

Project KESKALA: Studies on Ecologically Sustainable Fishing

Model-based evaluation of the management of pikeperch (*Sander lucioperca*) stocks using minimum and maximum size limits

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Pikeperch populations typically differ substantially in life-history traits. Here, we evaluated the potential of variable size limits to ensure ecologically and evolutionarily sustainable fishing of six important Finnish inland pikeperch stocks using a carefully parameterized age-, size-, and maturity-structured evolutionary population model. Individual growth rates of the Oulujärvi and Vesijärvi stocks were the fastest and least resource-limited. The Höytiäinen, Vanajavesi and Pääjärvi stocks were strongly regulated by density-dependent food availability. Minimum size limit ensuring the highest yields was clearly higher for the fast-growing stocks than for the strongly food-limited stocks. Implementation of a maximum size limit 200 mm above the minimum size limit (MSL) would allow the stocks to tolerate stronger fishing mortality rate, but the 200 mm slot appeared too wide to significantly prevent evolution towards earlier maturation. To ensure maximal stability of yield and minimal evolutionary effect, fishing mortality rates should be restricted to relatively low values.

Introduction

Inland fisheries are usually characterized by a large number of participants, mainly recreational fishers and an absence of direct regulations on the total fishing effort or the total catch (Arlinghaus *et al.* 2002). Recruitment overfishing is typically prevented by the use of minimum size

limit (MSL), and heavy fishing intensity is often also compensated by stockings (Coxw and Gerdeaux 2004). MSL can be used to maximize the yield from a single cohort by optimally taking into account the trade-off between individual growth and population level mortality (Ricker 1945). However, MSLs are rarely set based on quantitative population modeling and

an explicit management target. Instead, the general aim of applying MSL is to ensure one opportunity to spawn for most fish without specific information on the actual life-history variation among the managed stocks.

It is currently acknowledged that overfishing in inland waters is a far more widespread problem than previously thought, particularly in waters close to urban centers (Post *et al.* 2003, Allan *et al.* 2005). Too low MSLs and gillnet mesh sizes have contributed to declines of many now endangered salmonid stocks (Syrjänen and Valkeajärvi 2010), and they may also result in growth overfishing and cause unwanted evolution towards earlier maturation (Heikinheimo *et al.* 2006, Vainikka and Hyvärinen 2012, Kokkonen *et al.* 2015). Intensive fishing also truncates the size structure of the MSL-regulated population, and may through intensive competition for food among small, early maturing individuals (Ylikarjula *et al.* 1999) and trophic bottlenecks (Heath and Roff 1996), cause stunting. Overfishing tends to occur especially in waters with multiple private management units within the stock's distribution area (Saulamo and Thoresson 2005) stressing the importance of producing lake- and stock-specific management recommendations.

Maximum size limits are increasingly applied in rod fisheries where the fish can be released alive, but quantitative evaluations of their benefits are rare (Berkeley *et al.* 2004, Matsumura *et al.* 2011, Gwinn *et al.* 2015). Use of both minimum and maximum size limits restricts the total harvest rate and protects the largest individuals that are particularly valuable for the recruitment due to their larger offspring and potential indirect genetic benefits (Olin *et al.* 2012). Thus, management using an allowable size slot may decrease the risk of a population collapse and maintain more natural size structure and higher stock productivity than the management using only a MSL (Power and Power 1996, Gwin *et al.* 2015). However, determining an optimal slot-size for any given fish stock requires knowledge on the recruitment and its variation, individual growth, mortality, and size structure of the population (Brousseau and Armstrong 1987, Allen and Pine 2000, Isermann 2007). Such complete knowledge is rarely available for inland stocks, but population models with necessary simplifying assumptions can be used

to derive values that could be further adjusted in adaptive management over time (Gwin *et al.* 2015).

An additional concern in fisheries management arises from the evolutionary impact of fishing (Ricker 1981, Heino 1998, Heikinheimo *et al.* 2006, Kuparinen and Merilä 2007, Fenberg and Roy 2008, Jørgensen *et al.* 2009, Jørgensen and Fiksen 2010). Numerous studies provide evidence that fish maturation advances over time in intensively harvested stocks (Jørgensen *et al.* 2007, Kokkonen *et al.* 2015). In fishes, maturation usually occurs after an individual has reached some size threshold (Day and Rowe 2002) so that maturation is postponed when growth is slow and advanced when growth is fast. Adaptation to a high fishing mortality rate by decreased size at maturation may increase reproductive capacity of the stock, but simultaneously reduce biomass productivity through the allocation of resources to reproduction instead of somatic growth (Lester *et al.* 2004). Loss of large fish typically also decreases the value of the stock for recreational rod fisheries (Jacobson 1996). Therefore, extensive decreases in the size at maturation can be considered undesired (Law and Grey 1989, Laugen *et al.* 2014). However, relatively little attention has so far been paid to the evolutionary sustainability of inland fisheries, often lacking effective effort controls and thus managed using relatively strict size limits (Williams and Shertzer 2005, Lewin *et al.* 2006, Philipp *et al.* 2009, Cowx *et al.* 2010, Matsumura *et al.* 2011, Vainikka and Hyvärinen 2012). In general, models show that intensive harvesting induces evolution towards earlier maturation unless harvesting specifically targets only mature or small individuals (Law and Grey 1989, Heino 1998, de Roos *et al.* 2006, Dunlop *et al.* 2007, Jørgensen *et al.* 2009, Vainikka and Hyvärinen 2012). Implementation of a maximum size limit in addition to MSL might provide a tool to mitigate or reduce the negative genetic effects of fishing (Law 2007, Matsumura *et al.* 2011, Laugen *et al.* 2014). Bell-shaped selection curve as typically assumed for gill-nets has been shown to better maintain stock productivity over evolutionary time scales than trawl-fishing that corresponds management using only MSL (Jørgensen *et al.* 2009).

Minimum size limits and corresponding gill-net mesh size regulations are among the most commonly applied fisheries management measures in Finland (e.g. Heikinheimo *et al.* 2006, Milardi *et al.* 2011). In Finland, the pikeperch (*Sander lucioperca*) is one of the most valuable freshwater fish species in both commercial and recreational fisheries (Ruuhijärvi *et al.* 1996, Heikinheimo *et al.* 2006). It occurs both in the brackish waters of the Baltic Sea and, partially due to extensive stockings, in most major lakes up to the Arctic Circle in northern Finland (Milardi *et al.* 2011, Salminen *et al.* 2012). Prior to 2016, nationwide MSL of pikeperch was 370 mm when MSL was increased to 420 mm in inland waters. However, locally MSL may have been higher, and local deviations of up to 20% are now allowed by the Fishing Act. The pikeperch is a warm-water species living in Finland at the northern edge of its distribution range, and as such its recruitment is heavily dependent on water temperatures in summer (Heikinheimo *et al.* 2014). However, pikeperch is typically also stocked in large numbers and pikeperch stocks show large variation in individual growth likely due to both absolute food availability and density-dependence in food availability (Ruuhijärvi *et al.* 1996, Vinni *et al.* 2009). Generally, density-dependent food intake can be important in population regulation especially at high densities close to the carrying capacity (Lorenzen and Enberg 2002, Lorenzen 2008). Even in heavily-harvested, age and size truncated pikeperch populations, small individuals may be limited by the availability of suitably sized prey (Ginter *et al.* 2015).

Here, our primary aim was to study the ecological and evolutionary sustainability of six important Finnish pikeperch fisheries under varying MSL and allowable slot length regulations assuming either density-dependent or density-independent individual growth. We performed a simple evolutionary impact assessment (Jørgensen *et al.* 2007, Vainikka and Hyvärinen 2012, Laugen *et al.* 2014) by examining how the size at maturation would respond to the different size limit options. Size at maturation has been identified by both models and empirical data as the life-history trait which evolves most easily (Ricker 1981, Heino and Kaitala 1999, Olsen *et al.* 2004, reviewed by Jørgensen *et al.* 2007). For our purpose we used

an age-, maturity- and size-structured population model (Vainikka and Hyvärinen 2012) in which the individual growth follows the mechanistic growth model of Lester *et al.* (2004).

Material and methods

Overview of the model and the study populations

Age-, length- and maturity-structured discrete time model described by Vainikka and Hyvärinen (2012) was used in this study. Age structure was used only to parameterize the individual growth rate, and therefore the age is not indicated in the subsequent equations (all vital functions depend on body size). The seasonal order of functions in the model was: (1) spawning and recruitment, (2) maturation and density-dependent growth (including the calculation of food consumption), and (3) natural and fishing mortality. The population census occurs after mortality, which corresponds to the situation prior to spawning in the spring. Therefore, the size-at-age information derived from the model does not include any seasonal growth and all biomass yields are derived using the size of the fish after the growth season (for model parameters and their values see Appendix 1). The six modeled pikeperch lakes — Höytiäinen, Oulujärvi, Pääjärvi, Pielinen, Vanajavesi and Vesijärvi (see Appendix 2) — support nationally important inland pikeperch fisheries (Table 1). Höytiäinen is the most productive large pikeperch lake in Finland, and Oulujärvi and Pielinen are among the five largest lakes in Finland. Oulujärvi is the most important for commercial pikeperch fisheries whereas in the other lakes most catch is captured in recreational fisheries. Vesijärvi suffered from heavy eutrophication during the past decades, but currently water quality of all the study lakes is reasonably good (Table 1).

Spawning and recruitment

The total fecundity, G , of the sexually mature part of the female population (50:50 sex ratio) was defined as:

$$G = \frac{1}{2} \int_0^{\infty} [\gamma_0 + \gamma_1 m(l)] n_m(l) dl, \quad (1)$$

where $n_m(l)$ is the number of sexually mature individuals of length l at the time of spawning, and $m(l)$ is the body mass of a pikeperch at length l ; $\gamma_0 + \gamma_1 m(l)$ was set to zero when its value was negative. The parameters γ_0 and γ_1 were obtained using linear regression describing the dependence of individual absolute fecundity on the body mass of female pikeperch. If population-specific values were not available, the values of the geographically closest population were used (*see* Appendix 1). The constant pikeperch body mass-to-length ratio was assumed independently of resource levels. Body mass $m(l)$ at length l was defined as:

$$m(l) = a_0 l^{a_1}, \quad (2)$$

where a_0 and a_1 are the coefficient and exponent, respectively, whose values are obtained using non-linear regression and individual length and weight data (*see* Appendix 1).

As the temperature and stock recruitment data necessary to estimate the lake-specific

spawning stock biomass above which the recruitment might be overcompensatory were lacking (Heikinheimo *et al.* 2014), we chose to use the temperature-independent, Beverton-Holt-type recruitment function (Beverton and Holt 1957) that is based on the notion of finite spawning areas and has the convenient property of stabilizing population dynamics. The total number of surviving recruits (R) is given by:

$$R = \begin{cases} \frac{\eta G}{1 + \eta GK}, & \text{for deterministic recruitment} \\ \frac{\eta G}{1 + \eta GK} (1 + \gamma \phi), & \text{where } \gamma \geq -1 \text{ and } R \leq G, \\ & \text{for stochastic recruitment} \end{cases}, \quad (3)$$

where K is the Beverton-Holt constant (inverse carrying capacity), η is the constant determining the proportion of hatching recruits from eggs (i.e. egg–recruit scaling parameter; *see* Appendix 1), γ is a random number from approximate normal distribution (truncated to values > -1 in order to prevent negative recruitment) generated according to the central limit theorem by summing -6 and 12 random values (from 0 to 1),

Table 1. Environmental and pikeperch fisheries characteristics of the study lakes. Minimum size limit (MSL) refers to the limit that was applied in 2014. Fisheries parameters are averages for 2013–2015. Water quality parameters are for the surface (0–3.0 m) water during the open water seasons of 2010–2015 (obtained from open access databases of SYKE and ELY centres). Temperatures were measured between 25 July and 15 August. For some parameters mean \pm SD are given. The lengths of the thermic growing-season were obtained from the open access service of the Finnish Meteorological Institute.

