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The capability of harvestable slot-length limit regulation in conserving large and old northern pike (*Esox lucius*)

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In this experimental fisheries regulation study, we compared the effects of size-selective fishing according to minimum length limit (MLL, 40 cm) or harvestable slot-length limit (HSL, 40–64.9 cm) on population density, biomass, size and age structures, and sex ratio of the northern pike (*Esox lucius*). Data were collected during the years 2006–2013 in four 2.1–13.8 ha pristine forest lakes in southern Finland. In lakes where MLL fishing was carried out, pike density, biomass and size structure showed greater negative responses than in lakes where HSL fishing was carried out: mean length and age decreased, and large pike (≥ 65 cm) disappeared in just four years. HSL fishing affected the pike to a lesser extent, and large pike remained in the lakes, which is considered an essential feature of sustainable fishing. However, the results suggest that the number of large pike may decrease even under the HSL fishing strategy if the growth rate is slow and fishing is intensive, due to the high possibility of fish being caught before reaching the length beyond the upper HSL limit.

Introduction

The northern pike (*Esox lucius*) is a widespread and abundant cool-water predatory fish in the northern hemisphere. Pike plays a profound role in the ecosystem, since it can regulate the amount and composition of its prey species, as well as its own populations due to its highly cannibalistic behaviour (Raat 1988, Craig 1996, Sharma and Borgstrom 2008, Harvey 2009). In addition to its ecological importance, the pike is also an important and popular target species in recreational fisheries in Europe and North America. The popularity of pike as a gamefish stems from its large size and ferocity in fighting when hooked, as well as high catchability due to its abundance and aggressive feeding (Pierce *et al*. 1995, Paukert *et al*. 2001). As a result, the pike is very vulnerable to recreational fishing (Mosindy *et al*. 1987, Pierce *et al*. 1995, Pierce and Tomcko 2003), and requires sustainable management (Arlinghaus *et al*. 2010, Pierce 2010, Carlson 2016).

In developed countries, recreational fishing is the main factor affecting freshwater fish populations in many waterbodies, but its role in stock decline has been neglected until quite recently (Post *et al*. 2002, Allan *et al*. 2005, Cooke and Cowx 2006, Lewin *et al*. 2006, Post 2013). According to Post *et al*. (2002) and Lewin *et al*.

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(2006), the effects of recreational fishing on fish stocks include decline in population densities and changes in species composition, size distribution and trophic interactions. Targeting large individuals may cause truncation of age- and size distributions of a fish population, resulting in smaller mean size of fish. Fisheries-induced changes in life-history traits were observed in numerous marine and freshwater species for decades (Rose *et al*. 2001, Conover *et al*. 2009), including decrease in size and earlier maturation in perch (*Perca fluviatilis*) (Pukk *et al*. 2013), pikeperch (*Sander lucioperca*) (Mustamäki *et al*. 2014, Kokkonen *et al*. 2015) and pike (Edeline *et al*. 2007, Arlinghaus *et al*. 2009, Matsumura *et al*. 2011). Removal of large individuals by fishing favours early maturation and slow growth at the expense of fast-growing phenotypes which maturate later (Post *et al*. 2003, Cooke and Cowx 2004, Edeline *et al*. 2007, van Wijk *et al*. 2013). Intensive fishing may also alter fish behaviour, since actively swimming and fearless individuals are more likely to be caught (Härkönen *et al*. 2014). As activity in foraging and speed of growth are related, fisheries-induced selection is likely to favour more cautious and passive fish. Size-selective fishing may also be sex-selective, because females that usually grow faster and maturate later are more vulnerable to size-selective fishing than males (Lewin *et al*. 2006, Horppila *et al*. 2011).

Large females are essential to the vitality of a pike population, as they have higher absolute fecundity than smaller females (Craig 1996) and their progeny is also of better quality (Wright and Shoesmith 1988, Billard 1996, Kotakorpi *et al*. 2013). Eggs and larvae produced by large females are larger in terms of dry weight (*see* Kotakorpi *et al*. 2013) and consequently energy reserves in the yolk sacks are also greater (Ojanguren *et al*. 1996). This makes the larvae more resilient to starvation in their early life, less vulnerable to predation (Perez and Munch 2010) and more capable to use various prey items (Mehner *et al*. 1998). However, favourable effects of female size on offspring quality are not fully confirmed by studies carried out in natural environments (Pagel *et al*. 2015). This is due to a variety of factors affecting reproduction success, including the size-dependent timing of spawning (Murry *et al*. 2008), or trade-offs between different life-history strategies, e.g. growth benefit gained by increased activity *vs*. increased risk for predation (Estlander and Nurminen 2014).

From a fisheries management perspective, the detrimental effects of size-selective fishing can be diminished by regulating fisheries, for example by setting length limits for harvestable individuals. The most traditional of these regulation options is the minimum length limit (henceforth MLL). However, other approaches may be used, including maximum length limit, a combination of maximum and minimum length limits known as harvestable slot length limit (henceforth HSL), and the inverse of HSL, known as protected slot length limit (Paukert 2001, Arlinghaus *et al*. 2010, Carlson 2016). Traditional fisheries theories encourage harvesting large and old individuals in order to obtain maximum yield (Arlinghaus *et al*. 2010). As a result, severe size and age truncation has been observed in many commercially- and recreationally-exploited fresh- and brackish-water fish species like pikeperch (Kokkonen *et al*. 2015), perch (Pukk *et al*. 2013) and pike (Edeline *et al*. 2007, Pierce 2010, Carlson 2016).

In Finland, recreational fishing is hugely popular. According to the national fisheries inquiry, 1.5 million people, ca. 27% of the population, practise recreational fishing at least once a year (Natural Resources Institute Finland 2015). Pike is, after perch, the second most important catch species in recreational fishing in Finland. The recreational pike catch totalled ca. 7200 tonnes in 2014, of which less than 20% is released alive. The majority of catch, ca. 6300 tonnes, are caught from inland waters (Natural Resources Institute Finland 2015). Despite the popularity of pike recreational fishing, which also includes extensive use of effective fishing gears such as gillnets, there is no regulation of pike fishing in Finland. As recreational fishing may affect pike population structure and abundance (Jolley *et al*. 2008), it has likely affected negatively pike populations in many waterbodies in Finland. However, the impacts of recreational fishing are poorly documented. To maintain vitality of pike populations, it is important to develop sustainable practices for pike fisheries and to minimize the impacts of recreational fishing.

In order to better understand the effects of exploitation on pike stocks, we conducted an 8-year experimental pike fishery study, in which we monitored population responses to size-selective fishing by applying MLL of 40 cm and HSL of 40–64.9 cm in four protected forest lakes in southern Finland. Although size-based regulations (including of pike) have been evaluated in other studies (Arlinghaus *et al*. 2010, Pierce 2010, Matsumura *et al*. 2011, Gwinn *et al*. 2015), studies based on data from natural environments are still rare. This study offered a rare opportunity for long-term monitoring of two length limit-based regulation strategies in experimental but still natural environment without external fishing. Our aim was to compare the responses of pike population size, biomass and size and age-structure, when subjected to intensive fishing under MLL or HSL regulation. Our hypotheses based on earlier studies (Arlinghaus *et al*. 2010, Pierce 2010, Matsumura *et al*. 2011, Gwinn *et al*. 2015) were:

1. Pike density and especially biomass would decrease in MLL lakes, whereas in HSL lakes these parameters would be less affected due to conservation of large individuals.
2. Pike population structure would shift towards smaller and younger individuals in MLL lakes, while in HSL lakes large and old individuals remain in the population.
3. Female-to-male ratio would shift towards male dominance in MLL lakes, because females are more vulnerable to fishing. In HSL lakes the sex ratio would remain constant as large individuals (which are often female) are conserved.

