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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 that 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 euthrophic 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 potential 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 (Raat, 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

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

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 $a = 1, \ldots, a_{max}$. 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.

2.2 Biological processes

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

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

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

For conversions from length to weight, an empirical allometric relationship

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

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 empirical parameters defining the relationship for pike (Willis, 1989). The growth model by Lester et al. (2004) is based on the assumption that the exponent of the length-to-weight relationship is 3, and the corresponding value in Willis (1989) for typical pike populations is 3.059. For species or populations whose exponent of the length-weight-relationships differs substantially from 3, the generalized bi-phasic growth model by Quince et al. (2008) rather than the special case reported by Lester et al. (2004) may be more appropriate. Because the empirical exponent in Willis (1989) is fairly close to 3, we chose the simpler growth model by Lester et al. (2004) and assume an exponent of 3 (Table 1). Fish density D is then simply the sum of biomasses across all age classes,

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

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

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

where β_1 and β_2 define the shape of this relationship, D_u is a unit-standardizing constant, and h_{max} is the maximum immature annual length increment at $D = 0$ (Fig 1b, Table 1). According to equation (2), density-dependence in h also influences post-maturation growth.

The age-specific fertility f_a is defined as

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

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

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

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

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

where γ_1 and γ_2 are empirically derived parameters, and L_u is a unit-standardizing constant (Table 1). Annual reproductive investment g_a is calculated as

$$g_a = \omega \frac{J_a}{W_a}, \tag{9}$$

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

$$I_a = \delta_1 L_a + \delta_2, \tag{10}$$

where δ_1 and δ_2 are empirically derived parameters from data in Lindroth (1946) (R^2 = 0.44, $P <$ 0.001, Table 1).

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

$$s_0 = s_{0,\max} \exp\left(-\kappa G\left(B\right)\right), \tag{11a}$$

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

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

where μ is an exponent determining the rapidity of the transition between $s_{0,\max}$ and $s_{0,\min}$ through changes in hatched larvae density, and $B_{1/2}$ is the density of hatched larvae at which

$$s_0 = s_{0,\max} \exp(-\kappa/2) . \quad (11c)$$

The larval density B is the sum of age-specific larval production across all age classes,

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

Annual survival rates s_a at age are calculated by combining age-specific instantaneous natural mortality rates M_a with instantaneous fishing mortality rates F_a,

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

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

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

where X and Y are densities of “small” (i.e., age-2) and “large” pike (i.e., older than age-2), respectively, and L_a denotes the length of fish at age a, and τ_0, τ_X, τ_Y, and τ_L are empirically determined coefficients (Table 1). The half-year survival rates were translated into instantaneous mortality rates (Arlinghaus et al., 2009) using

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

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

$r_a = 1$ (constant, i.e., lack of a size-dependent maternal effect), (14a) or

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

where r_a is the relative early survival probability of pike offspring during the first month after hatching. Note that because age and size are strongly correlated in most fish, including pike, size-dependent maternal effects on offspring survival will also be age-dependent. The baseline assumption of a constant relationship between size of females and early survival of their offspring (equation 14a) represents the traditional assumption in fisheries models that the survival probability of offspring is independent of the female's size (e.g., Wright and Shoesmith, 1988). The second assumption of an asymptotic increase in relative early survival with the female's size (equation 14b) is based on recent experimental evidence about the differential relative survival of pike larvae spawned by five female pike ranging in total length between 33.5 and 99 cm. Equal numbers of larvae from each female were stocked into common garden ponds and offspring survival was measured over a period of one month after stocking (stocking May, 5, 2008; complete retrieval of survivors by draining of ponds, June, 12, 2008, Arlinghaus, Faller, Wolter & Bekkevold, unpublished data). Surviving offspring in the otherwise fishless ponds (so as to expose age 0 pike to strong intraspecific competition and intracohort cannibalism) were assigned to each of the five females using ten microsatellite loci, and relative survival rates of offspring as a function of female size was determined (Arlinghaus, Faller, Wolter & Bekkevold, unpublished data). Data were used to fit an asymptotic size-dependent maternal effect on early survival using equation 14b, and values for the parameters (λ_1, λ_2, and λ_3) were determined so as to provide the best fit to the data ($R^2 = 0.85$, Fig. 1d, Table 1). We coupled this relative survival function of offspring originating from a particular size (and hence age) class to the general stock recruitment function with overcompensation (equation 11a). Thereby, an initial relative survival advantage is maintained until recruitment to age-1, but not afterwards due to the lack of empirical evidence for size-dependent maternal effects on offspring traits being maintained after the first year of life in pike. Accordingly, equation (11a) was modified as

$$s_{0,a} = \frac{r_a}{\sum_{a=1}^{a_{max}} r_a k_a N_a \Big/ \sum_{a=1}^{a_{max}} k_a N_a} s_{0,max} \exp\left(-\kappa G\left(B\right)\right). \tag{11a′}$$