Variable/constant (symbol, unit)	Höytiäinen	Oulujärvi	Pääjärvi	Pielinen	Vanajavesi	Vesijärvi
Surface area (km ²)	282.6	887	13.5	894.2	102.6	107.4
WGS84 Latitude	62°46.54′	64°17.613′	61°3.958′	63°15.423′	61°9.419′	61°2.611′
WGS84 Longitude	29°42.939′	27°11.845′	25°7.974′	29°43.391′	24° 12.57′	25°35.52′
Total annual catch (tonnes)	100	100	1.8	70	22	27
Total annual catch per hectare (kg)	3.54	1.13	1.36	0.78	2.13	2.54
Minimum size limit (MSL) (l_{\min} , mm)	450	450	450	420	370	420
Fishing mortality rate (F , y ⁻¹)	1.5	0.7	0.6	0.7	1.6	1.0
Resource availability level (E/C)	1.5	2.0	1.0	2.0	1.12	2.9
Annually available resource (E , tonnes)	9661	5651	111	9293	360	1300
Length-at-age 6 (mm)	350.4	452.1	408.6	371.1	496.1	538.6
Total phosphorous ($\mu\text{g l}^{-1}$)	11 \pm 5	16 \pm 4	11 \pm 2	12 \pm 5	22 \pm 6	24 \pm 8
Total nitrogen ($\mu\text{g l}^{-1}$)	403 \pm 108	362 \pm 65	1470 \pm 132	366 \pm 48	738 \pm 375	438 \pm 74
Conductivity (mS m ⁻¹)	5.0 \pm 0.4	2.9 \pm 0.2	9.2 \pm 0.2	2.4 \pm 0.4	10.7 \pm 2.0	11.1 \pm 0.6
pH	7.1 \pm 0.2	6.8 \pm 0.3	7.2 \pm 0.2	6.8 \pm 0.2	7.5 \pm 0.4	7.7 \pm 0.3
Colour (mg Pt l ⁻¹)	52 \pm 25	69 \pm 20	82 \pm 15	67 \pm 17	41 \pm 13	19 \pm 4
Secchi depth (m)	2.6 \pm 1.0	2.0 \pm 0.5	1.9 \pm 0.3	2.4 \pm 0.9	1.8 \pm 0.4	2.1 \pm 1.1
Summer surface temperature (°C)	19.5 \pm 2.1	19.4 \pm 1.7	21.4 \pm 2.4	20.0 \pm 2.3	20.3 \pm 1.3	21.0 \pm 1.6
Thermic growing season (days)	155–165	155–165	175–185	155–165	175–185	175–185

and ϕ is the coefficient used to scale the variance in recruitment (Vainikka and Hyvärinen 2012). Normal distribution was chosen because we did not have data that would support better any other distribution. Parameter value of ϕ was adopted from Vainikka and Hyvärinen (2012) who estimated it for Oulujärvi. Recruits entered the population at constant size l_r .

Consumption dynamics

We assumed constant surplus production of prey fish without predator feedback so that pikeperch utilize a single unstructured resource pool E . This simplifying assumption was reasonable, since pikeperch undergoes several ontogenetic niche shifts along its growth and can flexibly switch between prey species according to their abundance (Peltonen *et al.* 1996). We assumed that individual pikeperch have a maximal annual feeding capacity c , which scales with body mass as

$$c(m) = c_0 m^{\alpha}, \quad (4)$$

where c_0 and α relate the maximal feeding capacity to body size in temperature conditions of Jyväsjärvi, central Finland (for the estimation of the parameter values, *see* Vainikka and Hyvärinen 2012) based on the bioenergetics model constructed by Keskinen *et al.* (2008). According to the parameterization, the amount of food consumed annually decreases rapidly with body mass: pikeperch with body mass of 100 g and 1000 g could consume max. 1579 and 6044 g of food, respectively. To account for density-dependent growth, we assumed that the resource available for each individual is inversely proportional to the total feeding pressure, C

$$C = \int_0^{\infty} c(l)n(l)dl, \quad (5)$$

where $n(l)$ is the number of individuals at length l right after reproduction has occurred. This results in the mean resources available to an individual $\bar{e}(l)$ at length as

$$\bar{e}(l) = c(l) \frac{E}{C}, \quad (6)$$

To account for the inherent variation in the individual-level availability of prey, we assumed that the realized availability of resource, $e_r(l)$ varies according to a normal distribution among individuals of the same size. In order to scale the variance in food availability with absolute food availability, the number of individuals at size l having realized the share of energy $e_r(l)$ (from here on e_r includes always this between-individual variation) was defined by the equation:

$$n\left(\frac{e_r}{c}, l\right) = n(l) \frac{1}{\sigma_e \sqrt{2\pi}} \exp\left[-\frac{\left(\frac{e_r(l)}{c(l)} - \frac{\bar{e}(l)}{c(l)}\right)^2}{2\sigma_e^2}\right], \quad (7)$$

where σ_e is the standard deviation of individual-level resource availability. The parameter value of σ_e (*see* Appendix 1) was found by comparing model-derived and observed population-specific standard deviations of length-at-ages and minimizing the difference by iteratively adjusting the σ_e value. This formulation simply means that $e_r(l)$ is normally distributed and translates into variance in individual growth rates. Individual fish cannot consume all available food due to behavioral restrictions, and we assumed that a Holling type II functional response describes the realized energy intake $i(l)$ at each level of individual energy share:

$$i(l) = \frac{e_r(l)}{1 + \frac{e_r(l)}{c(l)}}. \quad (8)$$

Type II functional response was chosen as it has often been determined as the best quantitative description of the empirically observed foraging responses of predatory fish (e.g., Buckel and Stoner 2000, Rindorf and Gislason 2005).

Maturation and growth

In the model, individuals mature with probability $p(l)$ according to a horizontal probabilistic maturation reaction norm (PMRN) (Heino *et al.* 2002):

$$p(l) = \left[1 + \exp\left(-\frac{l - l_{\text{mat}}}{\sigma_m}\right)\right]^{-1}, \quad (9)$$

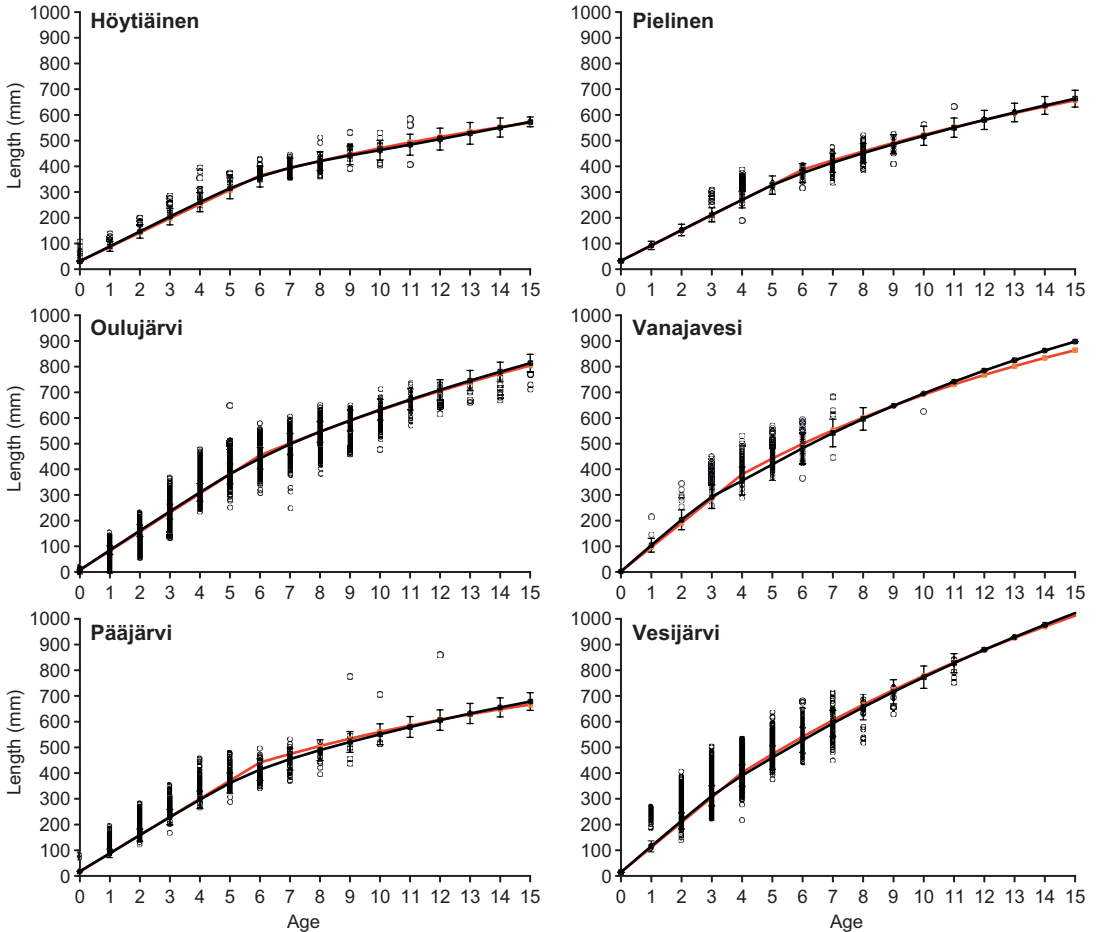


Fig. 1. Size distributions of sampled fish at the time of capture (circles, seasonal growth included) compared with the Lester *et al.*'s (2004) growth model fit (red line) and the growth rate produced by the model at the starting conditions (\pm SD, black line).

where σ_m defines the width of the length range at which maturation occurs, and l_{mat} is the length at 50% probability of maturing (*see* Appendix 1). Growth of maturing fish equals the growth of mature fish. Width of the maturation window, i.e. σ_m , was adjusted by visually matching the logistic-regression predicted proportions of mature fish (*see* below) with the parameterization of Eq. 9. For Vanajavesi, the σ_m value was reduced to 50 mm to avoid an unrealistically wide maturation window and potentially misleading population consequences resulting from very small spawners (*see* Appendix 1).

We used a mechanistic growth model of Lester *et al.* (2004) to describe individual growth. The length of an individual after a year

of growth was described by:

$$l_{t+1} = \left(\frac{3}{3+g} \right) l_t + \lambda(l) \frac{3h}{3+g}, \text{ when } l_{t+1} > l_t, \quad (10)$$

where g is the energetic gonadosomatic index (GSI, for juvenile fish, $g = 0$), λ is the multiplier that accounts for density-dependence in growth (Dunlop *et al.* 2007, Arlinghaus *et al.* 2009, Vainikka and Hyvärinen 2012), and h is the constant annual length increment in juvenile fish (Lester *et al.* 2004). The energetic GSI, g , was estimated together with the growth constant h using least-squares regression (*see* below and Appendix 1). The modeled growth rates matched well the observed growth rates (Fig. 1). The multiplier $\lambda(l)$ was calculated as:

$$\lambda(l) = \frac{i(l)/c(l)}{\lambda_0}, \quad (11)$$

where λ_0 is used to set the reference resource level corresponding to starting conditions (see Appendix 1), $i(l)$ is the realized energy intake (Eq. 8), and $c(l)$ is the maximal annual feeding capacity (Eq. 4). The constant λ_0 also implicitly accounts for the assimilation efficiency of consumed food and variation in thermal conditions among the lakes. The $i(l)/c(l)$ ratio indicates the resource level, i.e. how much an individual actually can consume in relation to the maximum intake capacity. If l_{t+1} was lower than l_t , the fish was assumed to die from starvation.