Material and methods

Study lakes

The study was conducted in Haarajärvi, Haukijärvi, Hokajärvi and Majajärvi which are small forest lakes in Hämeenlinna (southern Finland, 61°13´N, 25°12´E) during the years 2006–2013. Surface areas of the lakes are 13.8, 2.1, 8.4 and 3.4 ha, mean depths 6.1, 3.8, 2.2 and 4.6 m and maximum depths 12.0, 8.0, 6.0 and 12.0 m, respectively (Horppila *et al*. 2010). The lakes are nearly pristine, oligo-mesotrophic, and colored by humic substances. Mean water colour is 130 and 150 mg Pt l^{-1} in the less humic Hokajärvi and Haarajärvi, respectively, and 330 and 340 mg Pt l^{-1} in the more humic Haukijärvi and Majajärvi, respectively (Horppila *et al*. 2010). The lakes are not subjected to agricultural or industrial pollution, they are reserved for research use only, and recreational or professional fishing is not allowed. The lakes have strong temperature stratification, and subsequently display hypoxia in the hypolimnion, during both summer and winter. The sole exception is Haarajärvi, where the hypolimnion is well oxygenated throughout the year. Due to low euphotic depth and steep banks, the littoral vegetation zone is narrow (coverage 4%–15%), resulting in limited habitats for pike, except in Hokajärvi (littoral vegetation coverage 80%). Although the aforementioned conditions are normal for small humic lakes (Rask *et al*. 1999), they have profound effects on fish communities, restricting the species number and regulating species interactions (Olin *et al*. 2010). In all the lakes the dominating fish species are perch, roach (*Rutilus rutilus*) and pike. Other species include bream (*Abramis brama*) and bleak (*Alburnus alburnus*) in Hokajärvi and Haukijärvi, burbot (*Lota lota*) in Haarajärvi, Haukijärvi and Hokajärvi, as well as introduced whitefish (*Coregonus lavaretus*) and vendace (*Coregonus albula*) in Haarajärvi and tench (*Tinca tinca*) in Majajärvi (Olin *et al*. 2010).

Mark and recapture and pike removal

Pike population densities, biomass and size structures were determined using a capture-mark-recapture program in years 2006–2013 (Table 1). Multigear sampling was used to minimize the effect of gear selectivity and to increase catch and improve coverage. Fyke nets and wire traps were used during and after the spawning time of pike (late April to early–mid-May), starting immediately after ice melting and continuing 2–3 weeks. Fyke nets were placed in the spawning grounds of pike, and wire traps were placed evenly along the shoreline. During summer and autumn, pike were caught by gill-

nets and angling. As part of the standard experimental gillnet fishing program (CEN 2005) in the study lakes, Nordic multimesh gillnets (mesh size 5–55 mm) with stratified random sampling were used annually three times in July–August (Olin *et al*. 2010). When necessary to fulfil the target catch, additional gillnetting with 2 × 30 m gillnets of 45–60 mm mesh size was conducted in late autumn. Intensive angling was conducted annually between late August and early September, in which the whole littoral area was sampled at least four times during different days and times using a rowboat with 1–2 anglers. A variety of commonly used artificial lures, 5–12 cm in size, were applied: wobblers, jerkbaits, softbaits, spoons and spinners, but also live baitfish were occasionally used. Additional angling (on average three times per year per lake) was conducted alongside other sampling with the same methods as described above.

Pike of ≥ 30 cm were tagged with individually-coded Carlin tags in 2006 and Floy T-bar anchor tags in 2007–2013. Both types of tags were inserted into muscle tissue at the base of the dorsal fin. Pike of < 30 cm were not tagged due to assumed higher post-release mortality of these individuals. All pike were marked by finclipping (right or left pelvic fin depending on the year) in order to control the loss of individual tags. Tagged pike were kept for ca. 10 minutes in a large tub filled with water before releasing to determine the survival rate after handling. Severely injured pike and individuals included in the removal catch were immediately killed after being caught.

To compare pike population responses to fishing according to MLL and HSL regulations, pike populations in the four study lakes were subjected to two different size-selective removal procedures during 2008–2012: MLL of ≥ 40 cm in Hokajärvi and Majajärvi, and HSL of 40–64.9 cm in Haarajärvi and Haukijärvi. Target catch was 50% of the estimated spring biomass of ≥40 cm or 40–64.9 cm pike in MLL or HSL lakes, respectively. The MLL of 40 cm was selected, because this value roughly equals female pike maturation size in all study lakes. This size was also MLL for pike in Finland until 1993. The maximum length limit of 65 cm in HSL lakes was selected to ensure a reasonable

Table 1. Total numbers of pike caught, new and previously marked individuals (IDs) and total numbers of marked pike in autumn 2006 and in spring 2007–2013. Pike marking started in spring 2006. 'Total marked' values include numbers of individuals tagged in earlier years corrected with natural mortality estimates. HSL = harvestable slot-length limit regulation, MLL = minimum length limit regulation.

Lake	2006	2007	2008	2009	2010	2011	2012	2013
Haarajärvi (HSL)								
Total catch	44	62	82	80	55	32	52	38
New ID	38	45	50	36	25	12	26	23
Prev. ID	6	17	32	44	30	20	26	15
Total marked	57.0	50.6	90.7	131.8	112.6	92.0	71.7	61.0
Haukijärvi (HSL)								
Total catch	11	5	8	2	7	3	6	7
New ID	4	2	2	0	3	2	2	4
Prev. ID	7	3	6	2	4	1	4	3
Total marked	13.0	12.2	14.0	9.7	5.5	5.9	4.8	6.6
Hokajärvi (MLL)								
Total catch	17	14	31	37	31	31	36	25
New ID	10	9	22	26	22	22	26	16
Prev. ID	7	5	9	11	9	9	10	9
Total marked	40.0	32.0	35.0	34.7	23.1	21.2	25.2	30.6
Majajärvi (MLL)								
Total catch	19	17	26	18	5	9	12	8
New ID	2	6	12	7	3	5	4	4
Prev. ID	17	11	14	11	2	4	8	4
Total marked	46.0	34.1	35.6	33.9	15.9	13.3	11.2	5.2

number of pike also in the largest size class (≥ 5% of the total population). The rationale to compare (relatively low) MLL and HSL was to compare responses of "traditional" MLL-based regulation and HSL regulation where large pike are conserved.

