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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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1 **The conservation and fishery benefits of protecting large pike (*Esox lu-***
2 ***cius* L.) by harvest regulations in recreational fishing**

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23 ***cius* L.) by harvest regulations in recreational fishing**

24

25 **ABSTRACT**

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

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

43

44 **1. Introduction**

45 Fishing mortality has had, and continues to have, major impacts on wild fish populations (Worm et al.,
46 2009). However, it is only recently that fishing mortality exerted by recreational fishing has been
47 identified as contributing to fish stock declines (Post et al., 2002; Lewin et al., 2006). In both com-
48 mercial and recreational fisheries, positively size-selective exploitation is common (Lewin et al.,
49 2006). Therefore, naturally less abundant large and old fish within a stock tend to be removed at a
50 higher rate than small and young individuals (e.g., Braña et al. 1992; Paul et al., 2003). Traditional
51 fisheries theory encourages the resulting truncation of the size and age structure of the stock because
52 the decline of virgin population abundance relaxes intraspecific food competition, resulting in higher
53 per capita prey intake and increased production in terms of somatic body mass by on average small and
54 young and thus fast growing individuals (Schaefer, 1957; Silliman and Gutsell, 1958; Schäperclaus,
55 1960). Therefore, demographic truncation of the age and size distribution of a stock can be beneficial
56 from the perspective of maximizing fisheries yield (Silliman and Gutsell, 1958; Schäperclaus, 1960).
57 However, this yield-based fisheries management objective has been called into question as a viable
58 long-term approach to sustainable fisheries management (Larkin, 1977). It is particularly unsuitable as
59 a universal objective for recreational angling fisheries, because many anglers value the body size of
60 fish as memorable trophies or enjoy other body size-related determinants of angling quality (e.g., a
61 challenging fight with a large fish) more than maximized harvest biomass (Arlinghaus, 2006).
62 Moreover, conservation concerns have been raised that fishing-induced truncation of the age and size
63 structure of a population will impact recruitment dynamics and may destabilize populations (Berkeley
64 et al., 2004a; Hsieh et al., 2006; Anderson et al., 2008; Venturelli et al., 2009).

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

68 dynamics and destabilizes its abundance (Anderson et al., 2008). Secondly, in many fish stocks indi-
69 viduals of different sizes and ages reproduce at different times and locations (Wright and Trippel,
70 2009). This spreads larval production in time and space providing a buffer against environmental
71 stochasticity (Berkeley et al., 2004a). Thirdly, in many fish species the fecundity of a female increases
72 exponentially with its body length and linearly with its body weight (Wotton, 1998). This is due to
73 larger fish not only having a greater body volume for holding eggs, but also because they may devote a
74 greater proportion of energy to egg production rather than somatic growth (Edeline et al., 2007).
75 Therefore, strongly reducing the abundance of large fecund fish in a population might affect total egg
76 abundance (Berkeley et al., 2004a; Birkeland and Dayton, 2005). Finally, the existence of age and
77 size-dependent maternal effects on egg and larval survival is thought to influence recruitment dy-
78 namics in some marine and freshwater fish stocks (Berkeley et al., 2004a,b; Scott et al., 2006; Ven-
79 turelli et al., 2009).

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

92 life span as well as fishery selectivity and exploitation patterns (O'Farrell and Botsford, 2006; Ottersen,
93 2008; Venturelli et al., 2009).

94 In response to concerns about the conservation issues associated with pronounced age and size
95 truncation in exploited fish stocks, some authors have proposed to save large portions of old and large
96 fish from exploitation for demographic (Berkeley et al. 2004a; Palumbi, 2004; Birkeland and Dayton
97 2005) or evolutionary reasons (Law, 2007). This might also be beneficial from a fishing-quality
98 perspective (Trippel, 1993). However, few studies (for exceptions, see Berkeley, 2006 and Venturelli
99 et al., in press) have systematically investigated the impact of various simple harvest regulations on
100 fish populations and fishing quality in models with and without the existence of assumed age or
101 size-dependent maternal effects on egg and offspring survival. This gap of knowledge currently
102 precludes the derivation of robust management advice as to the appropriateness of different variants of
103 common harvest regulations to jointly meet conservation and fishing quality objectives.

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

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

125

126 **2. Methods**

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

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

142 **2.1 Population dynamics**

143 We use a deterministic Leslie-matrix population model. Such models classify a population into distinct
 144 stages (here age classes) and project their abundances in discrete time (Caswell, 2001). Our model is
 145 designed for application to fish species with a single breeding season per year, such as pike (Raat,
 146 1988), so that annual time steps can be used. In Leslie matrix models (see Caswell, 2001 for details),
 147 changes in the age structure and density of the population are described by $N(t+1) = KN(t)$ or

$$148 \begin{pmatrix} N_1(t+1) \\ N_2(t+1) \\ N_3(t+1) \\ \dots \\ N_{a_{\max}}(t+1) \end{pmatrix} = \begin{pmatrix} f_1 & f_2 & f_3 & \dots & f_{a_{\max}} \\ s_1 & 0 & 0 & \dots & 0 \\ 0 & s_2 & 0 & \dots & 0 \\ \dots & \dots & \dots & \dots & \dots \\ 0 & 0 & 0 & s_{a_{\max}-1} & 0 \end{pmatrix} \begin{pmatrix} N_1(t) \\ N_2(t) \\ N_3(t) \\ \dots \\ N_{a_{\max}}(t) \end{pmatrix}. \quad (1)$$

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

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

157 In each time step, the survival of individuals in age class a_{\max} is 0, whereas individuals at all other ages
 158 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

$$179 W_a = \alpha_1 (L_a / L_0)^{\alpha_2} \quad (3)$$

180 is used, where W_a is somatic weight at age a , L_u is a unit-standardizing constant, and α_1 and α_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 β_1 and β_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), ψ 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 γ_1 and γ_2 are empirically derived parameters, and L_u is a unit-standardizing constant (Table 1).