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

2.3 Recreational angling processes

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

$$V_a = \left(1 - \exp\left(-\eta L_a\right)\right)^{\theta}, \tag{15}$$

where V_a is the vulnerability of fish of age a with length L_a, and η and θ describe the shape of the relationship (Paul et al., 2003, Table 1). The total density N_V of vulnerable fish is then given by

$$N_V = \sum_{a=1}^{a_{max}} V_a N_a . \tag{16}$$

A realistic expectation about angler behavior is a response of angling effort E to the quality of the fishery (Post et al., 2003). As the quality of fishing measured in terms of angler satisfaction is often catch-dependent (Arlinghaus, 2006; Arlinghaus et al., 2008), increasing numbers of vulnerable fish are expected to increase the number of anglers spending effort on a particular fishery (Post et al., 2003). As empirical information on this effort dynamic is currently not available for pike fisheries, a general sigmoid numerical response of angling effort to fish availability, modified from Post et al. (2003), was 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 non-compliance mortality from illegal harvest of protected fish. On this basis, the number of dead fish d_a at age a is given by (Arlinghaus et al., 2009)

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

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

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

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

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

where ε and ζ are empirically derived constants, and C_u is a unit-standardizing constant (Table 1). The catch rate C_r of protected fish was calculated following Arlinghaus et al. (2009) on the basis of the number of illegal catch c_a at age a as

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

where

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

The instantaneous angling mortality F_a at age a is then simply

$$F_a = -\ln\left(1 - d_a/N_a\right). \qquad (21)$$

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 ha^{-1} yr^{-1}) and a high, yet realistic (Kempinger and Carline, 1978), maximum angling effort scenario (u = 250 annual angling-h ha^{-1} 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 and fishery variables for several typical angling regulations in pike management. Note that the parameter u represents a maximum potential angling effort level, which at equilibrium will not be equivalent to the realized angling effort due to the strong density-dependence in angling effort (Arlinghaus et al., 2009).

Output variables at long-term equilibrium (note that in every simulation equilibrium conditions were reached) were thought to be indicative of the long-term average benefits (or penalties) expected under different regulations; they included variables of the stock status and of fishery quality. Stock status was represented by pike abundance density for pike aged-1 and older and the spawning potential ratio (SPR) based on viable egg abundance (i.e., the ratio of viable eggs in the exploited equilibrium relative to the unexploited case). SPR is a common stock assessment tool to evaluate the degree to which fishing has reduced the potential population reproductive output (Goodyear, 1993). Recruitment overfishing is thought to occur when SPR ≤ 0.35 (Mace, 1994). To represent age truncation, we calculated the average age of spawners. In terms of fishery metrics, harvest (yield) and catches of large (i.e., from an angler's perspective so-called memorable) pike were evaluated. The length of memorable pike of 86 cm total length was taken from Anderson and Neumann (1996). We also calculated the harvesting efficiency, i.e. the ratio of harvest to total deaths due to fishing. This is a way to ethically evaluate conservation goals, as low harvesting efficiency values indicate that the majority of losses of individual pike are due to post release mortality rather than harvest (Pine et al., 2008). Sensitivity of results to parameter values was assessed by varying parameters independently by 10 % and calculating the resultant percentage of change for two response variables, absolute harvest and SPR. We further contrasted SPR values between the two maternal effect scenarios to investigate the robustness of the size-dependent maternal effect simulation results. We chose a moderate fishing mortality and a HSL-L 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 ha^{-1}, declining strongly and collapsing at a realized effort level of about 130 annual angling-h 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 ha^{-1}) relative to the unexploited case at low MinL-L and reasonably wide upper bounds for the HSL-L regulation (≥ 80 cm) when the realized angling effort levels exceeded about 100 annual angling-h 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 h ha^{-1} yr^{-1} resulted in a realized angling effort of only about 125 h ha^{-1} 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 annual angling effort per ha are displayed for illustrative purposes.

