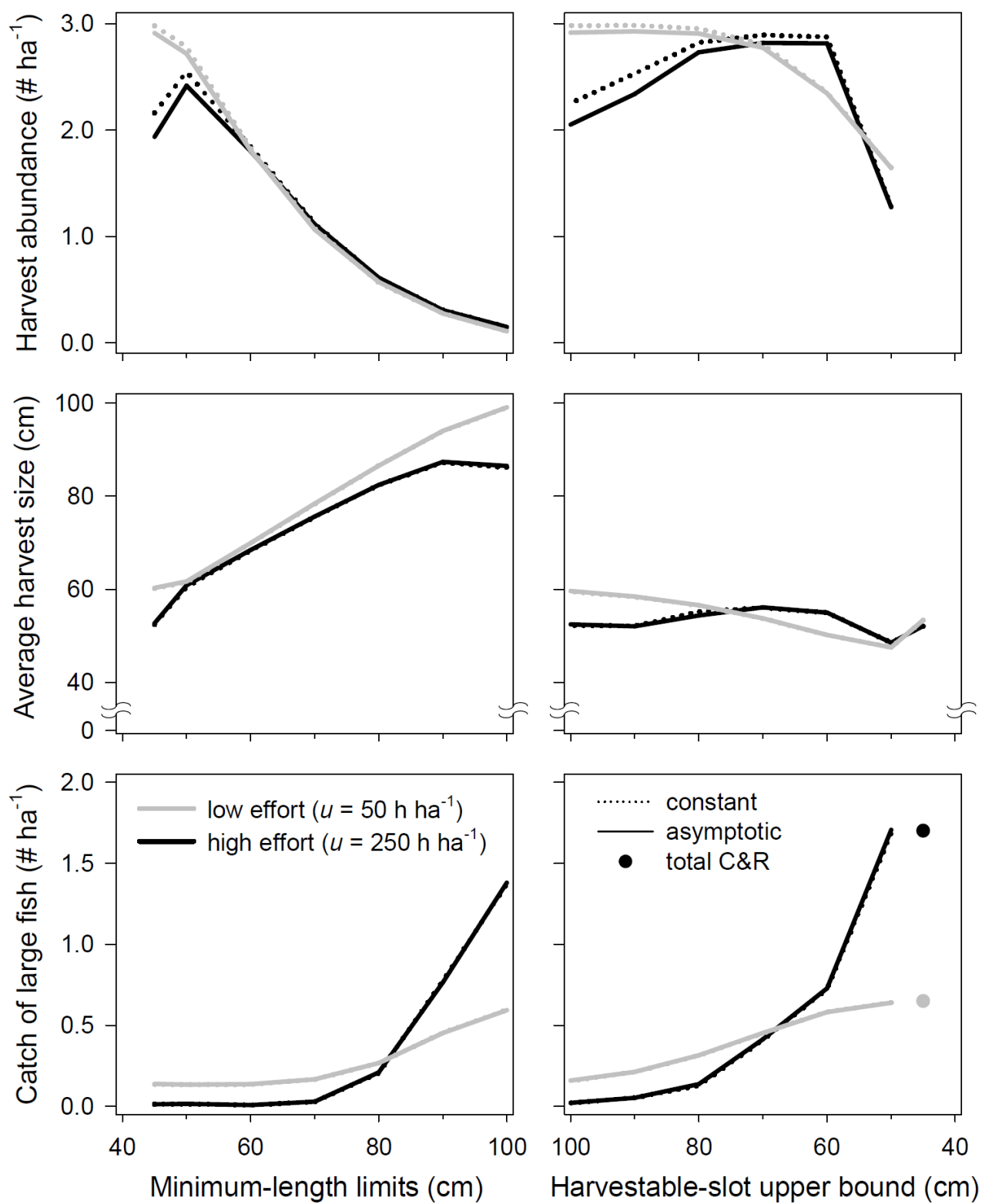
1045 Fig. 4



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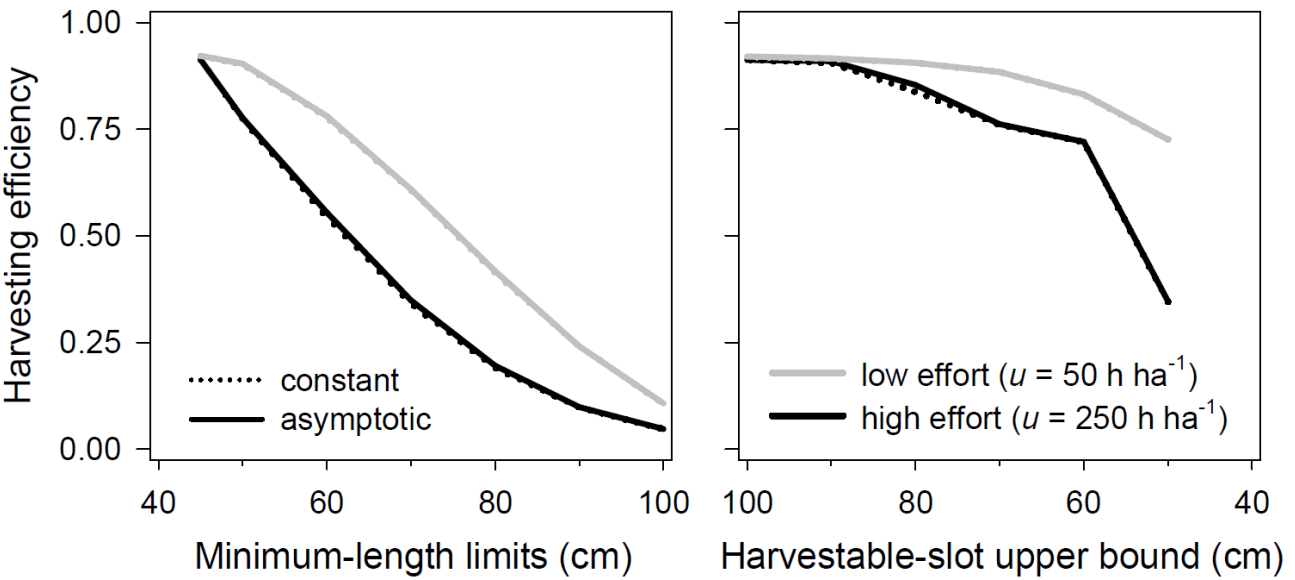
1048 Fig. 5



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1051 Fig. 6



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