222 Annual reproductive investment g_a is calculated as

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

224 where ω 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,

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

227 where δ_1 and δ_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,

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

234 where $s_{0,\max}$ is the maximum survival rate, κ 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,

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

239 where μ 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,

$$243 \quad B = \sum_{a=1}^{a_{\max}} \psi k_a N_a . \quad (11d)$$

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 ,

$$246 \quad s_a = \exp(-(M_a + F_a)) . \quad (12)$$

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 τ_0 , τ_X , τ_Y , and τ_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 Shoemith, 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 (λ_1 , λ_2 , and λ_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),

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

294 where V_a is the vulnerability of fish of age a with length L_a , and η and θ 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 ξ 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)

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

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 ϕ 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 ε and ζ 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

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

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

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

344 **2.4 Outline of analysis**

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

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

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

393

394 **3. Results**

395 **3.1 Impacts of angling mortality on the pike population**

396 Size-selective recreational fishing effort substantially affected the fish stock as indicated by reduced
397 equilibrium pike population densities (Fig. 3) and spawning potential ratio (SPR) values with in-
398 creasing effort levels (Fig. 4, top panels). The unexploited equilibrium pike abundance density was 25
399 pike aged 1 and older ha^{-1} , declining strongly and collapsing at a realized effort level of about 130
400 annual angling-h ha^{-1} in the absence of harvest regulations (Fig. 3). The population-level effects of
401 recreational angling were particularly pronounced at relaxed harvest regulations (i.e., low MinL-L or
402 wide HSL-L, see Fig. 3 and left area in the top panels in Fig. 4). For example, the pike abundance
403 density for fish aged 1 and older was reduced by 50% or more (i.e., $< 12.5 \text{ pike ha}^{-1}$) relative to the
404 unexploited case at low MinL-L and reasonably wide upper bounds for the HSL-L regulation (≥ 80
405 cm) when the realized angling effort levels exceeded about 100 annual angling-h ha^{-1} . Highest popu-
406 lation densities of pike aged 1 and older were maintained under total catch-and-release policies, but
407 population sizes at equilibrium were smaller than in the unexploited case due to hooking mortality (Fig.
408 3). Note that realized angling effort values in Fig. 3 correspond to regulation-specific maximum an-
409 gling effort levels u . Due to density-dependent effort (Fig. 2 f) realized effort was generally lower
410 than the maximum effort levels at equilibrium (Fig. 3). For example, at a MinL-L of 45 cm maximum
411 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
412 changes in the availability of pike due to harvesting, which reduced the attractiveness of the fishery,
413 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 $\text{ha}^{-1} \text{yr}^{-1}$) 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 $\text{ha}^{-1} \text{yr}^{-1}$), the SPR dropped below 0.35 at wide HSL-Ls with an upper
419 HSL-L bound of ≥ 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-
430 plementary Table 1). As to be expected, the decrease in the average age of spawners was most pro-
431 nounced 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-
437 serving a more natural age structure (Fig. 4, bottom panels). At the same time, however, only HSL-L

438 were effective in preserving old and large fish in a stock at high angling effort levels. For example,
439 while pike aged 7 years or older were extirpated at a maximum angling effort level of 250 angling-h
440 $\text{ha}^{-1} \text{yr}^{-1}$ with MinL-Ls < 80 cm, they were preserved in the stock under HSL-L regulations with an
441 upper bound of 80 cm or less, albeit at low relative abundances (Supplementary Table 1). In contrast to
442 the results in terms of SPR, the age truncation effect of recreational harvesting was largely unaffected
443 by size-dependent maternal effects on early survival (Fig. 4 bottom panels).

444 **3.2 Impacts of angling mortality on fisheries quality**

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

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

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

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

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

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

497 **3.3 Model sensitivity**

498 The sensitivity of the pike population model was investigated by analyzing changes in the absolute
499 harvest to modification of input parameter values (Table 2). As to be expected, the absolute harvest
500 was sensitive to changes in one parameter (μ) specifying the stock-recruitment relationship, and
501 maximum immature growth rate (h_{\max}). A 10% change of these parameters resulted in a change larger
502 than 10% in the absolute harvest. SPR was fairly insensitive to changes in parameter values. With the
503 exception of one parameter specifying life-time growth (h_{\max}), a 10% change of most parameters
504 caused only a few percent changes in the equilibrium SPR (Table 2). However, both absolute harvest
505 and SPR were sensitive to changes in both the exponent of the length-weight regression α_2 and the
506 exponent of the length-gonad weight regression γ_2 (Table 2).

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

509 vival with pike size were compared with a simulation run with a no size-dependent maternal effects on
510 early survival (Table 2). This relative SPR response variable (SPR with asymptotic maternal effect /
511 SPR with constant maternal effect) was largely insensitive to changes of individual parameters by \pm
512 10% (Table 2), indicating the robustness of the maternal effects results reported in this study.

513

514 **4. Discussion**

515 Many fisheries managers interested in managing stocks for maximized harvest tend to set a mini-
516 mum-length limit (MinL-L) in a way to allow at least one successful reproduction per individual and
517 facilitating aggressive exploitation for harvest afterwards (Schäperclaus, 1960). In pike, this objective
518 is usually achieved by setting the MinL-L to 45 - 50 cm because most pike individuals start to re-
519 produce at much smaller sizes (Raaf, 1988). However, our model results suggest that intensive recre-
520 ational exploitation of pike with low MinL-Ls can lead to recruitment overfishing and will also
521 strongly change the size structure of pike stocks resulting in the loss of large fish in addition to an
522 increase in the relative frequency of small and young size classes. This prediction agrees with various
523 empirical studies in exploited pike populations (e.g., Pierce et al., 1995; Jolley et al., 2008; Pierce, in
524 press). By contrast, our model suggests that a pike population can be effectively preserved, and SPR
525 values ≥ 0.35 achieved, by increasing MinL-L regulations to values > 50 cm. Increasing the MinL-L
526 also benefits the size-structure of pike stocks. For example, in a long-term study on the effectiveness of
527 various harvest regulations for maintaining size structure in pike stocks Pierce (in press) found that
528 MinL-Ls of 76.2 cm strongly increased the abundance of pike ≥ 50.8 and ≥ 61 cm total length across
529 various lake fisheries. However, such high MinL-Ls were not successful at increasing the abundance
530 of pike above 76.2 cm total length relative to reference lakes without MinL-L regulations, and only
531 maximum-length limits of 76.2 cm were able to conserve such large fish sizes in recreationally ex-
532 ploited 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 ≤ 80 cm were as effective as appropriately designed MinL-L
535 at avoiding recruitment overfishing in pike by keeping SPR values ≥ 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 – ≤ 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 appropriately chosen HSL-L by preserving large pike in the stock . In fact, our model indicated that
560 HSL-Ls of 45 – ≤ 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