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

Exploitation under HSL-Ls and MinL-L regulations resulted in substantial age truncation of the pike population as indicated by the decreasing average age of spawners at both angling intensity levels and for all types of regulations (Fig. 4 bottom panels). Thus, truncation of the age and size structure of thepike population is inevitable whenever anglers start cropping the stock (see also Supplementary Table 1). As to be expected, the decrease in the average age of spawners was most pronounced at the highest maximum fishing effort level and for strongly relaxed harvest regulations. While the average age of spawners was always three years or older across all harvest regulations at low maximum angling effort levels, it dropped to values below three years on average at high maximum angling effort densities for MinL-L regulations of < 80 cm and upper bounds for HSL-L of > 50 cm (Fig. 4). Generally, HSL-L regulations resulted in a lower average age of spawners compared to MinL-L regulations, while total catch-and-release policies were the most efficient regulations at preserving 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-h ha^{-1} yr^{-1} 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^{-1} yr^{-1} falling to 2 fish ha^{-1} yr^{-1} 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 ≥ 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 ≤ 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 ≥ 86 cm total length (Fig. 5 bottom panels). Generally, catches of large fish were low with values < 1 memorable pike ha^{-1} 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 was 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 (μ) 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 α_2 and the exponent of the length-gonad weight regression γ_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 survival 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 ± 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 (Raat, 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 ≥ 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 ≥ 50.8 and ≥ 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).

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

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

A further advantage of HSL-L over MinL-L in terms of fisheries variables related to the by far greater fraction of “wasted” fish under MinL-L regulations due to unwanted catch-and-release mortality compared to most HSL-L regulations with upper bounds > 60 cm. This results from the generally greater abundance of small pike that are vulnerable to the angling gear but must be released under 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 disproportionally greater fecundity of large individuals compared to small pike that maintains recruitment and subsequently fishing quality (harvest, catch of large fish) despite the largely inevitable declines in population abundance that result from intensive harvesting under all forms of harvest regulations, unless they become overly strict.

In our model we included an empirically measured asymptotic size-dependent maternal effect on early pike survival, which translated into a relative survival advantage to age 1 of offspring from larger females. The mechanistic reason for this effect in pike is related to inferior egg quality of first-time spawners and lower size-at-hatching (Hubenova et al., 2007), which translates into greater mortality of offspring from first-time spawners relative to offspring from larger repeat spawners through competitive disability or intracohort cannibalism (Skov et al., 2003). The size-dependent maternal effect we included in our model assumed the lack of any form of reproductive senescence in pike, which agrees with recent findings by Pagel (2009). One might still argue that we underestimate the importance of size-dependent maternal effects on offspring traits for pike recruitment because the maternal effect mechanism we incorporated in our model was constrained to the relative survival advantage of pike offspring from larger-sized females during the first month of like (Arlinghaus, Faller, Wolter & Bekkevold, unpublished data, Fig. 2d) translated into differential first year survival. Thereby, we did not account for potential survival advantages of differently sized larvae resulting from positively size-dependent intracohort competitive abilities and cannibalism (Skov et al., 2003) after age 1 later in life. Acknowledging the fundamental importance of body size for survival in pike (Haugen et al., 2006), one could indeed assume that offspring originating from large females might experience a survival advantage throughout their lifetime by having a persistent size advantage to offspring from small pike. However, there is no empirical support for this hypothesis in pike justifying our conservative assumption about size-dependent maternal effects on offspring survival in the present study. The possibility of other size-dependent mechanisms of maternal effects in pike, however, cannot be ruled out and should be investigated further. Our model is open to additions of important population dynamical 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 (Svärdson, 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 disproportionally 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 α_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 (α_2) is 3. Therefore, changes to the model structure might be needed if our model is applied to a specific pike population where α_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 literature (0.95-0.99, Willis, 1989). This reduces the problem of parameter sensitivity for α_2 if our model is to be applied to a real fishery. It nevertheless is worthwhile to estimate the density dependence of α_2 further and include this process in extensions of our model. Finally, further empirical studies are needed to obtain more precise estimates for γ_2, being the exponent of the length-gonad weight regression. So far, only one study (Edeline et al., 2007) has been published reporting this relationship, and further research for other populations is needed before our model can be considered of general applicability for pike.

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

We examined a range of angling intensities and a range of harvest regulations in the present 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 ha^{-1} 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 ha^{-1} 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 – ≤ 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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Table 1. Life-history parameters for a pike population exploited by recreational fisheries. Parameters and symbols are arranged according to biological and recreational angling processes. – indicates ratio scales or dimensionless parameters fitted to empirical data.