Mortality

In the model, there are three types of mortality: (1) natural, (2) fishing, and (3) starvation (negative growth). In biological reality, mortality is rather size- than age-specific (Sogard 1997, Lappalainen *et al.* 2000). Therefore, natural mortality M was defined as:

$$M = d_0 + d_1 \exp\left(\frac{-l}{l_0}\right), \quad (12)$$

where d_0 and d_1 define the size-independent and size-dependent mortality rates, respectively (Taborsky *et al.* 2003). The parameter l_0 is the size of natural mortality decay, i.e., the length at which the size-dependent mortality rate, $d_1 \exp(-l/l_0)$, decreases to $1/e = 36.8\%$ relative to its value at size $l = 0$ (Taborsky *et al.* 2003). The values of l_0 and d_1 were adjusted slightly from Vainikka and Hyvärinen (2012). With the used parameters, the recruitment of age 0 fingerlings by the end of the fourth year was 2.8%–5.9% depending on the individual growth rate. The corresponding age-specific natural mortality rates were ca. 1.2–1.6 for 0-year-old fish, 0.6–1.0 for 1-year-old, and 0.4–0.7 for 2-year-old fish.

Fishing mortality was defined as the product of size-specific probability to be exposed to fishing $f(l)$ and instantaneous fishing mortality rate F plus the discard mortality F_{pre} of released fish, i.e. fish under minimum size limit (l_{min}) or above maximum size (l_{max} , > 2000 mm for MSL-only scenario) (Coggin *et al.* 2007). Since recreational and commercial fisheries in Finland mainly use

gillnets, size limits do not directly translate into fishing mortality. Therefore, the probability to be exposed to fishing mortality $f(l)$ at length l was defined by two multiplied logistic curves as:

$$f(l) = \left[1 + \exp\left(\frac{l - l_{\text{max}}}{\sigma_{f,\text{max}}}\right)\right]^{-1} \left[1 + \exp\left(-\frac{l - l_{\text{min}}}{\sigma_{f,\text{min}}}\right)\right], \quad (13)$$

where $\sigma_{f,\text{min}}$ and $\sigma_{f,\text{max}}$ are the widths of the transition to and from fishing mortality, respectively. Similarly, released fish are exposed to discard mortality by:

$$f_{\text{pre}}(l) = \begin{cases} \left[1 + \exp\left(\frac{l - l_{\text{pre}}}{\sigma_{f_{\text{pre}}}}\right)\right]^{-1} - f(l), & f(l) < \left[1 + \exp\left(\frac{l - l_{\text{pre}}}{\sigma_{f_{\text{pre}}}}\right)\right]^{-1} \\ 0, & f(l) \geq \left[1 + \exp\left(\frac{l - l_{\text{pre}}}{\sigma_{f_{\text{pre}}}}\right)\right]^{-1} \end{cases}, \quad (14)$$

where $\sigma_{f_{\text{pre}}}$ is the width of the transition to discard mortality, i.e. the length range at which individuals recruit to fishing.

The total mortality Z was thus length-dependent as follows:

$$Z(l) = f(l)F + f_{\text{pre}}(l)F_{\text{pre}} + M(l), \quad (15)$$

where f is the proportion of realized fishing mortality, f_{pre} is the proportion of realized discard mortality and F_{pre} is the discard mortality rate of released fish. This translates to survival as:

$$s(l) = \exp[-Z(l)]. \quad (16)$$

The annual fisheries biomass yield (in grams), Y , for fish larger than l_y (700 mm for trophy fish, 0 mm for all the yield) from the population after spawning and growth can be calculated using Baranov's catch equation as:

$$Y = \int_{l_y}^{\infty} \frac{f(l)F}{Z(l)} \{1 - \exp[-Z(l)]\} n(l) m(l) dl. \quad (17)$$

With this information and similarly calculated information on the number of fish in the catch, also the mean size of fish in the catch can be calculated.

Estimation of growth and maturation

All accessible data were used to estimate pikeperch growth and maturation patterns in the study lakes (see Appendix 1). The data are long-

term averages rather than precise values. Individually back-calculated length-at-ages (using Fraser-Lee's equation; *see* Ricker 1992) were determined from scales for all the populations except the Oulujärvi one for which only the ages and sizes at capture were available. All individual length-at-ages were standardized to 1 January using the back-calculated size-at-age estimate or von Bertalanffy's growth function (Oulujärvi). Length at which 50% of pikeperch females mature, l_{mat} , was estimated for each population by fitting a logistic regression model of maturity *versus* total length in the beginning of the year. Females typically mature later than males (Lappalainen *et al.* 2003) and as such limit the reproductive capacity of the stock. For Höytiäinen and Pielinen, some of the juveniles were sexed microscopically. The final logistic regression was fitted using pooled sex data, but the average sex difference in $L_{p_{50}}$ values (5.9 mm in Höytiäinen and 34.2 mm in Pielinen) divided by two was added to the pooled sex estimate to account for the later maturation of females in comparison with males. For Vanajavesi, Vesijärvi and Pääjärvi, 50% of the unsexed juveniles were assumed to be females.

Lester *et al.*'s (2004) growth function was fitted to the individual back-calculated growth data using a general least-squares minimization and the estimated population average l_{mat} . For Oulujärvi, the growth model was fitted to age-at-length data (first standardized to 1 January). It should be noted that here the length at maturation (l_{mat}) refers to the length at which females mature ($L_{p_{50}}$) rather than the size at which they spawn for the first time (L_{50}).

Available data

In Höytiäinen, 261 pikeperch were sampled in 2013 for age and growth analyses. Of those, 248 individuals were used in the analyses of maturity. Fecundity information (total egg count) was available for 40 females. The size and age ranges were 49–585 mm and 0–11 yr, respectively.

The Oulujärvi data were gathered from 9349 fish captured between 1946 and 2014 (no data from 1947–1972) for which the exact capture date was available. Individual length was pro-

jected to 1 January by fitting von Bertalanffy's growth curve to continuous age-at-length data and reducing the predicted seasonal growth from each fish's length (using FSA 0.7.3 library and nls-based fitting in R 3.2.0, $p < 0.001$ for all parameters). As no additional maturity samples were collected since 2012, we used here the size at maturity estimate published by Vainikka and Hyvärinen (2012).

The Pielinen data consisted of 201 individuals obtained from commercial fishermen in 2013, and 171 individuals sampled by trolling in three different parts of the lake in 2014. The fish lengths and ages were 194–633 mm and 3–11 years, respectively. All data were used in the analyses of age, growth and maturity, but individual fecundity was available only for females collected in 2013 ($n = 30$).

The Pääjärvi data for age and growth analyses included 730 individuals collected during 2004–2012, 163 females for maturation analyses collected in 2004–2014, and 22 females for fecundity analyses collected in 2012 and 2014. The size and age ranges were, respectively: 72–860 mm and 1–12 years, 87–635 mm and 1–9 years, and 348–635 mm and 5–8 years.

The Vanajavesi data consisted of 660 individuals (145–1300 mm, 1–10 years) collected for age and growth analyses in 2005–2012, 98 individuals (365–825 mm, 3–7 years) collected for maturation analyses in 2012 and 2015 and 56 individuals (420–706 mm, 3–7 years) collected for fecundity analyses in 2012 and 2015.

The Vesijärvi age and growth data were from 3282 individuals (110–842 mm, 0–11 years) collected during 2004–2013. Maturation data from years 2005–2016 included 1472 females (64–815 mm, 0–12 years) and fecundity data from 2012 and 2015 included 35 individuals (370–528 mm, 4–7 years).

In Pääjärvi, Vanajavesi and Vesijärvi, we used Nordic multimesh gillnets (5–55 mm) supplemented with additional gillnets with large mesh sizes (30, 35, 40, 45, 50, 55, 60 and 70 mm). For fecundity analyses, we took a random sample of at least 50 eggs from the middle of both gonads and weighed them to get average fresh weight per egg. Total fecundity was calculated by dividing the total weight of gonads by the average egg weight.

Population level data used to parametrize recruitment, fishing mortality and resource environment

Total recreational pikeperch catches from Vesijärvi (years 2008–2011), Vanajavesi (years 2007–2010) and Pääjärvi (years 2008–2011) were available from survey reports based on inquiries sent to fishers that had bought a local fishing license (Ruuhijärvi and Ala-Opas 2014, Ruuhijärvi *et al.* 2014). For Oulujärvi, the total catch estimate was increased from the values used by Vainikka and Hyvärinen (2012) to 100 tonnes per year according to the most recent total catch estimates. For the much smaller Höytiäinen, the average total catch was estimated to be also 100 tonnes per year based on the fisheries questionnaire carried out in 2010 (H. Huuskonen unpubl. data), while for both Oulujärvi and Höytiäinen the reported annual peak catches exceeded 140 tonnes. For Pielinen, no data-based catch estimates were available, and we assumed the total catch to be around 70 tonnes annually (Table 1).

In the model, the carrying capacity coefficient of Beverton-Holt's recruitment function was adjusted iteratively until the equilibrium biomass yield corresponded the estimated yield with the assumed/estimated fishing mortality rate and the minimum size limit that was in use prior to 2016 (Table 1). For Oulujärvi, the fishing mortality rate estimate was taken from Vainikka and Hyvärinen (2012). The pre-fishing discard mortality rate was always 7.1% of the actual instantaneous fishing mortality rate (Vainikka and Hyvärinen 2012). Fishing mortality in Pääjärvi, Vanajavesi and Vesijärvi (Table 1) was estimated by subtracting natural mortality from total mortality. The total mortality was calculated by the catch curve method (Robson and Chapman 1961) using length distributions in standard Nordic gillnet catch data in 2010–2014 and age-length keys based on the previously described lake-specific age data. Only age groups 6–7 years in Pääjärvi and 5–7 years in the other two lakes were included in the calculations as these age groups are fully recruited to fishing (total lengths on average 410–570 mm) and are effectively caught by the largest mesh sizes (39, 43 and 55 mm from knot to knot) in Nordic gill-

nets (Van Densen 1987, Ruuhijärvi *et al.* 2014). Natural mortality for the age groups 5–7 years was 0.15 according to Lappalainen *et al.* (2005).

For Pääjärvi, Vanajavesi and Vesijärvi, an estimate of the total prey fish biomass was available from Ruuhijärvi *et al.* (2014). For Höytiäinen, Pielinen and Oulujärvi, the total available biomass was adjusted until an assumed level of resource availability was found (*see* Table 1). It is thus to be noted that population level parameters, especially for Pielinen, are based on expert assumptions rather than on the existing data, hence the yield estimates presented in this paper should be interpreted only in relative terms and with caution.