Population density, biomass and size and age-structure estimations

Population size estimates for tag-marked ≥ 35 cm pike were calculated for autumn 2006 and spring 2007–2013. Spring estimates had higher number of individuals as compared with the autumn estimates, and were used when possible. In 2006, the first pike were tagged in spring and thus only an autumn population estimate was possible. A modified Petersen method (Chapman version, Seber 1982: 60) was used to calculate pike population size in year t (N_t) by using following equation:

$$N_t = \frac{\left\{\left[\left(\sum_{t_0}^{t_{n-1}} T_{\geq 35\,\mathrm{cm}} S\right)+1\right](n+1)\right\}}{(m+1)-1} \quad (1),$$

where t_0 and t_n are the first and the latest tagging year, $T_{\geq 35\mathrm{cm}}$ is the total number of ≥ 35 cm tagged pike, S is the yearly survival rate, n is the sample size, and m is the number of marked fish in a sample. Since m/n ratios and sample sizes varied considerably among lakes and years, the upper and lower boundaries of 95% confidence limit interval were calculated by Poisson or binomial distribution as suggested by Seber (1982). As there was 0.5–1 year delay between tagging and recapturing and apparent recruitment to the catchable population during that time, the new recruits were excluded from the Petersen estimates by including only ≥ 35 cm pike in n and m (yearly length increment of 30–35 cm individuals was on average 5 cm) and by excluding 30–34.9 cm individuals tagged in preceding autumn from $T_{\geq 35\mathrm{cm}}$ in next spring. Pike biomass was calculated using population density estimates, length distributions and lake-specific length-mass power regression equations, which were $m = 0.005L^{3.0183}$ ($r^2 = 0.9792$) for Haarajärvi, $m = 0.0037L^{3.1168}$ ($r^2 = 0.991$) for Haukijärvi, $m = 0.0037L^{3.1127}$ ($r^2 = 0.9837$) for Hokajärvi and $m = 0.0043L^{3.0862}$ ($r^2 = 0.9915$) for Majajärvi, in which m = estimated mass (g), L total length (mm) and r^2 is the coefficient of determination describing the fit.

All pike were measured to the nearest 1 mm (total length). Removed pike and released large (≥ 65 cm) individuals were weighed to the nearest 1 g and 10 g, respectively. All individuals caught within a year were included in spring length distributions either by using their direct lengths (before the onset of growth) or estimated spring lengths (by subtracting estimated plus-growth based on back-calculated growth analyses). Sex of ripe individuals was determined by running reproductive products at spawning time, or from gonad preparation in cases when pike were killed. Age and back-calculated growth were determined by one experienced reader either from scales from released pike (n = 521) or cleithrum bones from removed pike (n = 728) using a Fraser-Lee equation (Frost and Kipling 1959) or a linear growth model (Casselman 1990). For the yearly age distributions, observed age for the aged individuals was used and for other individuals the age was estimated by using age-length keys based on back-calculated length at age data as described in Horppila *et al*. (2010). The pooled age distributions in 2006–2008 were used to estimate total mortality (Z) by the catch-curve method (Robson and Chapman 1961). The first fully-recruited age group was 4 yr. except in Haukijärvi, where the catch-curve could be fitted only to the catch of ≥ 9-yr. individuals. Z was estimated to be 0.21, 0.32, 0.27 and 0.23 in Haukijärvi, Majajärvi, Hokajärvi and Haarajärvi, respectively, and the corresponding r^2 values were 0.738, 0.852, 0.901 and 0.947. Annual mortality (A) was calculated as $A = 1 - e^{-Z}$, and $S = 1 - A$. Natural mortality (M) was assumed to be equal to total mortality (Z) in 2006–2008, i.e., before pike removal affected the demographic structure.

Statistical analyses

To detect changes in pike population structure, the year-to-year differences in frequencies of the size classes S (small = 30.0–39.9 cm), M (medium = 40.0–64.9 cm) and L (large

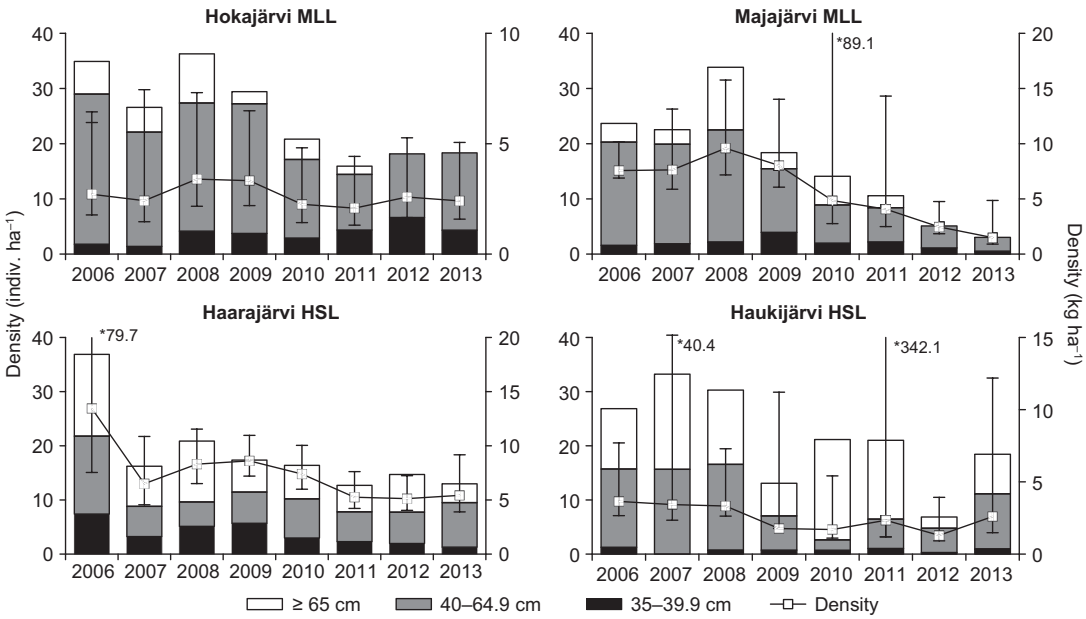

Fig. 1. Pike density estimates with 95% confidence limits and biomass estimates (columns) with proportions of 35–39.9 cm, 40–64.9 cm and ≥ 65 cm pike in research lakes in years 2006–2013. MLL = Minimum length limit, HSL = Harvestable slot-length limit. Removal fishing of pike ≥ 40 (MLL) or 40–64.9 cm (HSL) was conducted in 2008–2012.

≥ 65.0 cm), as well as female and male frequencies of pike were calculated by Fisher's exact test. Tests were conducted for each lake separately. Between-year differences were further examined by pairwise comparisons (Fisher's exact test) with the Bonferroni correction for multiple comparisons. Only pike of ≥ 30 cm total length were used in all statistical calculations, as this was the length threshold for tagging. In addition, our catching methods (spawning-time trapping, angling) for pike were poorly suitable for < 30 cm pike. The analyses were performed using R ver. 3.1.0.

A general linear model was applied to the data from each lake to investigate trends in pike population density, biomass and mean length and age, in response to HSL and MLL regulation in 2006–2013. In case of Haarajärvi, the year 2006 was excluded from density and biomass analyses, as the density estimate for 2006 was almost two times higher (with wide 95% confidence limits) than the estimates for 2007 and 2008, and thus considered not representative of initial pike population before the start of removal fishing. The above analysis was performed using SAS ver. 9.4.