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

584 We found that some model predictions as to the benefits of HSL-Ls and MinL-Ls for pike
585 conservation and fishing quality were affected by the presence of size, and thus age, dependent ma-
586ternal effects on early survival rate of pike. Ignoring such maternal effects on early life-history in pike
587 was predicted to lead to overestimation of the equilibrium spawning stock and of harvest abundance by
588 as much as 17% and 10%, respectively. This is in agreement with previous studies on the importance
589 of maternal effects on early life-history traits for recruitment dynamics and fishery resiliency in var-
590 ious marine (Scott et al., 2006; Berkeley, 2006; Carr and Kaufman, 2009; Lucero, 2009; Venturelli et
591 al., 2009) and freshwater fish stocks (Venturelli et al., in press). In pike, we found maternal effects on
592 early survival rates to be relevant for SPR, and to a lesser degree for harvest abundance, but these
593 maternal influences appeared largely irrelevant for other response metrics such as the average age of
594 spawners, average harvest size or the harvesting efficiency. We also found that maternal effects on
595 early survival of pike mattered more substantially at high than at low fishing effort levels. The diffe-
596rential importance of size-dependent maternal effects on early life-history traits for population and
597 fisheries variables and their dependency on the degree of fishing mortality is in agreement with other
598 modeling studies on marine fish by Lucero (2009) and O'Farrell and Botsford (2006). It results from
599 the greater age and size truncation associated with high fishing mortality such that size or age de-
600pendent maternal effects matter more under these situations because the relative reproductive value of
601 the otherwise less abundant large fish becomes more prominent. Note, however, that the beneficial
602 effects of saving large pike from harvesting for fisheries quality in our model holds irrespective of the
603 prevalence of size-dependent maternal effects on offspring survival. The reason relates to dispropor-
604 tionally 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-

629 namical processes if empirical evidence on alternative mechanisms of maternal effects or other bio-
630 logical or fishery processes accumulates for pike.

631 To add realism, we incorporated various processes of density-dependent compensation to
632 fishing mortality (e.g., growth, fecundity, recruitment), which were not included in previous pike
633 harvesting models (e.g., Dunning et al., 1982). We also included all known size-dependent relation-
634 ships on reproductive parameters from the recent pike literature, such as length-dependent gonad
635 weight (Edeline et al., 2007) and the positive relationship between size of females and egg sizes. Yet,
636 our model may suffer from omission of important processes, which might also influence population
637 dynamics of pike. In particular, we did not explicitly model size-dependent spawning timing in pike
638 and its possible relation to temperature, food abundance and subsequent growth and survival of
639 offspring. Yet, it is known from some inland water bodies that large-sized pike might spawn first in the
640 season (Svärdson, 1949; Pagel, 2009), and equally common are protracted spawning seasons lasting
641 6-8 weeks (Farrell et al., 2006; Pagel, 2009). Thus, size-dependent maternal effects on offspring
642 phenotypes and spawning timing can be confounded in pike, potentially inhibiting the expression of
643 maternal effects on offspring traits such as growth if early spawning coincides with low temperature
644 and low food availability. Indeed, Pagel (2009) reported a lack of a relationship between relative
645 reproductive success and size of female pike during a single spawning season in a natural lake, and he
646 also reported an inverse relationship between size of females and spawning timing. If these relation-
647 ships also hold for other years and ecosystems, our model does not fully represent pike population
648 dynamics and will need to be modified in the future. This is because even if size-dependent maternal
649 effects on offspring traits do not materialize in nature in our model fecundity was assumed to increase
650 disproportionately with size of female pike. This in turn implicitly fuelled a greater contribution to
651 future generation by a large spawning fish compared to a small female. However, the study by Pagel
652 (2009) suggests that a size-dependent “fecundity-effect” on relative reproductive success must not

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

658 Our model predictions were found to be reasonably robust against variation of most parameters,
659 however, some sensitive parameters were also identified. In particular, our model predictions were
660 sensitive to one parameter determining the stock-recruitment function in pike. We used a Ricker-type
661 stock-recruitment function reported by Minns et al. (1996) for pike, but the parameter values for this
662 function were associated with large standard errors. Although a Ricker stock-recruitment function is a
663 valid representation of pike recruitment (Edeline et al., 2008), this parameter uncertainty is an issue if
664 our model is to be applied to make detailed predictions. Moreover, the sensitivity of model predictions
665 to parameters specifying the stock-recruitment function suggests that all biological mechanisms af-
666 fecting the recruitment of pike to age 1 as a function of a given size and composition of the spawning
667 stock, such as all maternal influences on offspring survival (Venturelli et al., in press) or changes in
668 vegetation structure increasing the carrying capacity of ecosystems for young-of-the-year pike
669 (Grimm and Klinge, 1996), are important to develop sophisticated predictive models of pike popula-
670 tion development for a given fishery. Similarly, when our model is applied to a particular fishery there
671 is a need for a thorough assessment of the exponent α_2 in the length-weight regression, as this pa-
672 rameter exerted a large influence on the model predictions. Moreover, our growth model followed the
673 bi-phasic growth model by Lester et al. (2004), which assumes that the exponent of the length-weight
674 relationship (α_2) is 3. Therefore, changes to the model structure might be needed if our model is
675 applied to a specific pike population where α_2 substantially differs from 3. Fortunately, for a given
676 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 α_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 α_2 further and include this process in extensions of our model. Finally, further empirical
680 studies are needed to obtain more precise estimates for γ_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