Initial model conditions and non-evolutionary analyses

The initial equilibrium conditions for the simulation were defined based on the knowledge and data on average past fishing mortality rate, total yield, resource availability and the used minimum size limit (Table 1 and Appendix 1). Population dynamical equilibrium was defined as a stable 0 exponential population growth rate, S , for at least 30 years:

$$S = \ln\left(\frac{N_{t+1}}{N_t}\right), \quad (18)$$

where N represents the number of individuals in the population and $t > 30$.

We simulated full population dynamics with and without density dependence on growth using a range of MSL from 200 to 700 mm and a range of F from 0 to 4. In addition to MSL only, we considered a maximum size limit 200 mm above MSL. The 200 mm width was based on the recommendation that recreational anglers commonly use in Finland for pikeperch fisheries, i.e., using the slot of 450–650 mm. We show the two-dimensional figures as a function of fishing mortality rate for three MSL options, the current nationwide 420 mm, one 50 mm below and one 50 above the limit, i.e. 370 mm and 470 mm.

In stochastic simulations, population was re-created and simulated until population dynamical equilibrium for 100 times (defined as long term (30 year) average population growth

rate of zero). At each repeat, the spawning stock biomass (SSB) and total biomass yield were recorded for 100 years starting from the first year with population dynamical equilibrium. For each 100-year period, the probability of SSB or the total yield being below a predefined threshold value was calculated. The risk estimates were derived as averages of 100 risk estimates each based on 100 years of simulation. Thus, the final average and confidence intervals for SSB and biomass yield were derived from a total of 10 000 years of simulation. The SSB threshold levels were chosen somewhat arbitrary to correspond to about 1/3 of the contemporary total yield of each lake (Table 2).

Both deterministic and stochastic simulations of the yield were done using the fixed, estimated size at maturation without any evolution occurring in ecological time.

Evolutionary invasion analysis

Evolutionarily singular values of maturation size, l_{mat}^* , were found through numerical evolutionary invasion analysis (Metz *et al.* 1992, Geritz *et al.* 1998). In practice, we studied the diagonal of the pairwise invasibility plot (PIP) in each parameter setting and recorded the resident values below or above which the invasibility of a close mutant having lower or higher l_{mat} than the resident changed (Maynard Smith and Price 1973, Eshel 1983). The presence of multiple evolutionary endpoints was confirmed by the construction of full PIP. We considered the evolutionary endpoints (Evolutionarily Stable Strategies, ESS) as indicative of the amount of

potential evolutionary change without genetic restrictions, but aimed not at providing estimates for the rate of evolutionary change.

The resident environment that corresponds to each set of parameter values was found by simulating the resident population until a population dynamical equilibrium (*see above*). At a population dynamical equilibrium, the resident environment was defined by two variables: mean resources available to an individual, $\bar{e}(l)$, and recruit count of the resident population (numerator G in Eq. 3; for the mutant population the denominator G in Eq. 3 was replaced with the recruit count of the mutant population G^*). The fitness of a mutant with a slightly (ca. 2 mm) different l_{mat} was studied by simulating the mutant population given the constant resident environment parameters $\bar{e}(l)$ and G until the S of the mutant population converged to a value that represented the invasion fitness S^* . When $S^* > 0$, the mutant trait value was expected to be favoured by evolution, and when $S^* < 0$, the resident trait value yielded higher fitness than the mutant trait value.

The effect of evolution on yield was assessed by running the population into the population dynamical equilibrium using fixed, evolutionarily stable size at maturation while all other parameters were kept constant.

Results

Variation in growth and maturation among the study populations

The growth rate of the Vesijärvi pikeperch was

Table 2. Initial parameter values of the model in equilibrium start conditions. Yield at evolutionarily stable (ES) maturation size was calculated using the current fishing mortality rate (Table 1) and minimum size limit of 420 mm.

Parameter (unit)	Höytiäinen	Oulujärvi	Pääjärvi	Pielinen	Vanajavesi	Vesijärvi
Total population biomass (tonnes)	932	335	10.4	337	26.8	58.4
Spawning stock biomass (tonnes)	291	128	3.5	110	6.8	37.1
Threshold risky SSB level (tonnes)	40	40	0.7	25	7.5	10
Total yield (tonnes yr ⁻¹)	100	100	1.8	70	21.7	27.0
Yield of pikeperch > 700 mm (kg yr ⁻¹)	2.7	8698	10	472	188	4336
Recruitment (0 yr), R ($\times 10^6$ yr ⁻¹)	37.7	4.3	0.20	9.3	0.57	29.2
Recruitment success (%)	22.8	5.9	9.5	17.1	12.8	1.2
Required food (tonnes yr ⁻¹)	5796	1884	55	3098	170	334
Yield at ES maturation size (tonnes yr ⁻¹)	105.4	70.3	0.96	42.3	12.9	24.3

the fastest among the studied populations, which likely resulted from high food availability in the lake (Table 1 and Fig. 1). In contrast, the Höytiäinen pikeperch grew at the slowest rate despite the record-high total pikeperch catches in this lake (Table 1). Among the other stocks, the Pääjärvi and Pielinen pikeperch stocks could be classified as slow growing and those of Oulujärvi and Vanajavesi as fast growing. The l_{mat} value was lower in the southern populations than in the northern populations (see Appendix 1), but given the faster growth in the south, the actual lengths at 50% maturity differed relatively less.

Simulated contemporary stock status

Simulation of the model until a population dynamical equilibrium using each set of lake-specific parameters produced testable predictions for contemporary population-level measures (Table 2). Vesijärvi and Oulujärvi were found to produce the highest number of trophy pikeperch, as 16.1% and 8.7% of the biomass yield, respectively, was predicted to consist of pikeperch over 700 mm in length. On the other hand, in all of the other lakes, pikeperch over 700 mm made up less than 1% of the total yield. The Vesijärvi pikeperch stock produced the highest number of excess recruits as only 1.2% of the hatched larvae were predicted to recruit to the stock, whereas the best simulated larval survival was found for Höytiäinen which as such had the poorest capacity to tolerate recruitment overfishing (Table 2). The total prey fish consumption estimates were considerably large in all stocks as compared with the pikeperch yields (Table 2). The Höytiäinen pikeperch stock produced harvestable biomass at the lowest conversion efficiency (yield/consumption, 1.7%) and the Vanajavesi stock with the best efficiency (12.8%). However, these values are to be interpreted with caution as the estimates are based on assumptions of annual food intake with respect to body size in the beginning of the growth season and overall resource availability without direct information about temperature-dependence and individual conversion efficiency at variable food intake rates.

Biomass yields, general observations

Simulation of the population dynamics with instantaneous fishing mortality rates from 0 to 4 and minimum size limits from 200 mm to 700 mm revealed that MSL required to produce maximal yield increased with fishing mortality rate. Yet, the maximal biomass yields were obtained with low MSLs and at moderate fishing mortalities (Table 3). Implementing a maximum size limit 200 mm above the minimum size limit reduced the possibility of population extinction under heavy mortality, and also increased both the MSL and F values needed to reach the maximal theoretical biomass yield (Table 3). In general, the yields were higher using only MSL than using a combination of minimum and maximum size limits (Table 3). Density-dependence in growth made population responses to harvesting strongly compensatory, including partly unrealistic reductions of risk of population collapse under high fishing mortalities.

Biomass yields without density-dependence

Simulations with individually constant growth rate revealed that a 370 mm MSL would result in higher catches (given that F could be restricted to low values) than the two alternative MSLs in lakes with slow individual growth, i.e. in Höytiäinen, Pielinen and Pääjärvi (Fig. 2). In Vanajavesi, MSL of 420 mm would be optimal and in Vesijärvi and Oulujärvi, MSL of 470 mm would be the best of the three alternatives considered (Fig. 2). The Vanajavesi and Vesijärvi pikeperch stocks appeared resilient against very high fishing mortality rates ($F > 3.0$) due to early maturation in these lakes. However, in all other lakes, pikeperch population could disappear. With a 370 mm MSL, the critical fishing mortality rates leading to the population disappearance lied around 1.5, whereas an increase of MSL by 50 mm to 420 mm increased the critical F to values between 2–3 (Fig. 2). Given the fisheries management measures that were in force prior to the year 2016 and the approximated fisheries mortality rates (Table 1), MSL should be increased in Vanajavesi and in Vesijärvi to increase yields. On the other

hand, MSL could be decreased in Pääjärvi to 420 mm under the present fishing mortality rate (0.6) and the annual yield would increase by ca. 20%. In Höytiäinen, MSL could be decreased based on the individual growth rate of fish, but decreasing MSL to 370 mm at the current fishing mortality rate would lead to the population disappearance. Implementation of maximum size limit 200 mm above MSL would not essentially change the results, as under heavy fishing mortality rates most fish would be harvested before reaching the maximum size limit (Fig. 3).

Biomass yields with lake-specific density-dependence

The assumption of density-dependence in growth has the consequence that population reduction by fishing relaxes food competition and increases individual growth rates. Therefore, the peak yield was obtained with a higher fishing mortality rate than without density-dependence (Fig. 4). In the simulations, even the absolute maximum biomass yield was higher with density-dependence than without it, because a faster individual growth rate increases productivity and even marginally decreases natural mortality. Most notably, however, the density-dependent growth removed the benefit of increasing minimum size limits, as for all the lakes, the maximum biomass yield was obtained using the lowest MSL considered (Fig. 4). However, MSL of 370 mm did not protect the stocks from detrimental recruitment overfishing and stock decline under high fishing mortality rates (Fig. 4).

Implementation of maximum size limit 200 mm above the minimum size limit had only marginal effects also with density-dependent growth (Fig. 5). However, maximum size limit increased the benefit of high minimum size limit in Oulujärvi and Vesijärvi, as in these lakes the differences among MSL options (Fig. 4) diminished along the addition of maximum size limit (Fig. 5).

Variation in yield and spawning stock biomass

Stochastic simulations revealed that all the stocks except Oulujärvi pikeperch tolerate even $F = 4.0$ mortality, when MSL of 420 mm is used and growth is density-dependent (Fig. 6). However, 95%CI for biomass yield increases at high fishing mortality rates, and to ensure maximally stable yields, it would be necessary to sustain the fishing mortality rate between 0.5 and 1.5 (Fig. 6) except in Höytiäinen, where lower 95%CI limit did not decrease with increasing F .

In Höytiäinen, there is at maximum 0.8% risk of SSB falling below 40 tonnes limit within 100 years at $F = 4.0$ indicating that 420 mm efficiently prevents recruitment overfishing. In Oulujärvi, SSB reaches the 40 tonnes limit with certainty of 100% already at $F = 1.55 \text{ yr}^{-1}$ underlining the importance of limiting the instantaneous fishing mortality under $F = 1.05 \text{ yr}^{-1}$ (5% risk) or increasing the minimum size limit from 420 mm. In Pääjärvi, the stock reaches the 700 kg SSB limit at 100% certainty at $F = 3.1 \text{ yr}^{-1}$ and the risk exceeds 5% when the F exceeds

Table 3. Fisheries parameters producing the theoretical maximum sustainable yield without density-dependence in growth using only a minimum size limit (MSL) and a combination of minimum and maximum size limits (SL, maximum size limit 200 mm above MSL). Precision for the determination of F is 0.05 and for the size limit 10 mm.