Symbol		Equation	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 reproductive investment)		20	cm	Raat (1988)	G
α_1	(length-weight relationship)*	3	4.8×10^{-6}	kg	Willis (1989)	A
α_2	(length-weight relationship)	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}	–	$\exp(f_a)$ 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	$h\ ha^{-1}\ yr^{-1}$	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	–

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

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

Table 2. Sensitivity analysis of three variables [absolute harvest in terms of numbers of pike, spawning potential ratio (SPR), and SPR with asymptotic early survival relative to constant early survival with female size]. Parameter order and values follow Table 1. We chose an intermediate maximum angling effort (u = 150 h ha^{-1} yr^{-1}), a harvest regulation of a harvestable-slot length limit of 45 – 70 cm, and an asymptotic increase of early survival probability of offspring with their mother's size for the analysis of the first two variables. We also tested the constant maternal effect scenario for the first two variables and found qualitatively the same results. Percent changes for the first three variables when the default value of each parameter is altered by ± 10% are shown. Changes in response variables ≥ $|10\%|$ (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'_{0max}	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

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

Figure captions

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

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

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

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

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

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

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

Fig.1

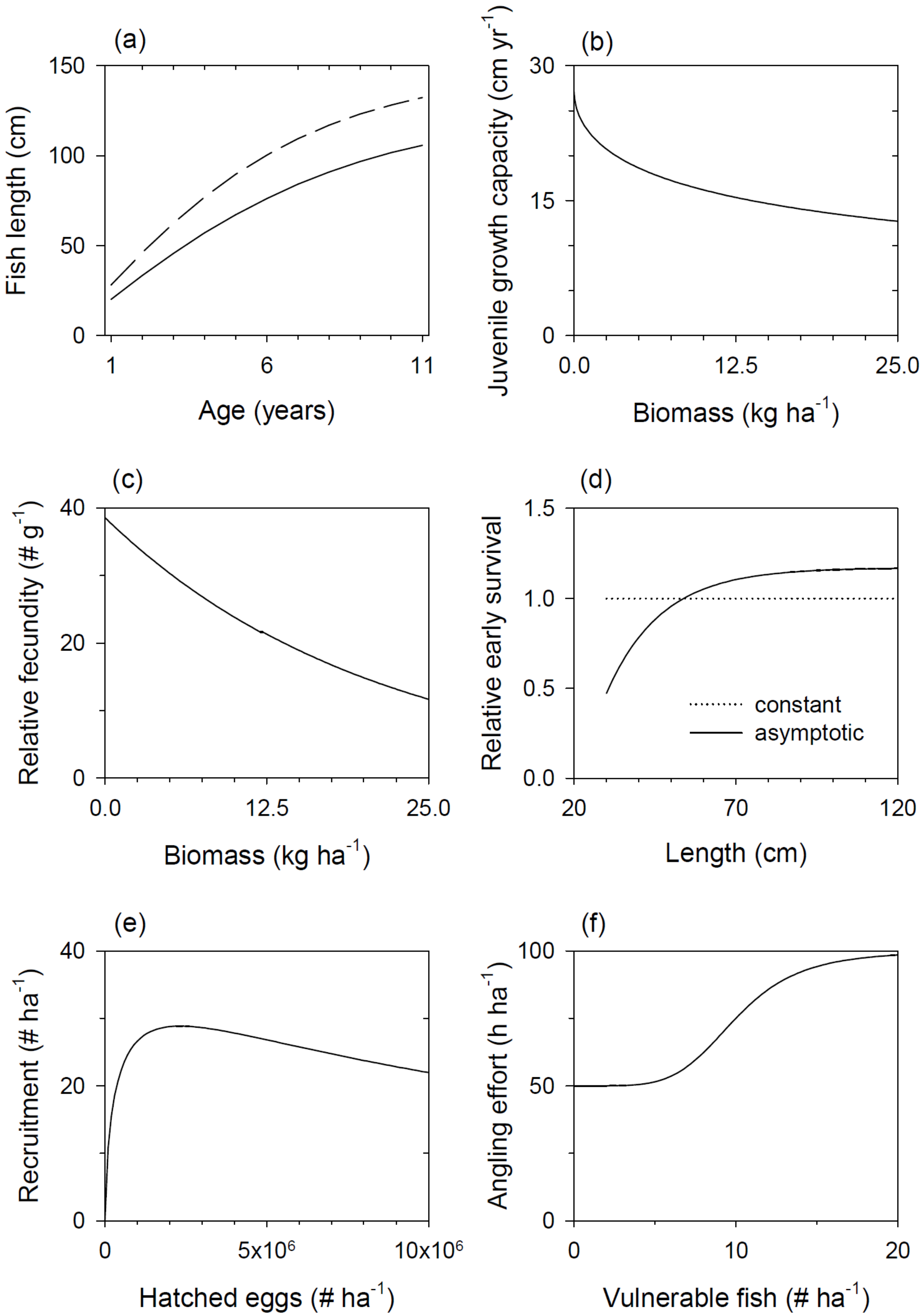
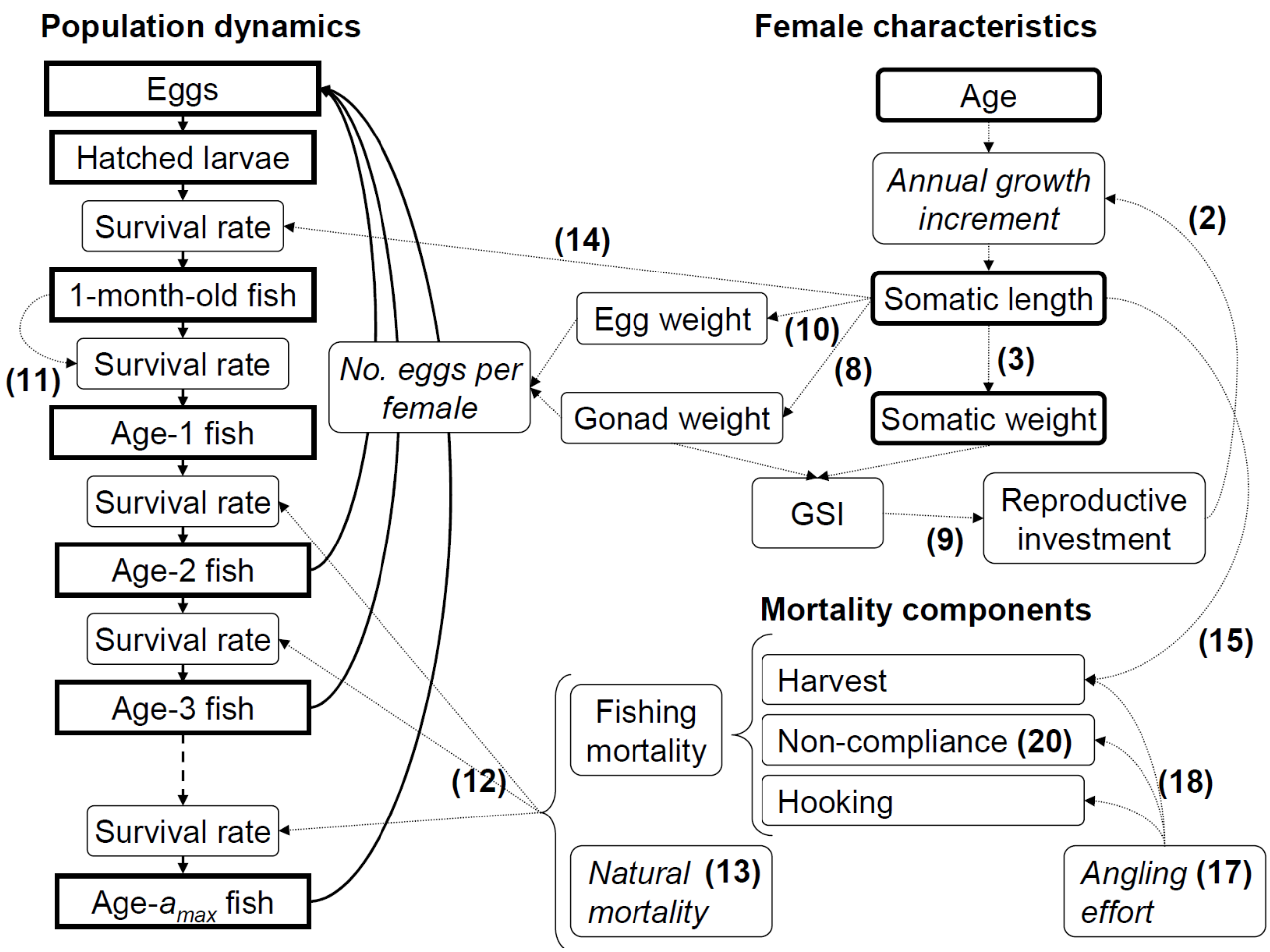