701 found in typical pike fisheries. A recent review showed that anglers can remove up to 80% of a target
702 population within a single angling season (Lewin et al., 2006), and annual exploitation rates for pike
703 with a moderate annual angling effort of 150 angling-h $\text{ha}^{-1} \text{yr}^{-1}$ ranged between 47 and 74% in con-
704 sumptive fisheries (Arlinghaus et al., 2009), but are lower in fisheries where anglers voluntarily release
705 pike (Pierce et al., 1995). The maximum potential angling effort levels used in our model reached 250
706 angling-h $\text{ha}^{-1} \text{yr}^{-1}$ but these values as well as the size-dependent vulnerability curves used were in
707 accord with field studies on pike (Kempinger and Carline, 1978; Pierce et al., 1995; Margenau et al.,
708 2003). We thus used realistic fishing intensities that can be expected in many pike fisheries world-wide
709 (Arlinghaus et al., 2009).

710

711 **5. Conclusions and Implications**

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

725 production as these fish typically have reduced egg quality (Hubenova et al., 2007). Preserving an
726 extended age structure, in turn, increases the stability of the stock (Anderson et al., 2008). It has been
727 speculated before that if the goal is to preserve large fish in a stock highly restrictive regulations are
728 needed in fisheries for esocid species (Dunning et al., 1982; Simonson and Hewett, 1999), and our
729 modeling results and recent findings by Pierce (in press) support this proposition. We conclude that
730 preservation of old and large fecund pike in an exploited stock through variants of harvested slot length
731 limits may offer benefits for conservation and increase fishing quality, in particular when angler value
732 the catch of large-sized pike and ethical arguments are present for limiting “cryptic” hooking mortality
733 associated with high minimum-length limits. However, non-compliance with regulations seems to be
734 common in pike fisheries (Pierce and Tomcko, 1998). To encourage rule compliance with unfamiliar
735 regulations, such as harvestable slot length limits, effective enforcement of regulations is needed along
736 with good communication of the underlying objectives of the novel regulation (Page and Radomski,
737 2006; Walker et al., 2007).

738

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749

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963

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 ion	Value	Unit	Source	Population**
Biological processes						
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
α_1	(length-weight rela- tionship)*	3	4.8×10^{-6}	kg	Willis (1989)	A
α_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)
β_1	(density-dependent	5	0.18190	–	Own calculations	(W)

	growth)					
β_2	(density-dependent growth)	5	0.56783	–	Own calculations	(W)
D_u	–	5	1	kg ha ⁻¹	unit	–
ψ	(hatching rate, constant)	6	0.735	–	Franklin and Smith (1963)	A
ρ	(density-dependent relative fecundity)	7	0.04818	ha kg ⁻¹	Craig and Kipling (1983)	W
γ_1	(relationship between female length and gonad weight)	8	1.01×10^{-5}	g	Own calculations	(W)
γ_2	(relationship between female length and gonad weight)	8	4.01	–	Edeline et al. (2007)	W
ω	relative caloric density of eggs compared to soma	9	1.22	–	Diana (1983)	A
δ_1	(relationship between female length and egg size)	10	2.95×10^{-5}	g cm ⁻¹	Lindroth (1946)	E
δ_2	(relationship between female length and egg size)	10	5.15×10^{-3}	g	Lindroth (1946)	E

$s_{0\max}$	(first-year mortality)	11	4.76×10^{-4}	–	$\exp(f_d)$ in Minns et al. (1996)	A
κ	(first-year mortality)	11	31.73	–	$-f_b$ in Minns et al. (1996)	A
μ	(first-year mortality)	11	0.31	–	f_c in Minns et al. (1996)	A
$B_{1/2}$	(first-year mortality)	11	1.68362×10^9	lar- vae ha ⁻¹	f_d^{1/f_c} in Minns et al. (1996)	A
τ_0	(natural mortality)	13	2.37 (small pike), 1.555 (large pike)	–	Haugen et al. (2007)	(W)
τ_x	(natural mortality)	13	-0.02 (small pike), 0.40 (large pike)	–	Haugen et al. (2007)	(W)
τ_y	(natural mortality)	13	-0.29 (small pike), -0.88 (large pike)	–	Haugen et al. (2007)	(W)
τ_L	(natural mortality)	13	0.25 (small pike),	–	Haugen et al. (2007)	(W)

			0.00 (large pike)			
λ_1	(early survival)	14	0.9191	–	See text	O
λ_2	(early survival)	14	4.1	cm^{-1}	See text	O
λ_3	(early survival)	14	0.059	–	See text	O
Angling processes						
η	(vulnerability)	15	0.25	cm^{-1}	See text	O
θ	(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 angling effort always present	17	0.5	–	See text	O
$N_{v,1/2}$	(numerical response of angling effort to fish availability)	17	10	fish ha^{-1}	See text	O
ξ	(numerical response of angling effort to fish availability)	17	5	–	See text	O
q	catchability	18, 20	0.01431	ha h^{-1}	Own value	O
ϕ	hooking mortality	19	0.094	–	Munoeke and Childress (1994)	A