Parameter (unit)	Höytiäinen	Oulujärvi	Pääjärvi	Pielinen	Vanajavesi	Vesijärvi
Minimum size limit						
Biomass yield (tonnes)	198.1	103.8	2.0	74.7	30.2	34.0
Fishing mortality rate (yr^{-1})	0.40	0.50	0.55	0.45	0.70	0.50
Minimum size limit (mm)	300	460	380	360	440	540
Minimum and maximum SL						
Biomass yield (tonnes)	191.7	88.0	2.0	69.1	25.5	24.6
Fishing mortality rate (yr^{-1})	0.45	0.80	0.65	0.55	1.15	0.95
Minimum size limit (mm)	310	480	400	370	470	640

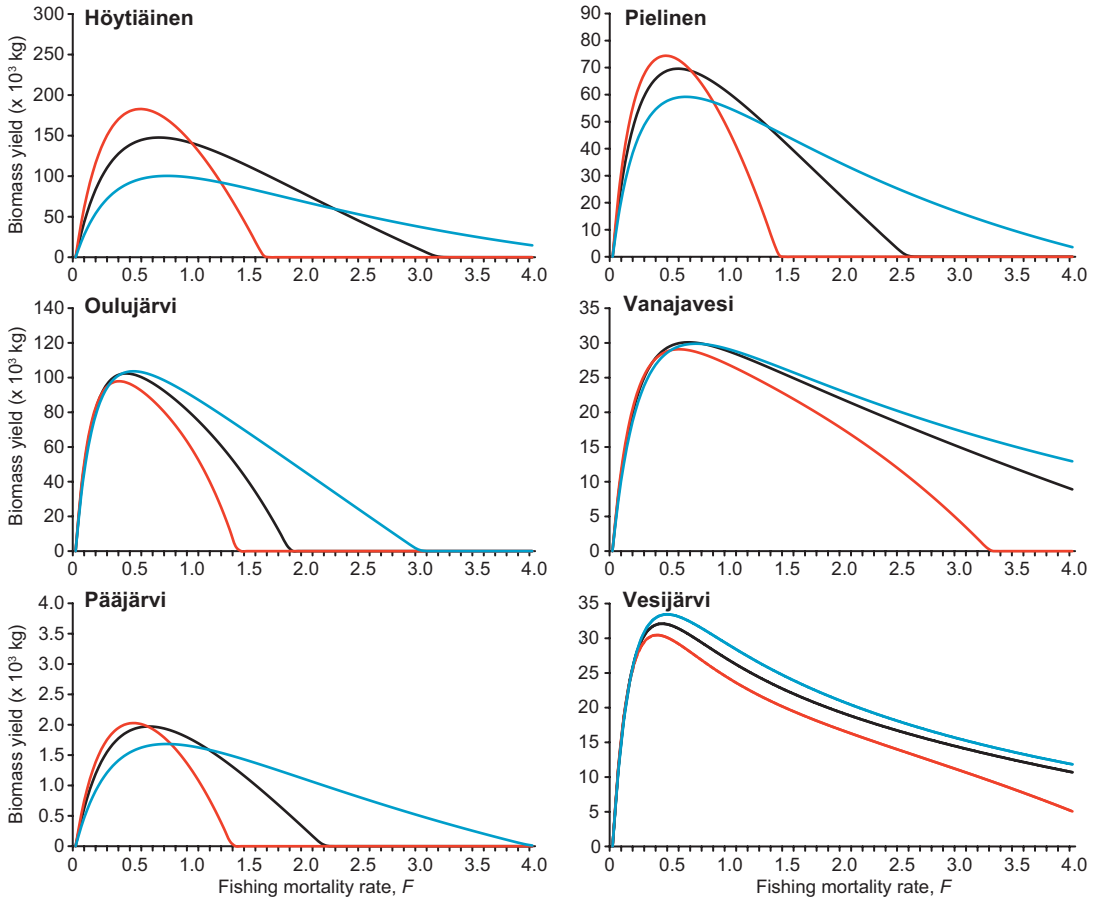


Fig. 2. Predicted deterministic biomass yields using three minimum size limits (MSLs): 370 mm (red line), 420 mm (black line) and 470 mm (blue line) as a function of varying annual instantaneous fishing mortality rate, without density-dependence in growth. The model was simulated with the currently observed parameter values, i.e. without evolution.

1.55 yr⁻¹. In Pielinen, SSB reaches the 25 tonnes risk limit with 5% certainty at $F = 2.1$ yr⁻¹ but it does not reach the limit with 100% certainty within the studied F interval. In Vanajavesi, SSB reaches the 7500 kg risk limit with 5% certainty at $F = 1.7$ yr⁻¹, and at $F = 4.0$ yr⁻¹, the risk increases to 0.99. In Vesijärvi, SSB reaches the 10 tonnes risk limit with 5% certainty at $F = 1.85$ yr⁻¹, and at $F = 4.0$ yr⁻¹, the risk increases to 91%.

Evolutionary effect

At nationwide MSL of 420 mm, the evolutionary impact of fishing was proportional to fishing mortality rate (Fig. 7). Already low fishing mor-

tality rates caused a substantial decrease in the evolutionarily stable size at maturation, while further increased fishing mortality rate had less impact on the size at maturation (Fig. 7). The use of an allowable slot of 420–620 mm did not significantly improve the situation in stocks other than in the fast-growing Vesijärvi stock, as the evolutionarily stable size at maturation was only a few millimeters greater than with MSL only. However, the predicted evolutionarily stable size at maturation without fishing was unrealistically high for Vesijärvi (687 mm), and given the current size at maturation, the evolution would follow the lower alternative path and decrease the size at maturation even below 200 mm under high fishing mortality rates (Fig. 7). Assuming the current fishing mortality

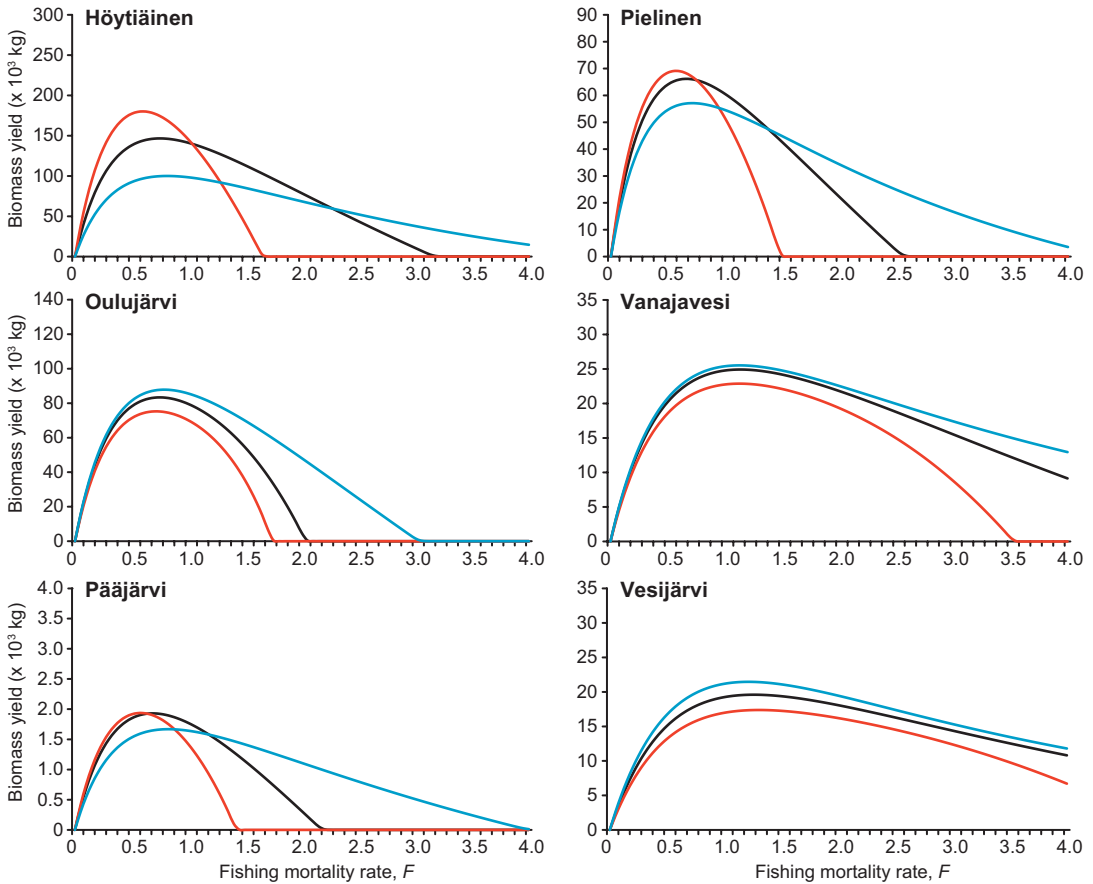


Fig. 3. Predicted deterministic biomass yields using three minimum and maximum size limit combinations: 370–570 mm (red line), 420–620 mm (black line) and 470–670 mm (blue line) as a function of varying annual instantaneous fishing mortality rate without density-dependence in growth. The model was simulated with the currently observed parameter values, i.e. without evolution.

rate, MSL of 420 mm, and evolution of size at maturation until evolutionary equilibrium, the fisheries yield would increase slightly in Höytiäinen but decrease significantly in the other lakes (Table 2).

Discussion

We were able to parameterize individual growth rate, size-dependent fecundity and maturation patterns for six important Finnish pikeperch stocks and simulate biomass yields of these stocks with alternative minimum and maximum size limit combinations. Despite presumably large uncertainties in the stock-level parameters, our simulations revealed how variation in

life-history traits led to different outcomes under common management measures. As expected, fast growing, early maturing pikeperch stocks as those of Vanajavesi and Vesijärvi appeared to tolerate high fishing mortality at nationwide MSL of 420 mm. However, yields from these stocks could be improved, if MSL was increased. At the other extreme, late maturing stocks such as the Oulujärvi one face a high risk of population decline and even disappearance at national MSL of 420 mm. On the other hand, early maturing and slow growing populations such as those of Höytiäinen and Pielinen tolerate relatively heavy mortality when nationwide MSL of 420 mm is used, and yields from these stocks would be maximized using even smaller MSL than the currently set 420 mm. However, improving catches