Results

Pre-treatment conditions

Prior to pike removal experiment, pike average density estimates for 2006–2008 (except in Haarajärvi 2007–2008) were 14.8 and 9.2 indiv. ha^{-1} in HSL-lakes Haarajärvi and Haukijärvi, respectively, and 11.4 and 16.5 indiv. ha^{-1} in MLL-lakes Hokajärvi and Majajärvi, respectively (Fig. 1). Corresponding average biomass estimates were 9.3, 11.3, 8.1 and 13.3 kg ha^{-1} in Haarajärvi, Haukijärvi, Hokajärvi and Majajärvi, respectively. In each of the study lakes all size classes (S, M and L) were present (Fig. 1). Large pike (≥ 65 cm) comprised on average 12.8% and 46.8% of the estimated total density and biomass, respectively, in Haarajärvi; 21.9% and 46.6%, respectively, in Haukijärvi; 7.2% and 19.4%, respectively, in Hokajärvi; and 5.5% and 19.8%, respectively, in Majajärvi. Pike average lengths (2006–2008 average) were 42.7, 53.0, 46.7 and 45.3 cm, average ages 7.0, 9.2, 7.4 and 6.7 years and female percentages 40.7%, 45.0%, 46.%8 and 39.4% in Haarajärvi, Haukijärvi, Hokajärvi and Majajärvi, respectively.

Pike removal catches

Pike removal catch during 2008–2012 in HSL lakes (Table 2) totalled 309 individuals and 150 kg (2.0–2.5 kg ha^{-1} yr^{-1}) and 32 individuals and 26 kg (1.9–3.6 kg ha^{-1} yr^{-1}) in Haarajärvi and Haukijärvi, respectively. In MLL lakes, Hokajärvi and Majajärvi, the corresponding numbers were 204 individuals and 123 kg (2.0–3.8 kg ha^{-1} yr^{-1}) and 108 individuals and 76 kg (3.5–5.9 kg ha^{-1} yr^{-1}). The removal catch by weight, which was set up by spring biomass estimates, declined clearly in MLL lakes during the removal years but in HSL lakes it either fluctuated (Haukijärvi) or remained quite stable (Haarajärvi) reflecting the changes in or stability of the estimated total biomass (Table 2 and Fig. s1).

Pike average removal percentages (and ranges) of the estimated total biomass (H_b) in 2008–2012 were higher in MLL lakes Hokajärvi (50.1%, 39.6%–57.3%) and Majajärvi (73.2%, 34.6%–137%) than in HSL lakes Haarajärvi (27%, 22.6%–35.5%) and Haukijärvi (47.1%, 23.8%–83.8%). The percentages of the removed numbers of individuals (H_n) differed less clearly between treatments. In MLL lakes, Majajärvi and Hokajärvi, average H_n in removal years (2008–2012) were 60.4% and 39.6%, respectively, and in HSL lakes, Haukijärvi and Haarajärvi, 54.7% and 31.6%, respectively. The H_n values for medium sized pike (40–64.9 cm) in the removal years were almost identical between the treatments: 68.6% and 48.3% in MLL lakes Majajärvi and Hokajärvi, respectively, and 71.9% and 46.7% in HSL lakes Haukijärvi and Haarajärvi, respectively.

Responses in population density and biomass

Estimated pike population abundances decreased significantly in both MLL lakes (Fig. 1 and Table 3). In Majajärvi, both estimated density and biomass decreased (by 82.0% and 88.7%, respectively, from 2006–2008 to 2013). In Hokajärvi, estimated biomass decreased significantly

Table 2. Annual pike removals from study lakes in 2008–2012 including numbers and weights removed per hectare, and removal percentages of estimated biomass removed (≥ 40 or 40–64.9 cm individuals), and percentages of females in removal catch. HSL = harvestable slot-length limit regulation, MLL = minimum length limit regulation.

Lake	2008	2009	2010	2011	2012
Haarajärvi (HSL)					
Removal (indiv. ha^{-1})	4.9	4.3	4.6	4.6	4.0
Removal (kg ha^{-1})	2.5	2.0	2.0	2.3	2.1
Removal (% of biomass)	24.3	22.6	24.7	35.5	27.9
Removed females (%)	55	37	59	50	37
Haukijärvi (HSL)					
Removal (indiv. ha^{-1})	2.9	4.9	1.9	2.4	3.4
Removal (kg ha^{-1})	2.7	3.6	1.9	2.5	2.2
Removal (% of biomass)	23.8	72.5	23.8	31.7	83.8
Removed females (%)	0	50	50	25	57
Hokajärvi (MLL)					
Removal (indiv. ha^{-1})	4.3	7.1	4.6	3.6	4.6
Removal (kg ha^{-1})	3.6	3.8	3.0	2.0	2.3
Removal (% of biomass)	39.6	54.0	57.3	49.3	50.5
Removed females (%)	65	58	63	53	63
Majajärvi (MLL)					
Removal (indiv. ha^{-1})	7.7	7.1	4.4	6.5	6.2
Removal (kg ha^{-1})	5.9	4.4	4.0	4.7	3.5
Removal (% of biomass)	34.6	47.5	57.4	89.4	137.0*
Removed females (%)	38	70	60	37	50

* Removal catch in 2012 exceeded estimated biomass.

(by 43.7%), but the 15.2% decrease in density was statistically insignificant. In HSL lakes, estimated density and biomass decreased only little, and not significantly, in the course of the study (Fig. 1 and Table 3). In Haarajärvi, density and biomass estimates for 2013 were 26.7% and 30.1% lower than the average level in 2006–2008. In Haukijärvi, the between-year variation was high during the study (Fig. 1), but the density and biomass estimates for 2013 were respectively 25.1% and 38.8% lower as compared with those for the pre-treatment levels.

Responses in population structure, age and sex distribution

Mean length of pike decreased significantly in both MLL lakes (Table 3), the decrease being 9.5% in Hokajärvi and 6.8% in Majajärvi towards the end of the experiment (Table 4). In HSL lakes, Haarajärvi and Haukijärvi, no significant changes in mean length were detected (Table 3). In HSL lakes, large (≥ 65 cm) pike that were released comprised a substantial part of the total biomass (Haarajärvi 26.8%–53.8%; Haukijärvi 30.2%–87.6%) during the study period, indi-

Table 3. Development of pike density, biomass, mean length and age in 2006–2013 analysed by general linear model. Significant values of the effect of year are set in boldface. HSL = harvestable slot-length limit regulation, MLL = minimum length limit regulation.