ε	(non-compliance mortality)	20	1.25	–	Sullivan (2002)	X
ζ	(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 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 survival ¹	
	+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
α_1	-2.7	2.0	4.2	-4.2	-0.1	0.3
α_2	-44.4	0.4	63.3	-59.3	1.0	2.0
h_{\max}	10.7	-12.3	13.5	-12.3	1.5	-1.1
β_1	-4.2	3.8	-3.4	5.0	0.2	0.5
β_2	-4.8	4.4	-2.3	4.5	-0.1	0.5
ψ	5.1	-6.3	-0.8	1.3	-0.3	0.5
ρ	-2.5	1.6	5.0	-4.2	0.6	0.4
γ_1	3.2	-4.1	-2.6	3.2	0.1	0.2
γ_2	55.3	-65.9	-11.1	25.3	-8.0	2.9
ω	-2.3	1.6	-1.7	2.2	0.1	0.1
δ_1	-2.0	1.6	0.8	-0.5	0.7	0.0
δ_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
κ	-9.3	9.1	1.9	-1.0	1.0	-0.2
μ	27.3	-31.7	-3.2	5.5	-1.4	1.6
$B_{1/2}$	1.9	-3.3	0.0	0.8	0.3	0.3

τ_0 (small pike)	6.4	-8.0	0.1	0.3	-0.1	0.3
τ_0 (large pike)	1.6	-2.5	-0.1	0.7	-0.1	0.4
τ_x (small pike)	-0.1	-0.3	0.1	0.1	0.1	0.1
τ_x (large pike)	-1.2	0.4	0.1	0.2	0.2	0.0
τ_y (small pike)	1.1	-1.6	-0.3	0.6	-0.1	0.4
τ_y (large pike)	1.5	-1.9	1.0	-0.8	0.2	0.5
τ_L (small pike)	-1.8	1.3	0.5	-0.2	0.4	0.0
τ_L (large pike)	0.0	0.0	0.0	0.0	0.0	0.0
λ_1	-1.1	0.0	0.3	0.8	0.3	0.8
λ_2	1.4	-2.7	0.8	-0.1	0.8	-0.1
λ_3	5.7	-6.9	-0.5	1.0	-0.5	1.0
η	-3.4	2.2	-2.9	2.4	0.1	0.1
θ	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
ξ	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
ϕ	-2.1	1.4	-0.4	0.8	0.1	0.1
ε	-0.2	-0.6	0.1	0.6	0.4	0.9
ζ	-0.6	-0.4	0.6	0.6	0.9	0.9

986 ¹ SPR relative to the case when the constant size-dependent early survival is assumed.

987

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 ha^{-1} and open squares indicate a cor-
1007 responding high maximum potential angling effort density $u = 250$ annual angling-h 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.