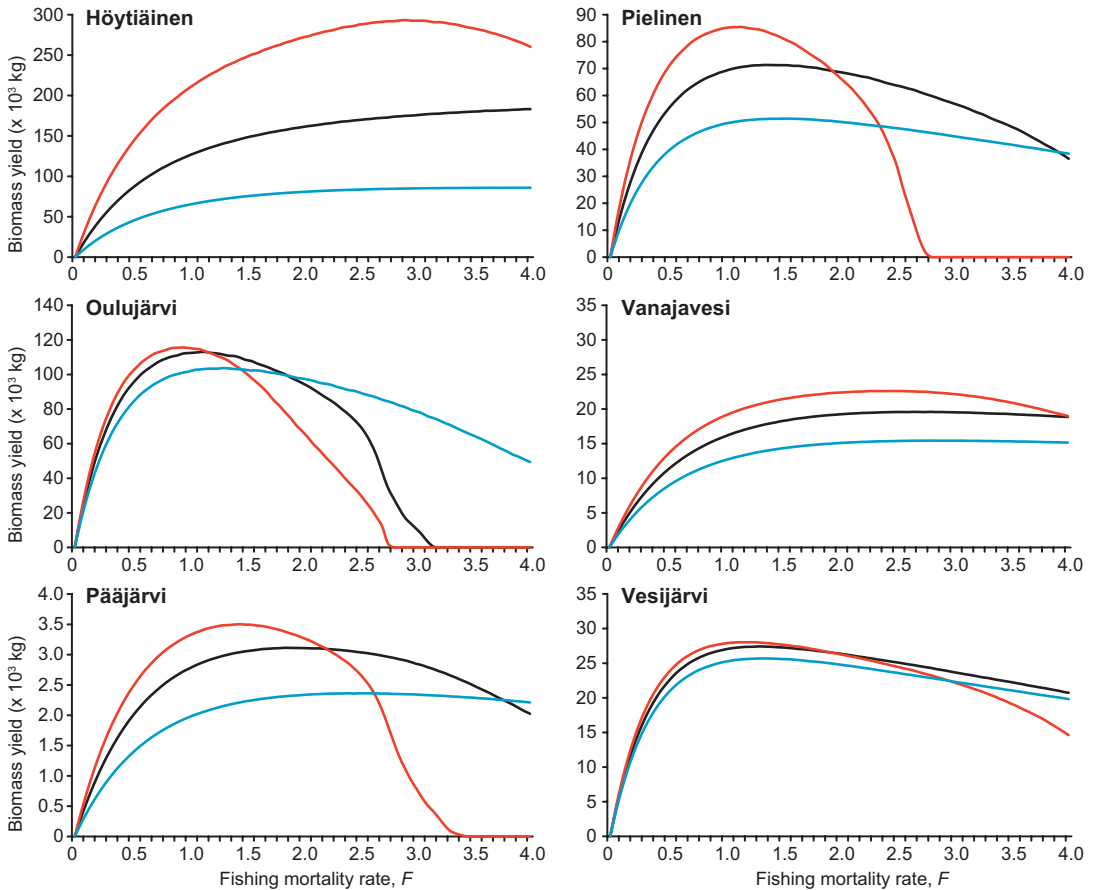


Fig. 4. Predicted deterministic biomass yields using three minimum size limits (MSLs): 370 mm (red line), 420 mm (black line) and 470 mm (blue line) as a function of varying annual instantaneous fishing mortality rate, when assuming lake-specific density-dependence in growth. Note that the theoretical yields can exceed those observed without density-dependence because the individual growth rate is increased due to fishing-induced increase in per capita food availability. The effect is the stronger the lower is the original per capita food availability. The model was simulated with the currently observed parameter values, i.e. without evolution.

by decreasing MSL would require simultaneous decrease in the total fishing mortality rate, i.e. a reduction in the fishing effort for which there are limited management tools in Finland. Implementation of a maximum size limit 200 mm above MSL did not increase the theoretical maximal biomass yield from any of the populations.

Length at the age of six years varied from 350 mm in Höytiäinen to 526 mm in Vesijärvi. According to the length-at-age listing for various European pikeperch stocks (Argillier *et al.* 2012), the growth rates of the pikeperch stocks studied here are typical for northern Europe, while in France the length of pikeperch at the age of 6 years can be even 710 mm. Notably,

the growth rate of pikeperch in Vesijärvi was faster than in Swedish Hjälmarén (length 394 mm at the age 6) that has been used as a good example of successful management after MSL was increased to 450 mm (Argillier *et al.* 2012). As such, it would be highly recommended to increase MSL in Vesijärvi, Vanajavesi and Oulujärvi to at least 450 mm or even to 500 mm (cf. Table 3).

Reproductive biology of pikeperch has been little studied and quantitative estimates of size and age at maturation as well as size-dependent fecundity are rare (Lappalainen *et al.* 2003). Lappalainen *et al.* (2003) reported that the mean length at 50% maturity (TL_{50}) of female pike-

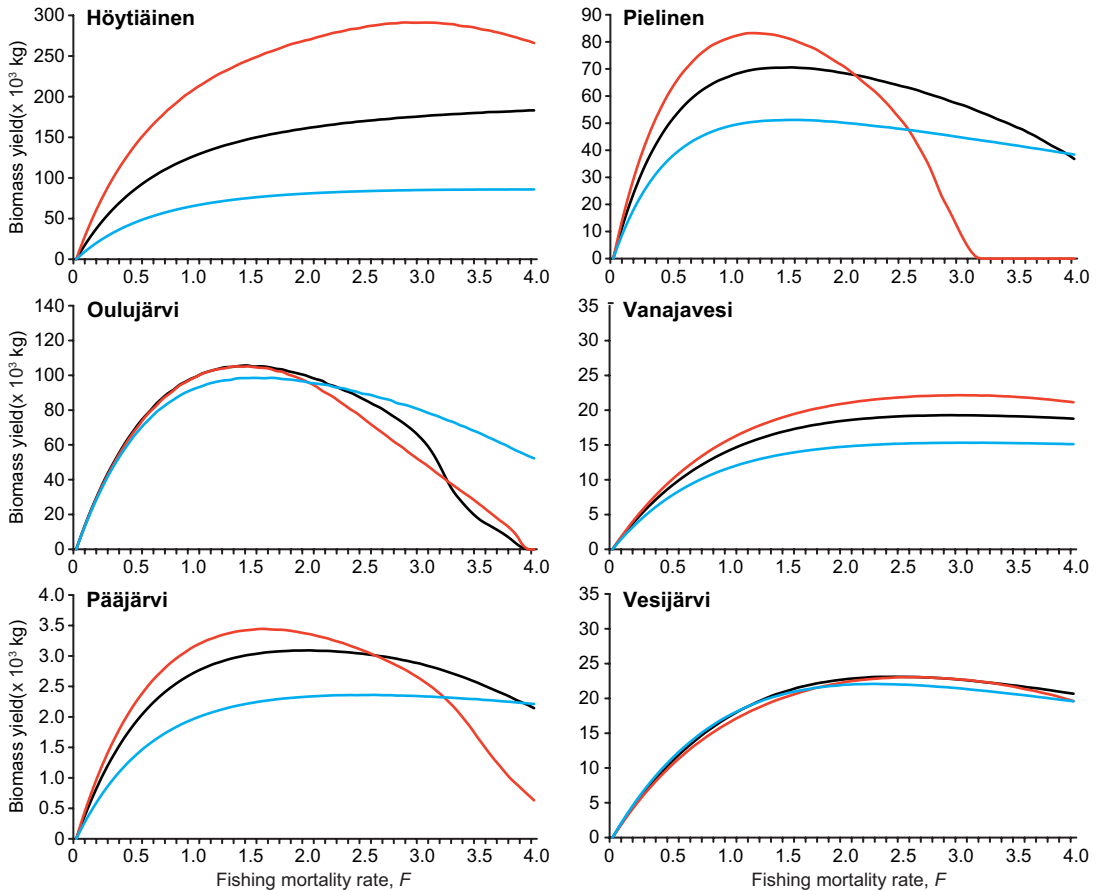


Fig. 5. Predicted deterministic biomass yields using three minimum and maximum size limit combinations: 370–570 mm (red line), 420–620 mm (black line) and 470–670 mm (blue line) as a function of varying annual instantaneous fishing mortality rate, when assuming lake-specific density-dependence in growth. Note that the theoretical yields can exceed those observed without density-dependence because the individual growth rate is increased due to fishing-induced increase in per capita food availability. The effect is the stronger the lower the original per capita food availability is. The model was simulated with the currently observed parameter values, i.e. without evolution.

perch belonging to the Baltic Sea and freshwater Finnish and Swedish populations varied between 280 and 460 mm. In female walleye (*Sander vitreus*), a close relative of pikeperch, the probability of maturation is dependent on surplus lipid reserves which depend on water temperature (growing degree days) and prey availability and its energetic content in the growing season before spawning (Henderson and Nepszy 1994, Madenjian et al. 1996). Male pikeperch guard the offspring for some weeks after spawning which may affect maturation as well. In nest-guarding bluegill sunfish, *Lepomis macrochirus* populations removal of large males by fishing has even been suggested to cause stunting due to earlier

maturation of males and their subsequent allocation of resources into reproduction instead of growth (Beard et al. 1997, Jennings et al. 1997) warranting need for research on the same mechanism in pikeperch.

The study lakes included a wide variety of environments as they differed in the level of productivity (food availability), morphology, water colour and geographical location (water temperature) (see Table 1). This is also due to the fact that pikeperch was introduced to lakes and regions where it had not naturally occurred (Salminen et al. 2012). In four out of the six lakes in this study, pikeperch stocks are not original but introduced by transferring individ-

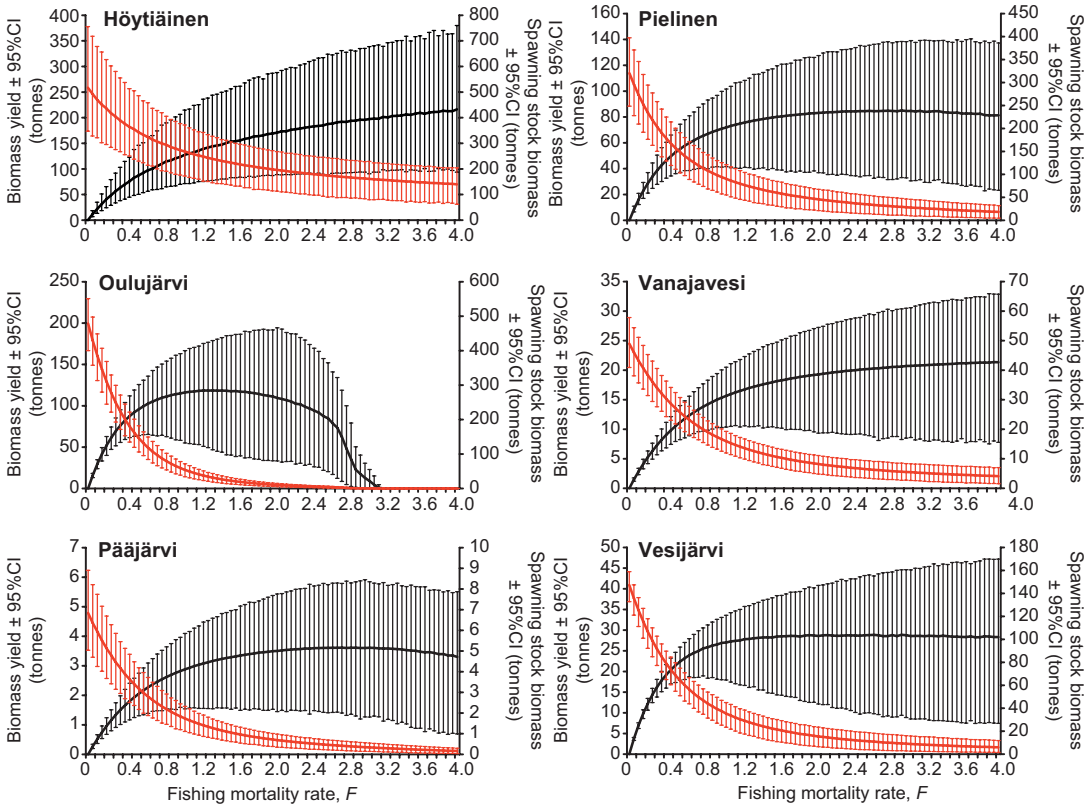


Fig. 6. Stochastic simulations of mean \pm 95%CI biomass yield (black) and spawning stock biomass (red) as a function of instantaneous annual fishing mortality rate using the minimum size limit (MSL) of 420 mm and assuming density-dependent growth and the current size at maturation, i.e. no evolution.

uals from another lake. The pikeperch stock of Vanajavesi has been introduced to Pääjärvi, Vesijärvi and Oulujärvi, where it matures at different lengths and ages than in Vanajavesi. Thus, our study suggests that maturation in pikeperch is strongly driven by environmental variables. However, we cannot exclude rapid contemporary evolution as partial explanation, as mortality patterns among the lakes with pikeperch of common origin also differ and such differences have been observed to translate into genetic differences in a relatively short time in grayling *Thymallus thymallus* (Haugen and Vøllestad 2001). Anyhow, our results contradict the claim of Henderson and Morgan (2002) of walleye maturation age being genetically determined. Similarly with walleye, maturation size appeared inversely related to the temperature sum of the growing season, as the pikeperch populations in the northern study lakes matured at a larger size

than the populations in the southern study lakes (Henderson and Morgan 2002).