Lake	Effect	Estimate	SE	df	*t*	*p*
Haarajärvi (HSL)						
Density	Intercept	17.941	2.399	5	7.48	0.0007
	Year	–0.926	0.446	5	–2.08	0.0924
Biomass	Intercept	10.335	1.064	5	9.71	0.0002
	Year	–0.478	0.198	5	–2.42	0.0602
Mean length	Intercept	41.758	0.953	6	43.83	< 0.0001
	Year	0.277	0.189	6	1.47	0.1928
Mean age	Intercept	7.4009	0.4877	6	15.17	< 0.0001
	Year	–0.0726	0.09658	6	–0.75	0.4807
Haukijärvi (HSL)						
Density	Intercept	9.707	1.436	6	6.76	0.0005
	Year	–0.667	0.284	6	–2.35	0.0573
Biomass	Intercept	12.247	1.977	6	6.19	0.0008
	Year	–0.941	0.392	6	–2.40	0.053
Mean length	Intercept	55.423	3.534	6	15.68	< 0.0001
	Year	–0.835	0.700	6	–1.19	0.2777
Mean age	Intercept	10.2383	1.035	6	9.89	< 0.0001
	Year	–0.4254	0.205	6	–2.08	0.0833
Hokajärvi (MLL)						
Density	Intercept	11.937	1.493	6	8.00	0.0002
	Year	–0.299	0.296	6	–1.01	0.3507
Biomass	Intercept	9.240	0.878	6	10.53	< 0.0001
	Year	–0.673	0.174	6	–3.87	**0.0083**
Mean length	Intercept	48.325	1.256	6	38.47	< 0.0001
	Year	–1.081	0.249	6	–4.34	**0.0049**
Mean age	Intercept	7.6899	0.27	6	28.48	< 0.0001
	Year	–0.1752	0.05347	6	–3.28	**0.0169**
Majajärvi (MLL)						
Density	Intercept	20.862	2.304	6	9.06	0.0001
	Year	–2.098	0.456	6	–4.60	**0.0037**
Biomass	Intercept	16.394	2.181	6	7.52	0.0003
	Year	–1.821	0.432	6	–4.21	**0.0056**
Mean length	Intercept	46.417	0.805	6	57.68	< 0.0001
	Year	–0.691	0.159	6	–4.33	**0.0049**
Mean age	Intercept	7.2631	0.1846	6	39.34	< 0.0001
	Year	–0.198	0.03656	6	–5.42	**0.0016**

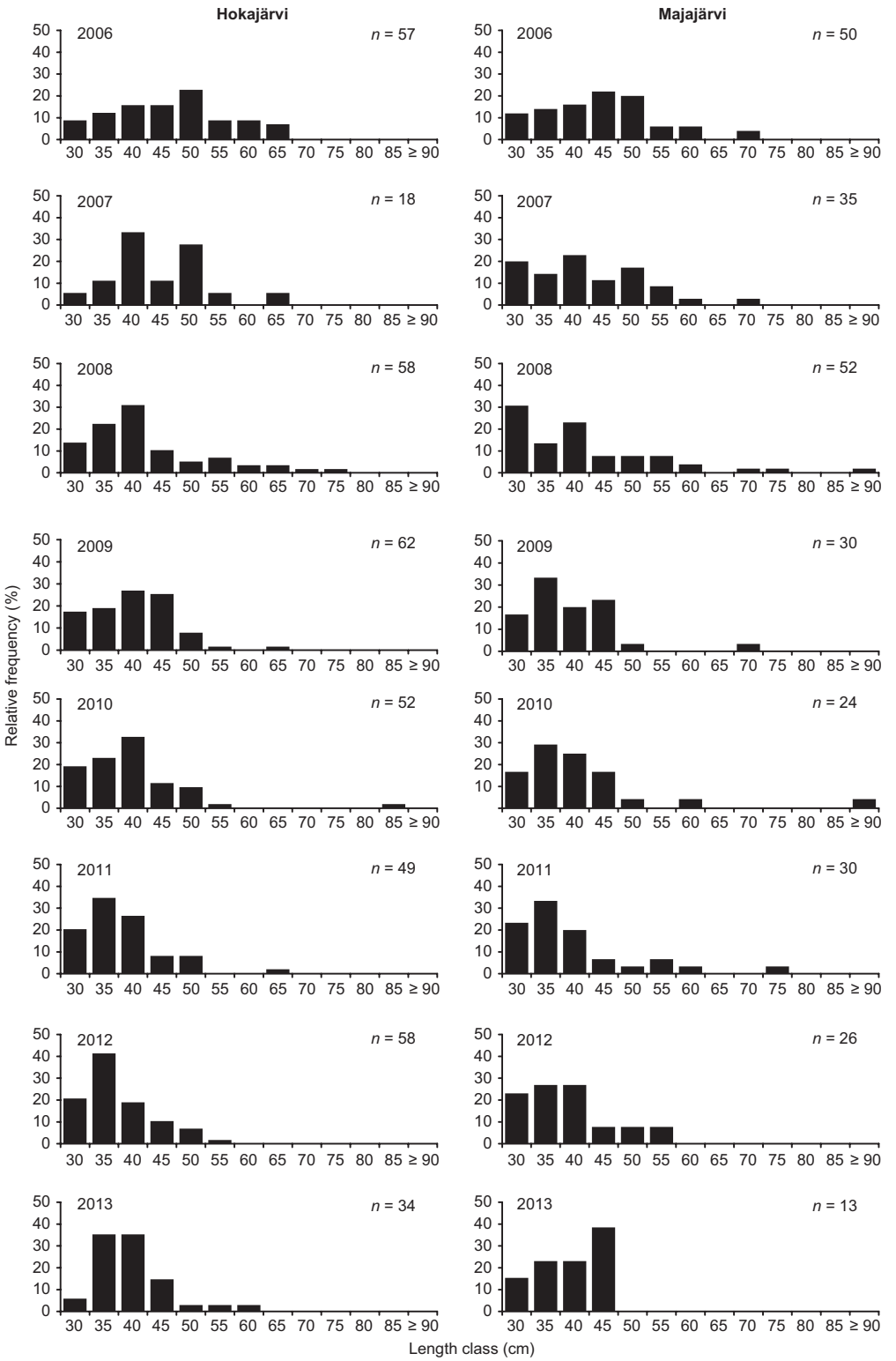

Fig. 2. Pike length frequency distributions in MLL-lakes in spring in years 2006–2013. Removal fishing of pike ≥ 40 cm was conducted in 2008–2012.

cating low mortality due to handling. Large pike disappeared completely from both MLL lakes four years after the start of pike removal (Figs. 1 and 2). In MLL lake Hokajärvi, removal gradually led to the dominance of < 45 cm pike (Fig. 2). This was evidenced by significant differences in annual frequencies of S, M and L size classes (Table 4) between pre-removal and "late removal" years. For example, the frequencies in 2006 differed from the frequencies in 2011 and 2012; and the frequencies in 2007 from the frequencies in 2011 (Fisher's exact test: p = 0.020, < 0.001 and 0.019, respectively). In the other MLL lake (Majajärvi), length distributions in the years 2012 and 2013 were severely truncated as compared with those in the years before pike removal (Fig. 2). However, the differences between the annual frequencies of size-classes S, M and L were not significant (Fisher's exact test: $p > 0.05$), as truncation took place within the medium size-class. In HSL lake Haarajärvi, intensive fishing of M-sized pike did not prevent high recruitment to harvestable size. In 2013 the frequency of M-sized pike (40–64.9 cm) was the highest in the study period (60.4%, Table 4), and differed significantly from the frequencies in 2006, 2008 and 2009 (Fisher's exact test: p = 0.0064, < 0.001 and 0.001, respectively). The size-structure distribution remained rather unchanged during the study as either 35–39.9 cm or 40–44.9 cm pike dominated every year (Fig. 3). In the other HSL lake (Haukijärvi), the

Table 4. Total numbers of ≥ 30 cm pike caught, female percentages, mean lengths and weights, and frequencies of small (S), medium (M) and large (L) pike in the study lakes in the years 2006–2013. HSL = harvestable slot-length limit regulation, MLL = minimum length limit regulation.