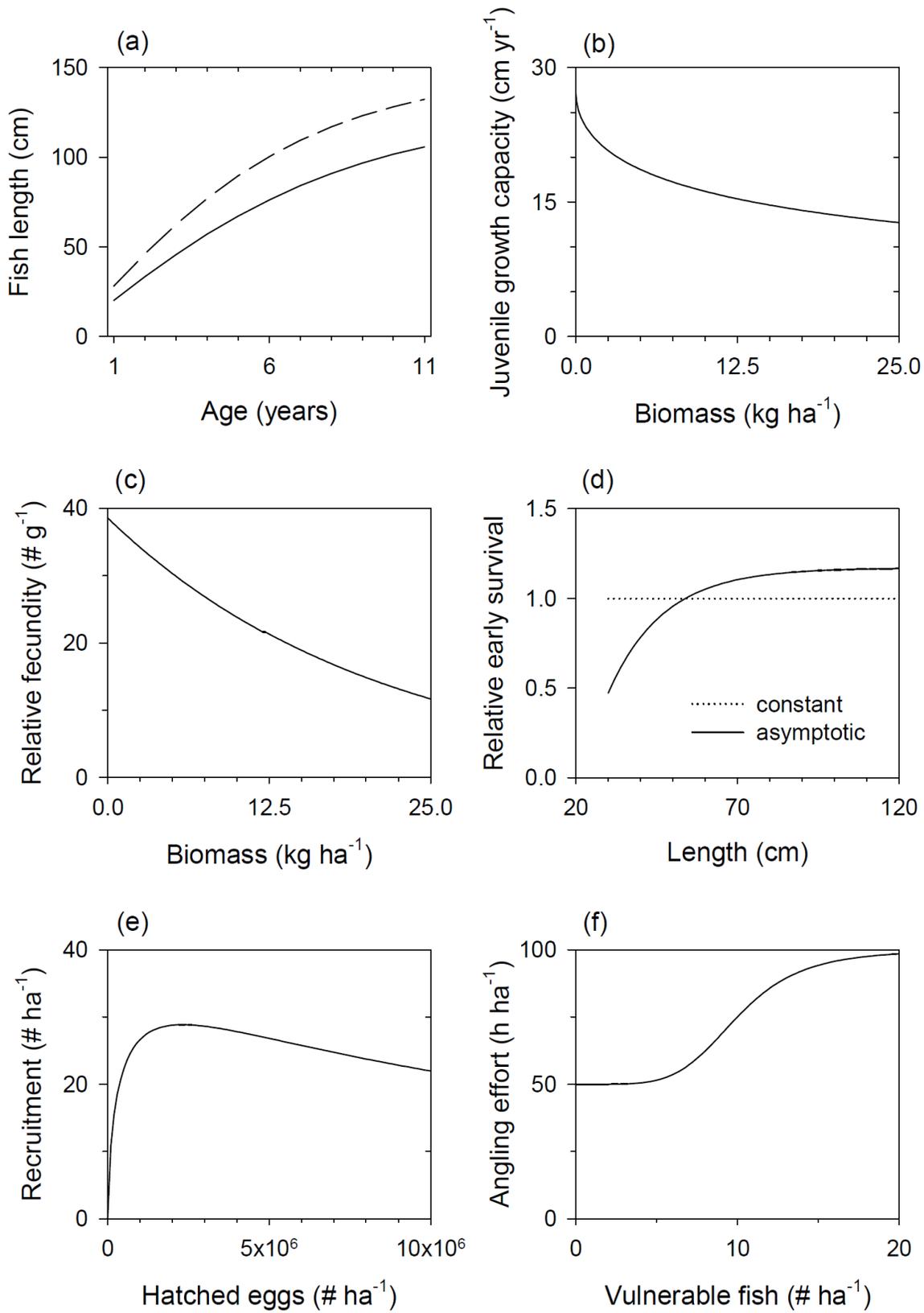
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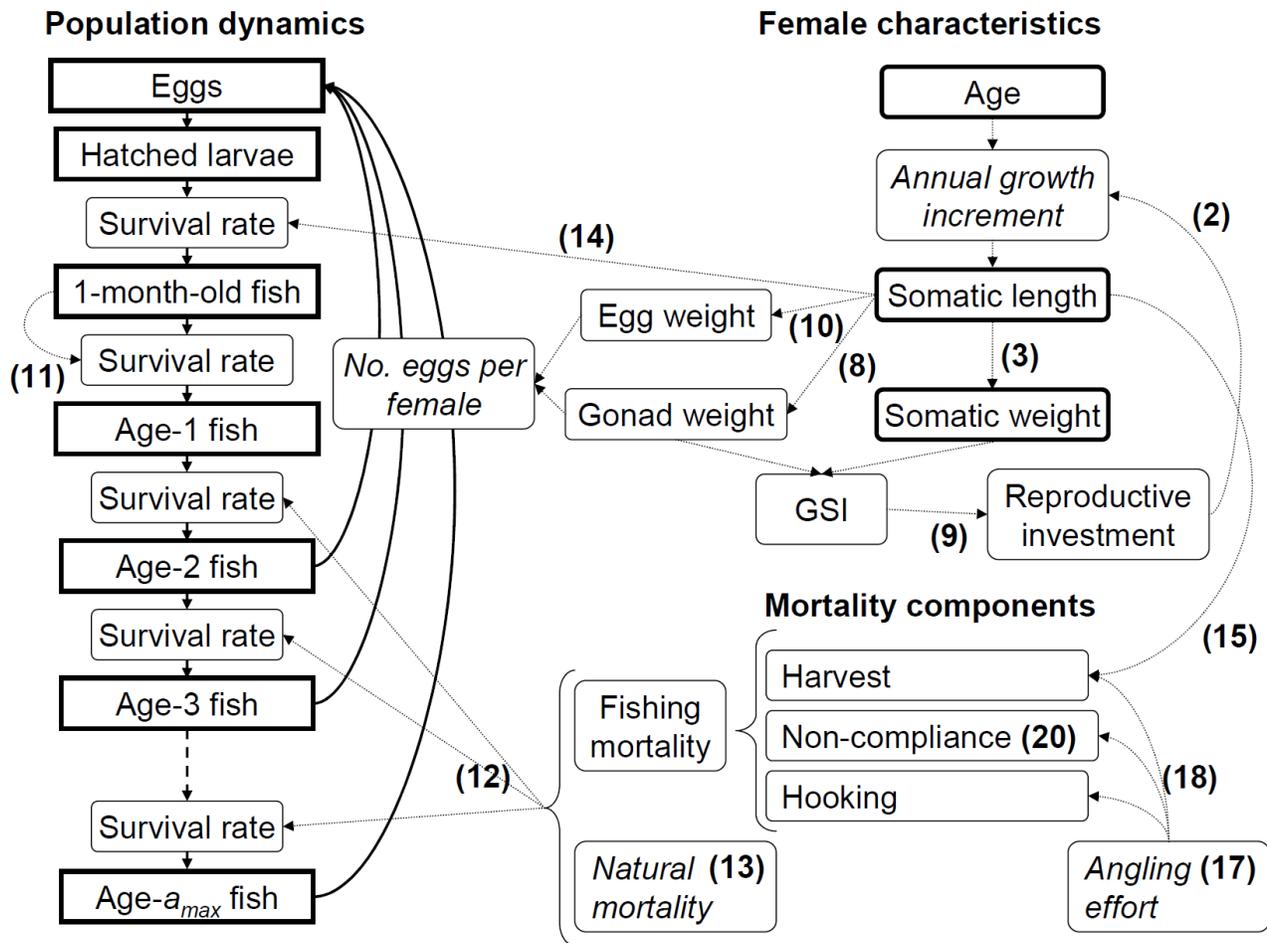
1020 Fig. 5. Equilibrium harvest of pike (in terms of numbers, top panels), equilibrium average size of
1021 harvested pike (total length in cm, middle panels) and equilibrium catch of large fish ≥ 86 cm total
1022 length in response to two levels of maximum angling effort (low and high by varying the 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.