(a)
Fish length (cm)
150
100
50
0
1
6
11
Age (years)
(b)
Juvenile growth capacity (cm yr-1)
30
15
0
0.0
12.5
25.0
Biomass (kg ha-1)
(c)
Relative fecundity (# g-1)
40
20
0
0.0
12.5
25.0
Biomass (kg ha-1)
(d)
Relative early survival
1.5
1.0
0.5
0.0
constant
asymptotic
20
70
120
Length (cm)
(e)
Recruitment (# ha-1)
40
20
0
0
5x10^6
10x10^6
Hatched eggs (# ha-1)
(f)
Angling effort (h ha-1)
100
50
0
0
10
20
Vulnerable fish (# ha-1)

Fig. 2



Population dynamics
Eggs
Hatched larvae
Survival rate
1-month-old fish
Survival rate
(11)
Age-1 fish
Survival rate
Age-2 fish
Survival rate
Age-3 fish
Survival rate
Age-a_{max} fish
No. eggs per female
(14)
(12)
Female characteristics
Age
Annual growth increment
(2)
Somatic length
Egg weight
(10)
(8)
(3)
Gonad weight
Somatic weight
GSI
(9)
Reproductive investment
Mortality components
(15)
Fishing mortality
Harvest
Non-compliance (20)
Hooking
(18)
Natural mortality (13)
Angling effort (17)