Lake	2006	2007	2008	2009	2010	2011	2012	2013
Haarajärvi (HSL)								
≥ 30 cm pike caught	111	90	179	122	112	103	97	53
Female (%)	44.4	35.5	42.2	36.4	49.5	42.2	33.8	45.2
Mean length (cm)	43.4	43.0	41.6	40.8	42.8	43.3	44.6	44.5
Mean weigth (g)	577	557	515	453	514	534	636	559
S, 30–39.9 cm (%)	60.4	53.3	68.7	65.6	43.8	50.5	48.5	34.0
M, 40–64.9 cm (%)	30.6	36.7	21.2	28.7	48.2	40.8	40.2	60.4
L, ≥ 65 cm (%)	9.0	10.0	10.1	5.7	8.0	8.7	11.3	5.7
Haukijärvi (HSL)								
≥ 30 cm pike caught	20	12	12	12	10	10	15	17
Female (%)	38.5	66.7	30.0	54.5	70.0	40.0	55.6	81.8
Mean length (cm)	51.5	54.8	52.5	50.5	59.7	52.3	43.7	48.2
Mean weigth (g)	994	1172	1095	962	1746	1264	584	904
S, 30–39.9 cm (%)	20.0	16.7	25.0	33.3	20.0	20.0	53.3	29.4
M, 40–64.9 (%)	65.0	58.3	58.3	50.0	30.0	60.0	40.0	64.7
L, ≥ 65 cm (%)	15.0	25.0	16.7	16.7	50.0	20.0	6.7	5.9
Hokajärvi (MLL)								
≥ 30 cm pike caught	57	21	61	63	56	51	58	36
Female (%)	37.5	41.7	61.4	63.3	59.2	40.0	48.1	42.4
Mean length (cm)	48.5	47.2	44.5	42.3	42.1	40.6	40.1	42.3
Mean weigth (g)	751	660	598	490	502	421	390	461
S, 30–39.9 cm (%)	21.1	28.6	39.3	36.5	46.4	56.9	62.1	44.4
M, 40–64.9 cm (%)	71.9	66.7	54.1	61.9	51.8	41.2	37.9	55.6
L, ≥ 65 cm (%)	7.0	4.8	6.6	1.6	1.8	2.0	0	0
Majajärvi (MLL)								
≥ 30 cm pike caught	50	36	54	30	24	32	26	15
Female (%)	33.3	45.5	39.5	60.7	47.6	39.3	40.0	26.7
Mean length (cm)	47.0	45.1	43.8	42.1	43.0	42.2	41.1	42.2
Mean weigth (g)	713.2	631.2	670.3	516.2	640.2	548.0	445.8	466.8
S, 30–39.9 cm (%)	26.0	36.1	45.3	50.0	45.8	59.4	50.0	46.7
M, 40–64.9 cm (%)	70.0	61.1	49.1	46.7	50.0	37.5	50.0	53.3
L, ≥ 65 cm (%)	4.0	2.8	5.7	3.3	4.2	3.1	0	0

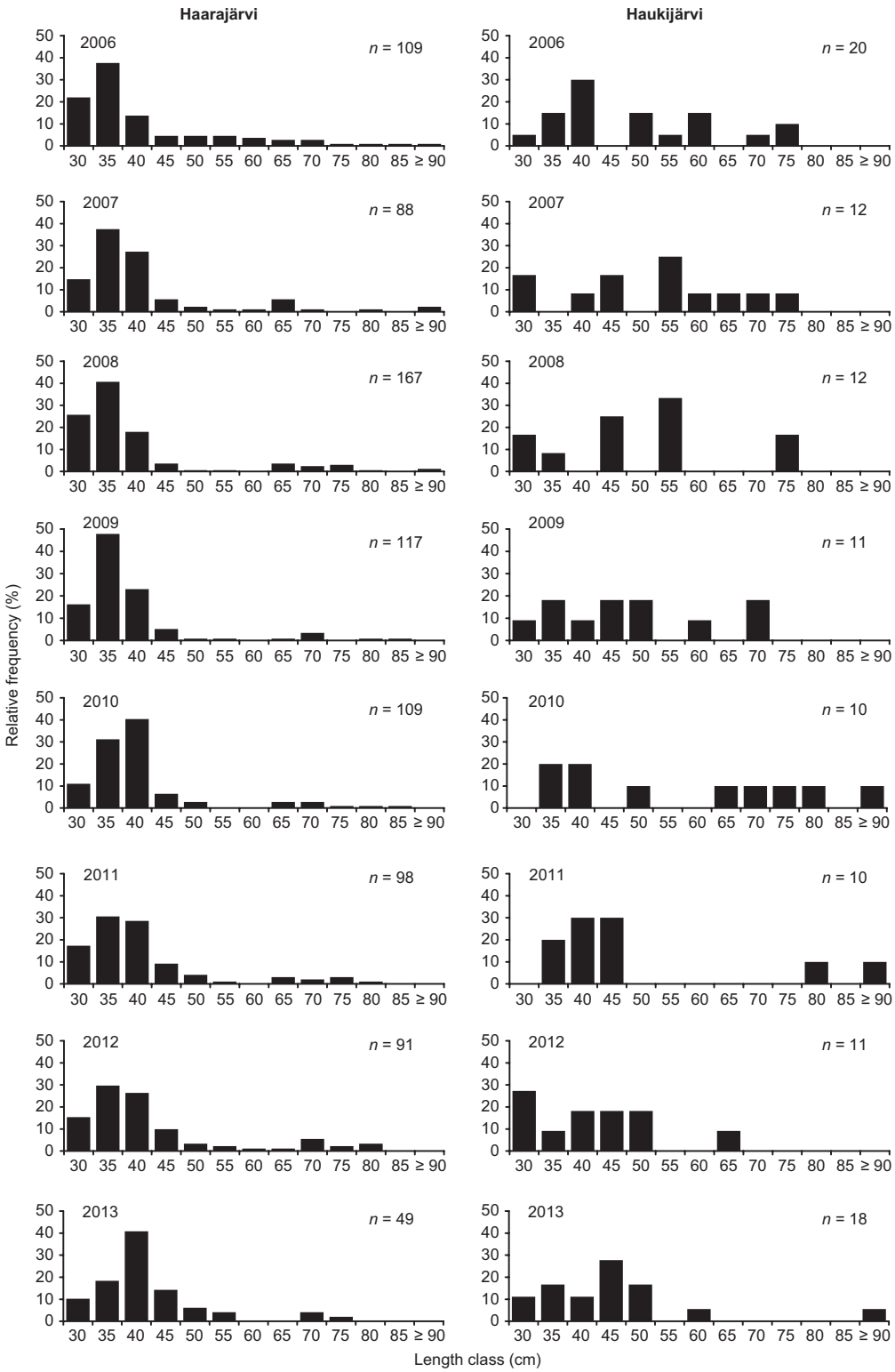

Fig. 3. Pike length frequency distributions in HSL-lakes in spring in years 2006–2013. Removal fishing of pike 40–64.9 cm was conducted in 2008–2012.