In oligo-mesotrophic Pääjärvi with low food availability and low temperature sum due to large water volume (likely lower than the location-based estimate in Table 1), pikeperch matured at a rather old age and large size most probably due to the long time needed for reaching the nutritional status enabling energy allocation to reproductive products. Low food availability in Pääjärvi possibly also explained the low fecundity of female pikeperch in Pääjärvi as compared with that in the other southern lakes. Pikeperch in the nearby Vesijärvi had high food resources, and they matured earlier and smaller than Pääjärvi pikeperch. Furthermore, annual within-lake variation in the average energetic condition of the walleye has been found to affect the maturation probability (Henderson and Morgan 2002). However, annual variation in the

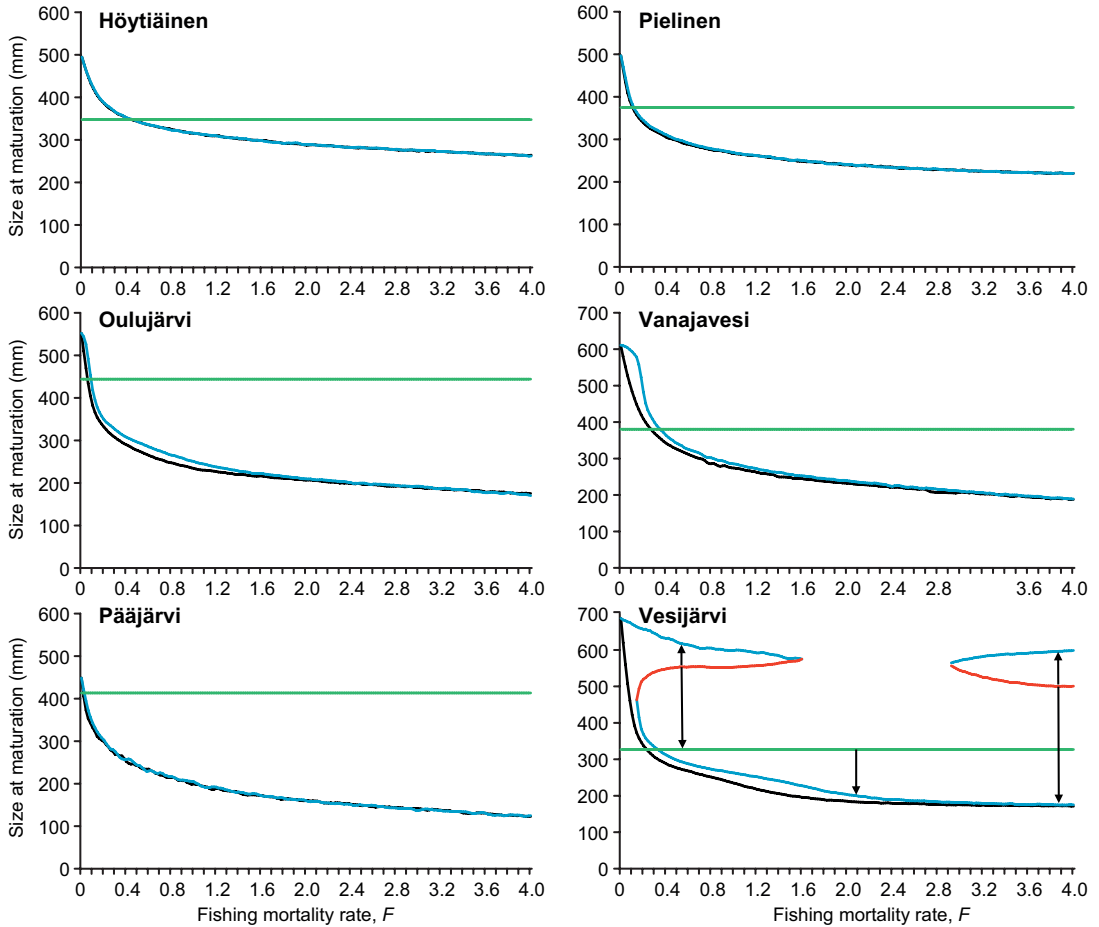


Fig. 7. Evolutionary impact of fishing on the evolutionarily stable size at maturation using minimum size limit (MSL) of 420 mm (black line) and a combination of MSL of 420 mm and maximum size limit of 620 mm (blue line). The red line in the Vesijärvi panel represents the fitness minimum. Above the fitness minimum the maturation size is expected to evolve towards the upper alternative ESS (blue line) and below towards the lower alternative ESS (black line) as indicated by the arrows. The lines represent running average smoothed (span 3) numerical solutions of deterministic ESS values, i.e. the non-smoothness results from the precision of numerical analysis rather than stochastic simulation. The green reference lines indicate the current size at maturation.

maturation size would have significant effects on population dynamics only through recruitment, and as such, our stochastic simulations took into account the potential temporal variation in the size at maturation as well as variation in the temperature conditions.

Kokkonen *et al.* (2015) showed that the size and age at maturity had decreased in both male and female pikeperch in the Archipelago Sea in the cohorts 1993–2006. Length at maturity has been suggested to be used as an indicator of negative effects of intensive fishing in data poor fisheries (Lappalainen *et al.* 2016). Sample size

as low as 35–70 females per year could reveal ecologically relevant trends in maturation schedules of fish (Lappalainen *et al.* 2016). Given the strong impact of size at maturation on somatic growth, recruitment and fisheries yields, regular assessments of maturation patterns of the most important freshwater pikeperch stocks should be carried out. Because positively size-selective fishing is also expected to result in relatively strong selection differential for slower growth rate (Williams and Shertzer 2005, Vainikka and Hyvärinen 2012), fisheries monitoring programs should regularly record also changes in the

average length-at-ages. Reasons for temporal changes in growth rate could then be further partitioned between mechanisms arising from earlier maturation and other factors by predicting the change in growth that would result from a shift in maturation pattern alone (Pardoe *et al.* 2009).

Pikeperch is a potent predator and regulator of prey fish stocks (Vehanen *et al.* 1998). However, pikeperch prefers small prey fish (Turesson *et al.* 2002, Keskinen and Marjomäki 2004), and a heavily fished, size-truncated pikeperch stock can forage only on a very narrow size range of prey fish. Based on very simple bioenergetics calculations, we estimated that for example the current Oulujärvi pikeperch stock would consume 1.9 million kilograms of prey fish annually, according to Vehanen *et al.* (1998) mainly smelt (*Osmerus eperlanus*), but also whitefish (*Coregonus lavaretus*), perch (*Perca fluviatilis*) and vendace (*Coregonus albula*). However, the diet of pikeperch has likely changed over time in lakes to which it has been (re-)introduced as a result of significant changes in the whole fish community. This is particularly likely in Höytiäinen and Oulujärvi where the pikeperch stocks rapidly increased after (re-)introductions (*see* Vainikka and Hyvärinen 2012 for Oulujärvi, and Haakana and Huuskonen 2008 for Höytiäinen) and reached the current levels less than 10 years ago, but no published reports yet exist about the pikeperch-induced fish community changes in these lakes.

It is notable that the total consumption estimate for the Oulujärvi pikeperch stock for example is an order of magnitude greater than the commercial catch of vendace in Oulujärvi demonstrating that fisheries management decisions affect strongly the species interactions and potential catches of prey and their predators (Vehanen *et al.* 1998). This also shows that the importance of density-dependent growth cannot be overlooked in fisheries models (Persson and de Roos 2006). Based on our simulations, an increase of MSL or corresponding stocking of juvenile pikeperch in already slow-growing populations would likely readily translate to shortage of suitably sized prey fish, and further decrease in fisheries yields (*see* also Milardi *et al.* 2011) by increased natural mortality, also through cannibalism (Argillier *et al.* 2012) and less effi-

cient conversion of prey fish biomass to surplus somatic growth. On the other hand, increasing the number of large predatory pikeperch might affect the size-distribution of prey fish populations, and through feedback mechanisms (including cannibalism), increase the per capita availability of suitably sized prey as predicted by models (Van Leeuwen *et al.* 2008) and observed by culling the old prey individuals (Persson *et al.* 2007). Thus, there remains a need to build multispecies population models that allow cannibalism to assess the importance of such size-dependent predator-prey interactions (Claessen *et al.* 2003). In a single-species setting, density-dependence in growth makes the populations more resilient to fishing mortality, because the remaining fish typically grow faster due to the increased per capita availability of prey. Increased individual growth rate, on the other hand, can lead to earlier maturation and more efficient recruitment further amplifying the compensatory response.

Recruitment success of pikeperch is strongly dependent on the temperature during the first summer of fry growth because the winter survival is typically negatively size-dependent (Heikinheimo *et al.* 2014). Size-dependent population dynamical interactions between 0-year-old pikeperch and their zooplankton and fish prey ultimately explain the growth variation during the first summer (Persson and Brönmark 2002). The strength of negatively size-dependent winter mortality can depend on the duration of ice-cover period in winter and the water temperatures in the previous summer (Lappalainen *et al.* 2000). Despite the negative impact on recruitment, negatively size-dependent predation mortality of young pikeperch is an important selective force favoring fast juvenile growth and late maturity (Abrams and Rowe 1996, Vainikka and Hyvärinen 2012). We did not consider the resource dynamics or temperature-dependence explicitly in our model, but information on these processes could be further incorporated in models. Real-time updating of environmental data in simulation models could even help to produce near-future projections for fish stock development and help fisheries managers or automated license-sale systems to adjust fisheries regulations and potential need for stockings on annual or even monthly basis.

MSLs have been used for long in the management of pikeperch and walleye (*Sander vitreus*) stocks (Brousseau and Armstrong 1987). However, MSLs as well as bag limits are often considered ineffective management measures as they fail to decrease the total harvest rate, and they often rather decrease than increase the abundance of large fish (Dunning *et al.* 1982, Van Poorten *et al.* 2013, Gwinn *et al.* 2015). It has also been argued that minimum size limits do not protect stocks from overfishing even if the fishery is based fully on catch and release, since always some proportion of the fish will die to accidental injuries (Post *et al.* 2003). This is particularly true for pikeperch as it is more sensitive to catch and release stress than other percids or pike (Arlinghaus and Hallermann 2007). Our simulations showed that MSL based regulation works poorly in increasing the number of large individuals in a stock or protecting against negative evolutionary changes. Instead, heavy fishing mortality combined with a minimum size limit leads to a heavily truncated size-distribution of fish, and a large number of undersized individuals in comparison to legally harvestable size classes. Effective removal of large pikeperch by fishing efficiently eliminates not only potential for cannibalism, but also for positive predation effects on often abundant cyprinids that remain too large for small pikeperch (Peltonen *et al.* 1996).