Fig. 3

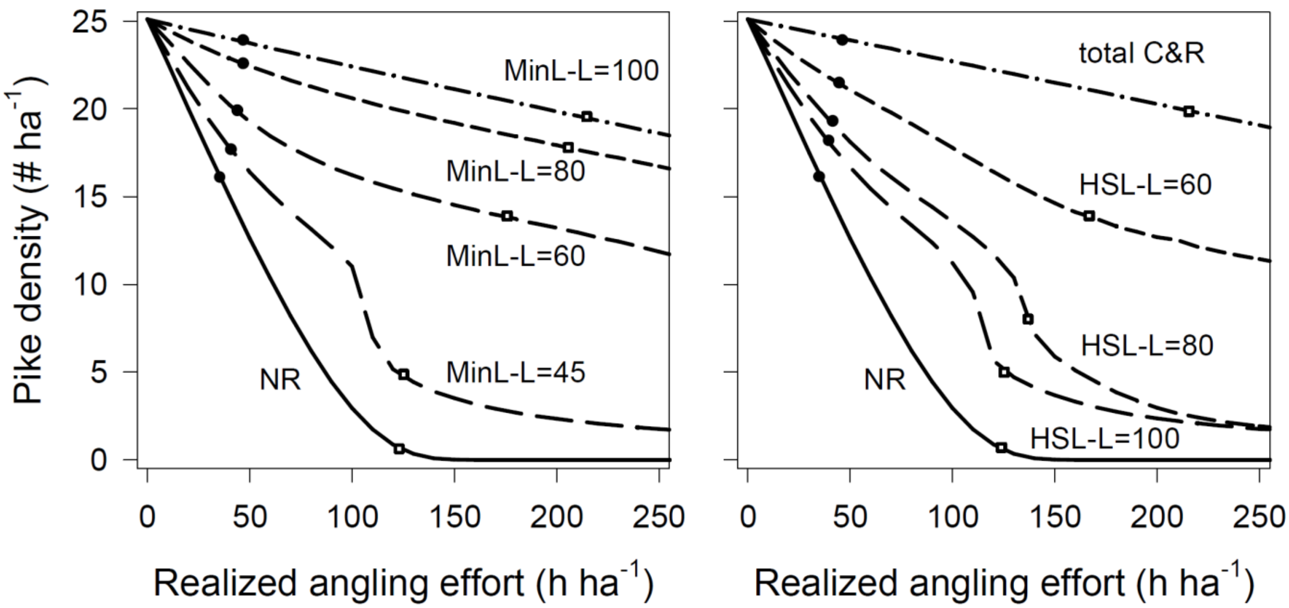