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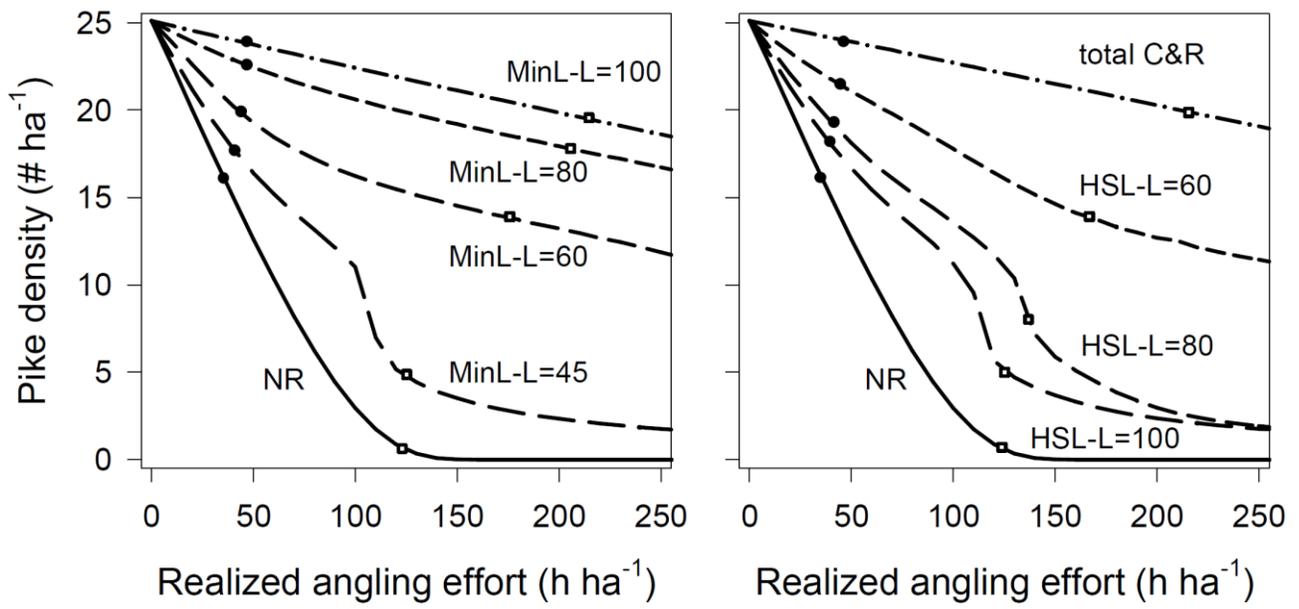
1028 Fig. 6. Harvesting efficiency (total harvest in numbers relative to total deaths) at equilibrium in re-
1029 sponse to two levels of maximum angling effort (low and high by varying the parameter $u = \text{maximum}$
1030 $\text{angling effort in annual angling-h ha}^{-1} \text{ yr}^{-1}$) at minimum-length 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.