According to evolutionary fish population models, biomass yields typically decrease if size at maturation decreases and fisheries regulations are not adjusted (Law and Grey 1989, Jørgensen *et al.* 2009, Vainikka and Hyvärinen 2012). Based on our simulations as well, the biomass yields generally decrease in response to decreasing size at maturation. However, as in the case of the Höytiäinen stock, the biomass yield can even increase, when the minimum size limit is decreased to compensate for the advanced maturation. Thus, MSL-based management of pikeperch stocks is expected to lead to a positive feedback loop between advancing maturation and further decreases of MSL. At worst, this development could continue until the fish stock productivity does not anymore support the particular fishery. Notably, maturation trends were observed to decline also before the northern cod (*Gadus morhua*) stock collapsed (Olsen *et al.*

2004). Thus, MSL as the only management measures should be questioned and complemented with either maximum size limits or effort restrictions (*see also* Gwinn *et al.* 2015).

Implementing a bell-shaped selection curve using specific gears or maximum size limits in addition to MSL has been suggested as a solution to protect large spawners and to avoid negative evolutionary consequences of fishing (Jørgensen *et al.* 2009, Laugen *et al.* 2014). However, our simulations showed that implementation of a maximum size limit 200 mm above the 420 mm MSL would have only a marginal effect on the evolutionary stable size at maturation, as with contemporary fishing mortality rates most pikeperch would be harvested before they grew the necessary 200 mm to reach the size refuge. In such a situation as well as without any maximum size limit, large MSLs generally cause less evolutionary changes than low MSLs because they limit the total harvest rate with constant F (Vainikka and Hyvärinen 2012). However, the presence of an alternative evolutionarily stable size at maturation even at very high fishing mortality rates in Vesijärvi (Fig. 7) shows that suitably adjusted combinations of minimum and maximum size limits could maintain a large size at maturation in sexually reproducing populations. Because the alternative ESS was found only in the fast growing Vesijärvi population with relatively high 420–620 mm slot, the optimal size slot reducing the evolutionary impact of fishing would be lower and/or narrower than this for most pikeperch populations (Berkeley *et al.* 2004, Jørgensen *et al.* 2009). Thus, the current tendency to increase minimal mesh sizes in gillnet fishing does not necessarily reduce the evolutionary impact of fishing, but increases it. Based on evolutionary considerations, the gillnet mesh sizes should rather be decreased than increased, but at the same time, the total numbers of gillnets used should be decreased from the current levels. However, evaluation of the true consequences of evolutionary bistability in maturation size, as often observed in invasion fitness based models (Gårdmark and Dieckmann 2006) would require the use of individual based models with sexual reproduction and some information about the inheritance of maturation schedules (*see* Dunlop *et al.* 2009).

A probably important factor that we did not include in our model is the positive maternal effect of large females on the survival of juveniles. In walleye, the population reproductive rate has estimated to be considerably higher when old females are abundant, and age- or size-based maternal effects were considered to be important stabilizing mechanisms in the dynamics of heavily exploited populations (Venturelli *et al.* 2010). Recent observations suggest that size-dependent maternal effects might be important also in pikeperch population dynamics (M. Olin unpubl. data). Our unpublished simulation results also show that size-dependent maternal effects generally decrease the magnitude of negative evolutionary changes.

As a conclusion, our results show that the only efficient way to ensure both ecologically and evolutionarily sustainable fishing is to restrict total harvest rates. Maximum size limits decrease the evolutionary impact on size at maturation to some extent especially at low harvest rates, and maximum size limits help fish populations to tolerate higher fishing mortality rates than MSL-based regulation only. However, maximum size limits alone do not ensure that any fish would survive until reaching the size refuge provided by the maximum size limit, and as such they do not eliminate the need for total harvest restrictions (Olin *et al.* 2017). The very different life history traits in all of the studied pikeperch populations stresses the need for unique, data-informed fisheries management plans for every heavily exploited stock. The nationwide MSLs of 420 mm is a rather good compromise but any MSL-based management has drawbacks such as potential stunting, loss of trophy fish and inevitable evolution towards maturation at smaller size. As an alternative, an optimal combination of minimum and maximum size limits giving the highest yield with the least evolutionary impact should be considered lake-specifically depending on the growth rate, maturation properties of and the fishing pressure on the pikeperch population.

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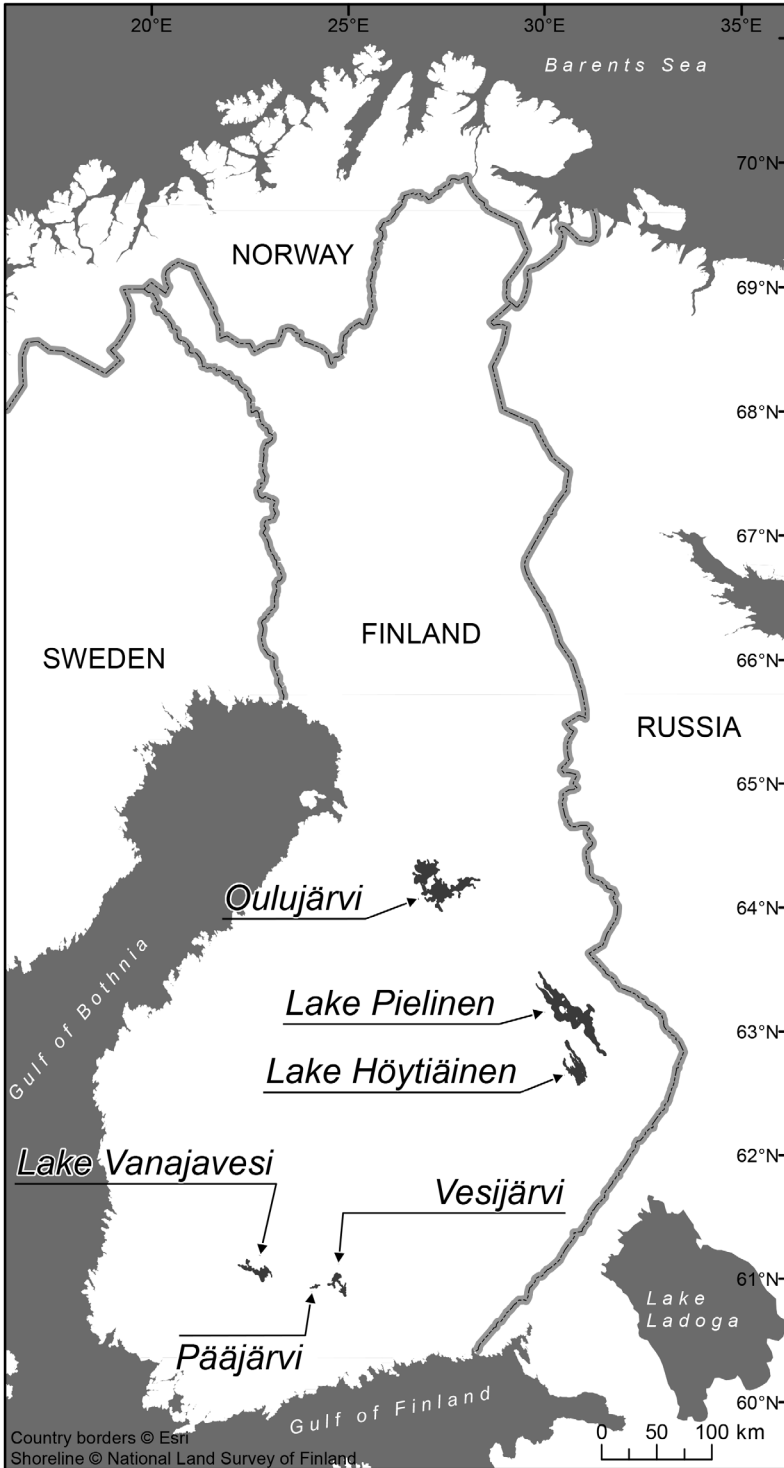
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Appendix 1. Parameters of the model and their values in the order of appearance in the text with references to equations.

Variable/constant name (unit)	Symbol	Höytiäinen	Oulujärvi	Pääjärvi	Pielinen	Vanajavesi	Vesijärvi	Appears in equation
Fecundity intercept	γ_0	-61260	-17958	-2234	-17958	-66599	-41303	1
Fecundity slope (g^{-1})	γ_1	220.6	122.6	124.2	122.6	222.6	188.3	1
Length-to-mass equation's coefficient	a_0	4.54×10^{-6}	3.45×10^{-6}	6.04×10^{-6}	4.66×10^{-6}	3.63×10^{-6}	2.06×10^{-6}	2
Length-to-mass equation's exponent	a_1	3.105	3.168	3.039	3.089	3.145	3.252	2
Egg-recruit scaling parameter	η	0.01	0.01	0.01	0.01	0.01	0.01	3
Scaling parameter for variance in recruitment	ϕ	0.79	0.79	0.79	0.79	0.79	0.79	3
Beverton-Holt carrying capacity constant	K	2.05×10^{-8}	2.19×10^{-7}	4.46×10^{-6}	8.91×10^{-8}	1.53×10^{-6}	2.93×10^{-6}	3
Recruit body length (initial value for l) (mm)	l_i	31.0	8.0	17.5	32.5	2.0	14.4	10
Maximum food intake coefficient	c_0	107.72	107.72	107.72	107.72	107.72	107.72	4
Maximum food intake exponent	c_1	0.583	0.583	0.583	0.583	0.583	0.583	4
Standard deviation of individual-level resource availability	σ_e	15.3	0.8	3.0	29.7	1.7	7.7	7
Length at which 50% of pikeperch females mature ($L_{p_{50}}$) (mm)*	l_{mat}	347.5	444.0	413.3	374.7	380.5	326.8	9
Width of the length range at which maturation occurs (mm)	σ_m	31	25	29	25	50 (79)	24	9
Juvenile growth increment (mm)	h	55.6	74.4	70.6	59.1	94.6	97.1	10
Broad-sense gonadosomatic index	g	0.201	0.161	0.236	0.160	0.225	0.185	10
Reference resource level	λ_0	0.565	0.638	0.125	0.636	0.500	0.680	11
Size-independent mortality rate (y^{-1})	d_0	0.15	0.15	0.15	0.15	0.15	0.15	12
Size-dependent mortality rate (y^{-1})	d_1	2.75	2.75	2.75	2.75	2.75	2.75	12
Size of natural mortality decay (mm)	l_0	115	115	115	115	115	115	12
Width of the transition from fishing mortality (mm)	$\sigma_{f,max}$	10	10	10	10	10	10	13
Width of the transition to fishing mortality (mm)	$\sigma_{f,min}$	10	10	10	10	10	10	13
Width of the transition to discard mortality (mm)	$\sigma_{i,min}$	80	80	80	80	80	80	14
Discard mortality rate of undersized fish (y^{-1})	F_{pre}	0.107	0.050	0.050	0.043	0.114	0.071	15
Minimum size of "trophy" fish (mm)	l_{pre}	700	700	700	700	700	700	17

*Note that the $L_{p_{50}}$ values represent the size at which the maturation process begins, not the size at the first spawning.



Appendix 2. Locations of the study lakes. Parts of the map that are owned by ESRI have been used under the agreement between LUKE and ESRI, and those owned by the National Land Survey of Finland (Maanmittauslaitos) are now in the public domain and can be used without permission.