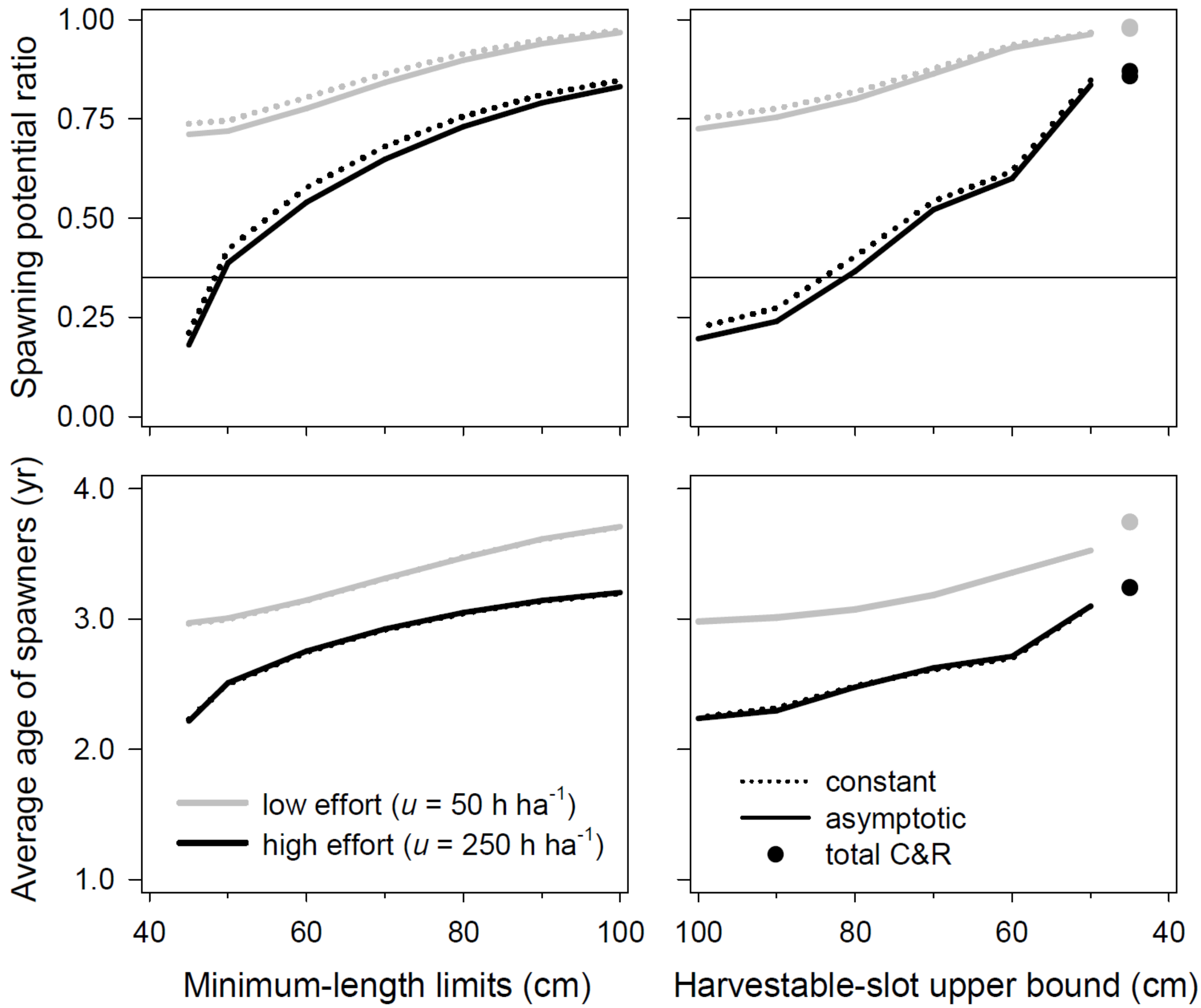
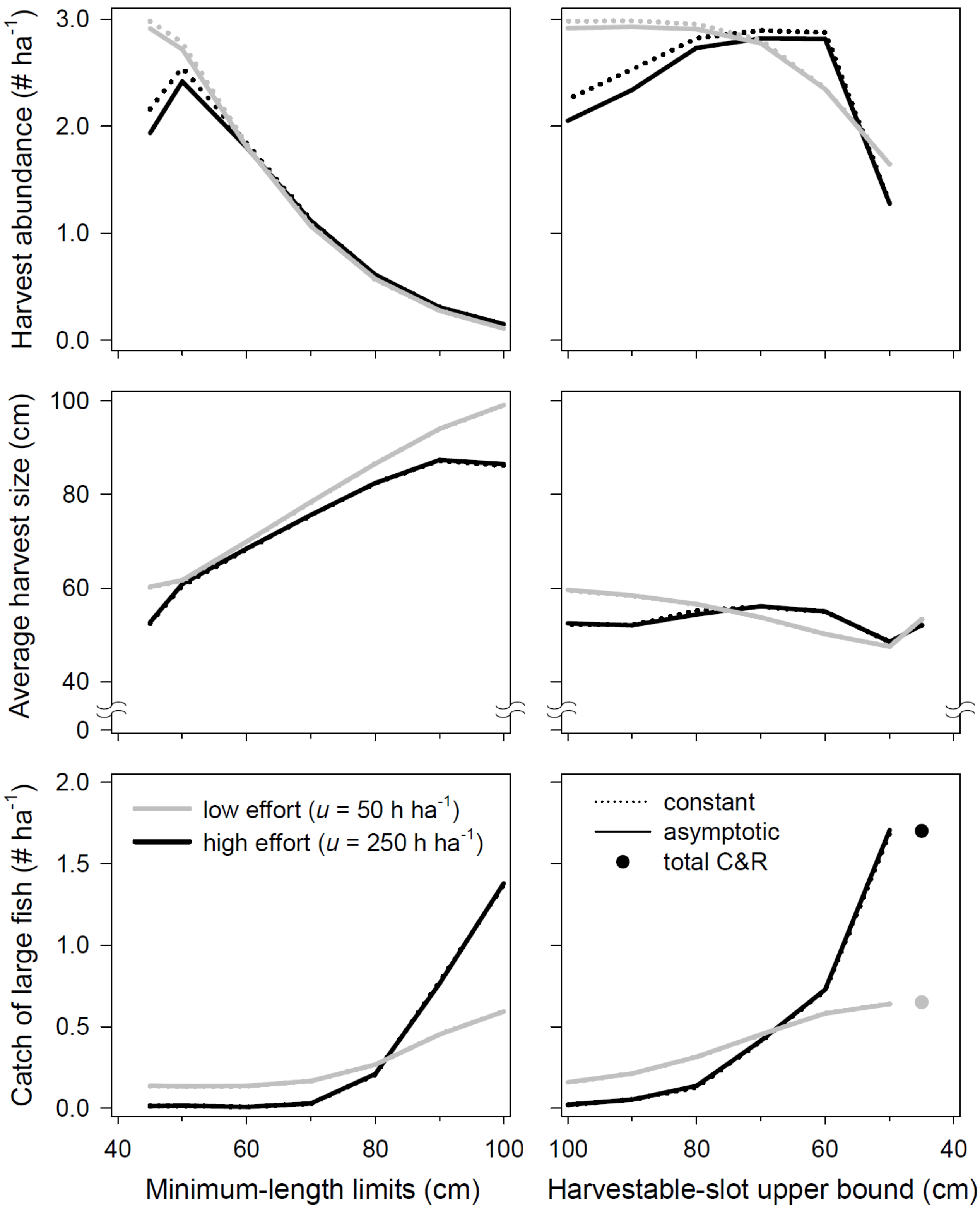