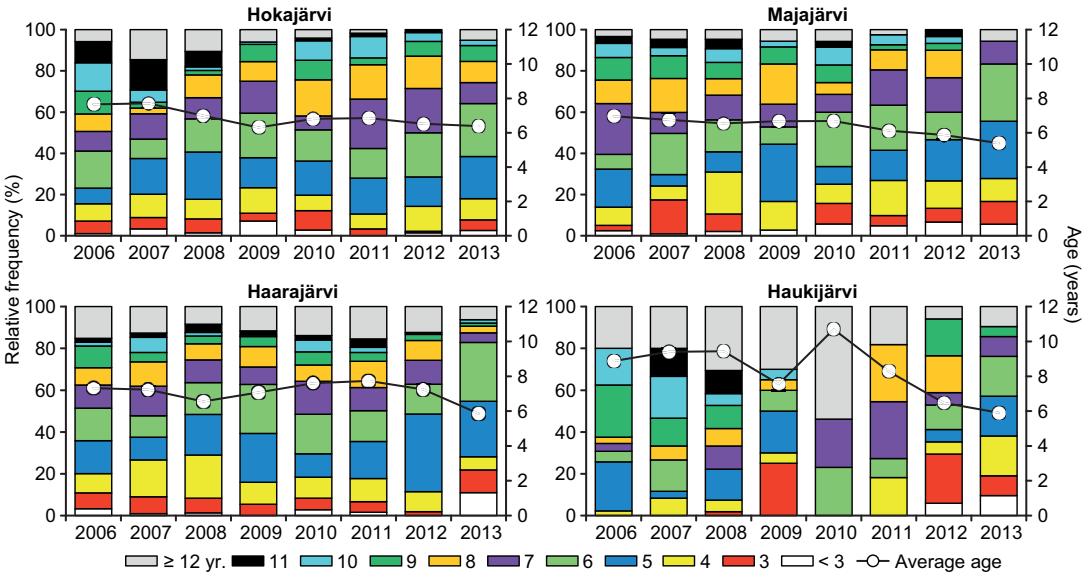

Fig. 4. Pike age distribution and average age in study lakes in 2006–2013.

frequencies of S-, M- and L-sized pike fluctuated between years (Fig. 3 and Table 4), and there was no significant response to removal (Fisher's exact test: $p > 0.05$).

The average age of pike decreased significantly during the course of the study in both MLL lakes (Hokajärvi and Majajärvi; Fig. 4 and Table 3). From 2006–2008 (average) to 2013, the average age decreased from 7.4 to 6.4 years (14.3%) in Hokajärvi and from 6.7 to 5.5 years (20.2%) in Majajärvi. In HSL lakes Haarajärvi and Haukijärvi, no decrease was detected, as in Haarajärvi the mean age was quite consistently between 6.6 and 7.7 years in 2006–2012, being the lowest (5.9 years) in 2013; and the pike mean age in Haukijärvi fluctuated considerably, being the highest (10.7 years) in 2010 and lowest (5.9 years) in 2013 (Fig. 4). The pike populations in all the lakes consisted of several age classes but the share of younger age classes (especially < 3 years) increased during the study period indicating increased recruitment (Fig. 4). Interestingly, large pike (≥ 65 cm; average age 13.5, 12.2, 11.7 and 12.9 years of age in Hokajärvi, Majajärvi, Haukijärvi and Haarajärvi, respectively) disappeared completely from the MLL lakes, but smaller pike of comparable age remained in the populations until the end of the study.

Average female percentages during the study were 41.2%, 54.6%, 49.2% and 41.6%, in Haarajärvi, Haukijärvi, Hokajärvi and Majajärvi, respectively (Table 4). Contrary to our hypotheses, there were no significant changes in female-to-male ratio in any of the lakes during the study years (Fisher's exact test: $p > 0.05$), although female percentages in removal catches were higher than female percentages in total catches, except in Haukijärvi (Tables 2 and 4).

Discussion

Responses of pike population to size selective fishing by HSL or MLL

According to our study, HSL regulation retained large pike in the lakes and maintained pike population abundance close to the original levels despite, which is considered an essential feature in sustainable fishing (Arlinghaus *et al*. 2010, Gwinn *et al*. 2015). In contrast, the abundance of large individuals decreased rapidly in the MLL lakes and large pike vanished in just four years. Our study supports earlier studies (Snow and Beard 1972, Kempinger and Carline 1978, Pierce *et al*. 1995, Arlinghaus *et al*. 2010, Pierce 2010) criticizing MLL fishing (especially if the

threshold length is set too low) as being unable to maintain either pike fishery yield or diverse size-structure for conservational purpose. Our results also concur with the meta-analysis by Pierce (2010), that implementation of maximum size-limits improves population size structure in terms of presence of large pike, but has less effect on population density as compared with lakes where MLL was applied. In both MLL lakes, the biomass response was more evident than the response in density, which is logical as the biomass estimate is affected not only by density, but also by size structure, and the catchability of large individuals seemed to be higher than that of smaller ones.

The study revealed that pike populations in different lakes may respond differently to similar size-selective fishing. Pike populations responded differently (but in both cases negatively) to MLL regulation in Majajärvi and Hokajärvi. In Majajärvi, both pike density and biomass collapsed, while mean size decreased, and size structure was truncated. In Hokajärvi, pike density decreased only little, but biomass almost halved, as size structure was truncated and mean size decreased. Truncation of the size distribution was also evidenced by changes in frequencies of S-, M- and L-sized pike between pre-removal and late removal years in Hokajärvi, but in Majajärvi changes in frequencies of size-classes were not found, as the number of large pike was low, and truncation took place within medium size-class. Differences in population-density responses between Hokajärvi and Majajärvi are likely explained by considerably greater removal percentage in Majajärvi in 2011 and 2012, which led to a collapse of the pike population. Also, the lake morphology features such as small size, steep banks, narrow euphotic layer and consequently narrow vegetated zone may have contributed to the population decline in Majajärvi, as pike were observed to gather along the shoreline where they are easily caught. Furthermore, the large vegetated littoral areas in Hokajärvi may have contributed to effective reproduction and compensatory recruitment of small pike (Bry 1996), which may partly explain why pike density was less affected in Hokajärvi.

HSL regulation seemed to be more sustainable than MLL, as there were no decrease (although quite close) in either lake in population density, biomass and mean size, and large pike remained in populations until the end of the study. Changes in frequencies of S-, M- and L-sized pike expressed increased recruitment and growth in Haarajärvi, indicating that HSL regulation would not have decreased population abundance even if the experiment was continued. The pike size structure in Haukijärvi practically did not change, but these results are quite difficult to interpret, as the length distribution showed high year-to-year fluctuation, which is likely due to small sample size. Small populations are also prone to high between-year variation due to environmental and demographic stochasticity (Lande 1993).