1034





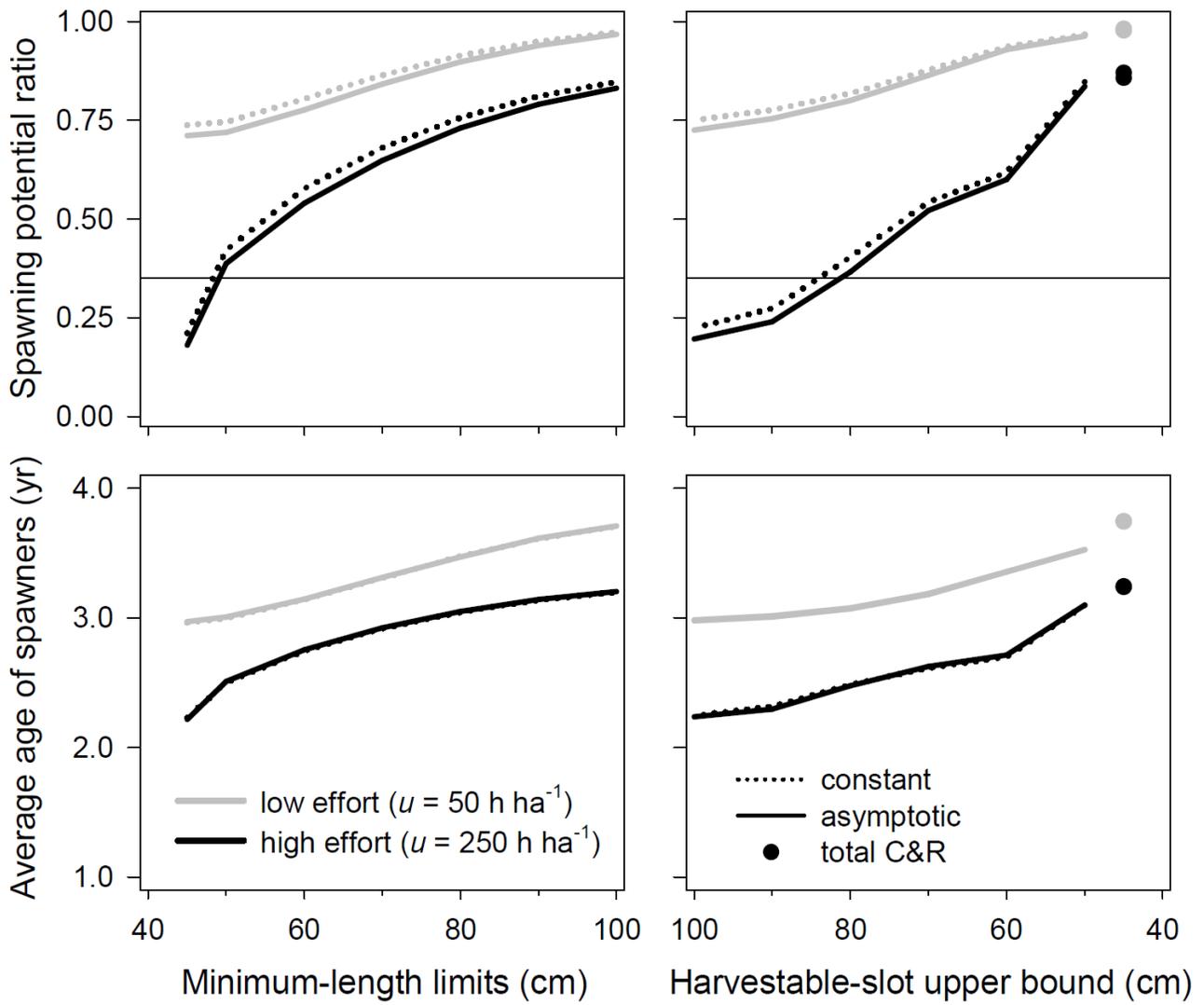
1042 Fig. 3



1043

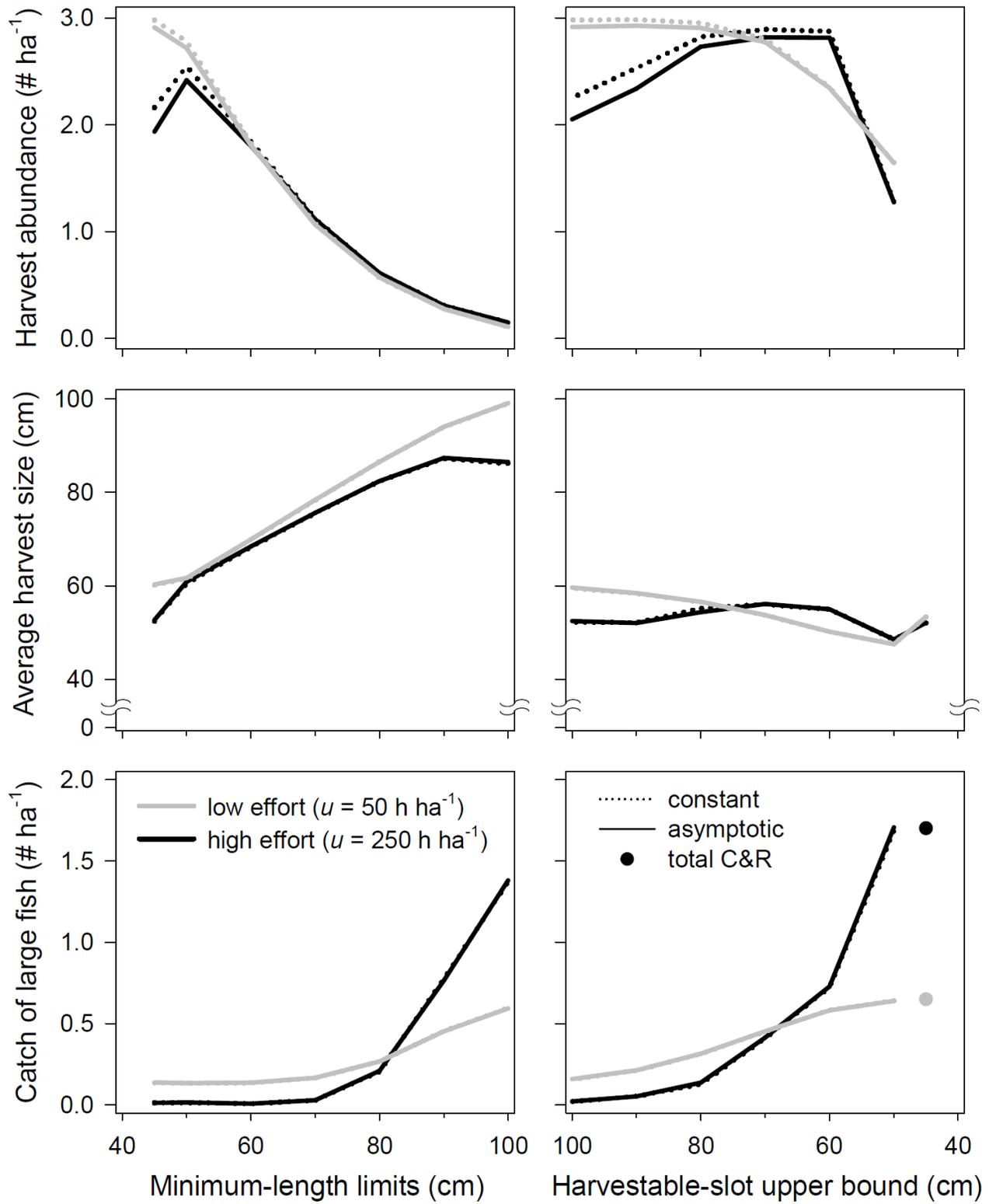
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1045 Fig. 4



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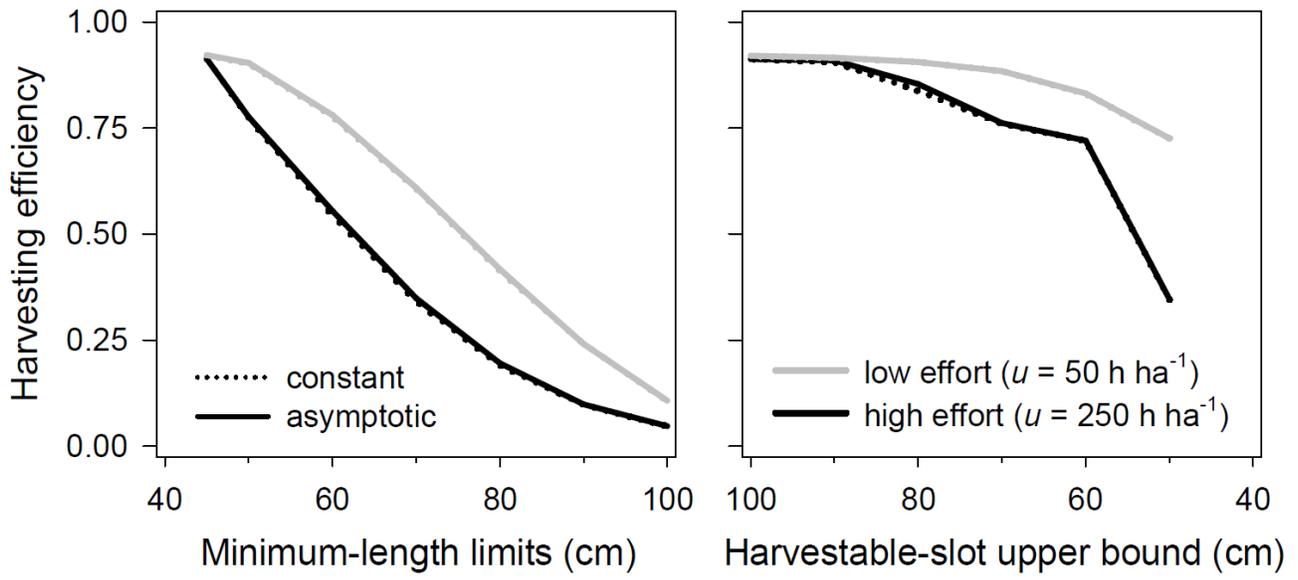
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1050

1051 Fig. 6



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