Pike density (# ha^{-1})
Realized angling effort (h ha^{-1})
MinL-L=100
MinL-L=80
MinL-L=60
MinL-L=45
NR
total C&R
HSL-L=60
HSL-L=80
HSL-L=100
NR
Realized angling effort (h ha^{-1})
0
5
10
15
20
25
0
50
100
150
200
250

Fig. 4



Spawning potential ratio
1.00
0.75
0.50
0.25
0.00
Average age of spawners (yr)
4.0
3.0
2.0
1.0
low effort (u = 50 h ha-1)
high effort (u = 250 h ha-1)
constant
asymptotic
total C&R
40
60
80
100
100
80
60
40
Minimum-length limits (cm)
Harvestable-slot upper bound (cm)

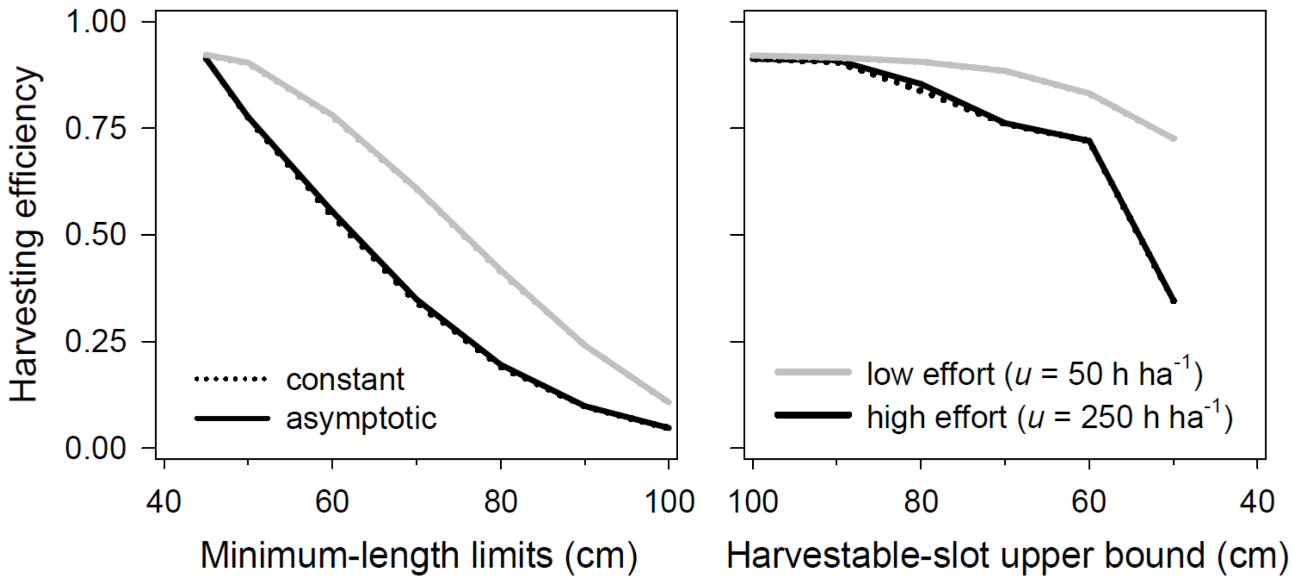
1048 Fig. 5



1049

1050

1051 Fig. 6



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