Our study also indicated that the age structure of the pike population may be less affected by fishing than the size structure. Although mean length and age decreased, large pike vanished and size distributions were severely truncated in both MLL-regulated lakes, the effect on age distribution was not as evident as compared with variations in the size structure. Old (≥ 12 years) pike remained to some extent in Hokajärvi and Majajärvi until end of the study. This finding implies that even though large individuals were not especially targeted in the MLL lakes, they were vulnerable to fishing as Pierce and Tomcko (2003) have suggested, indicating that fishing was positively size-selective, favouring slow-growing and passive individuals at the expense of fast-growing and actively-feeding ones. This may have an adverse effect on pike population productivity via genetic selection, as the share of fast growing genotypes decreases in the population (Cook and Younk 1998, Lewin *et al*. 2006). According to our study, HSL regulation will reduce the risk of positively size-selective fishing. Therefore, we concur with the results of recent studies (Arlinghaus *et al*. 2010, Pierce 2010) that recommend protection of large pike, whose higher energy need and activity increases their probability of being caught in recreational fishing (Lewin *et al*. 2006, Pierce and Tomcko 2003).

MLL regulation should decrease the number of female pike more than that of male pike, as large pike are more likely to be females whose probability to be caught under this regime is high (Craig 1996, Lewin *et al*. 2006). This was found

in our study as well, as more females than males were included in the removal catch. However, female-to-male ratio did not shift towards male dominance even in the MLL lakes, where large individuals were targeted. Due to the higher catchability of females, they may have been overrepresented in the pike density data which in turn masked the possible reduction in the share of females in the populations. Another explanation could be earlier maturation of females due to faster growth (first author's unpubl. data) which increased their relative abundance in recruiting year-classes as was observed for perch (Olin *et al*. 2017). However, our sex-distribution data on young pike was too scarce to verify this. In the long run, female-selective fishing is documented to have detrimental effects on recruitment (Lewin *et al*. 2006).

Reliability of the results

The advantage of HSL over MLL in this study could be partly explained by smaller removal percentage of biomass as a result of release of large individuals, which, despite their small number, comprised a large share of the pike biomass. However, when considering removal percentages of removed numbers, the difference was less obvious, and removal percentages of medium-sized pike (40–64.9 cm) were almost identical between the treatments. At the end of the experiment, when large pike had completely vanished from both MLL lakes and removal catch consisted almost solely of medium-sized pike, the main difference between the treatments was the release of large pike in HSL lakes, and not the contrasting harvest rates between the fishing regimes. Our study indicates how MLL and HSL would work in practical fisheries management in situations where fish population with initially low (or zero) harvest rate faces sudden increase in fishing pressure. In this scenario, initially high kept catch in MLL lakes would decrease eventually to the levels of HSL lakes but the size structure under HSL would be more diverse including large individuals and fishing is thus more sustainable. In the long run, HSL lakes may continue producing relatively high harvests, as large individuals are able to spawn and produce strong year-classes, whereas in MLL lakes the reproductive potential of the small-sized spawning stock is lower and the catch would probably decrease further.

As our population density and biomass estimates were based on mark-recapture data, we followed the prerequisites for the Petersen-Chapman method and collected representative length and weight data to ensure the reliability of estimates. According to Ricker (1975), the assumptions for reliable estimates with the Petersen-Chapman method are: (1) the marked and unmarked fish have the same natural mortality, (2) the marked and unmarked fish have same possibility of being caught, (3) there is no mark loss, (4) random mixing of marked fish to a population, (5) all marks are detected and reported, (6) there is only negligible recruitment to the catchable population during the recovery time. Assumptions 1–5 were fulfilled, since marking pike with T-bar anchor tags did not considerably increase the mortality in earlier studies and tag loss was negligible (Pierce and Tomcko 1993, Sharma and Borgstrøm 2008). Pike capture and recapture were conducted extensively on each lake to enable equal catchability for all pike. As pike handling, tagging and tag recording was conducted by trained personnel, mishandling, unreported tags, etc., unlikely affect the results. Fish passage from other lakes or rivers was restricted, because the study lakes are connected to other lakes only by small brooks which are either totally or at least partially impassable. Since lakes are reserved for research use only, no other fishing mortality than ours was expected to happen as there was only minimal evidence of illegal fishing. The major potential biases in our approach are related to the assumption concerning recruitment during recovery time. This was taken into account by including larger (≥ 35 cm) individuals in the analyses than had been earlier marked (≥ 30 cm) thereby excluding new recruits from the estimates. Possible error sources of the mark-recapture procedure and calculation with the Petersen method and comparison Bayesian estimates are more extensively discussed in the study of Kuparinen *et al*. (2012), which uses partially the same data from the years 2006–2009. Also regarding the catch-curve method, by which Z was estimated, the

key assumptions of this method were fulfilled: (1) there were no observed trends in recruitment during 2006–2008, (2) there was no fishing mortality during this period, (3) due to the multiple gears and sampling periods, there was relatively constant selectivity at age for the analysed ages ≥ 4 years. Older fully-recruited age group in Haukijärvi as compared with that in other lakes (9 years *vs*. 4 years) was not due to slower growth but lack of some smaller age groups in the data, which is likely explained by the small population size prone to high between-year variation (Lande 1993).

HSL in managing sustainable fisheries

Although HSL fishing proved to be better than MLL in maintaining population density, biomass and diverse size-structure, our results indicate that HSL fishing alone may not be sufficient to retain large individuals in a population, as we observed slightly decreasing numbers of large pike in both lakes with this type of fishing regulation. This implies that the fishing mortality of harvestable-sized pike in relation to growth rate was too high to let a sufficient amount of new recruits enter the largest size-class to maintain large pike over a longer period. Therefore, as suggested by Arlinghaus *et al*. (2010), fishing pressure has to be proportional to growth rate to ensure adequate recruitment of individuals exceeding the maximum length limit. Adjusting fishing pressure to a sustainable level may thus involve, beside HSL regulation, also other fisheries management tools such as bag limits, banning or restricting certain gear types, or restricting fishing areas or times (for example at spawning grounds or at spawning time) in order to control the fishing pressure on the pike population, as for example Paukert *et al*. (2001) and Pierce (2010) suggest.

Determining appropriate length limits for pike is an important task. The lakes we studied are small and have low production and slow pike growth (first author's unpubl. data). Therefore, the maximum length limit of 65 cm applied in this study is not likely to be valid everywhere. In their modelling study, Arlinghaus *et al*. (2010) suggested that ideal slot length limit for maintaining large pike is achieved by setting MLL of 45 cm and maximum length limit of 75–80 cm. In Sweden, in response to the declining pike stock in the coastal waters of the Baltic Sea, HSL is set to 40–75 cm with the daily bag limit of three pike. Recreational fishing is usually positively size-selective (Cook and Younk 1998, Lewin *et al*. 2006), and therefore implementing HSL regulation would be a promising tool to improve the sustainability of recreational fishing by maintaining high ecological status, and improving angling quality while still allowing a moderate mortality of medium-sized pike for subsistence fishing or low mortality by catch and release fishing.

Although implementing HSL regulation may decrease the maximum yield compared with that of MLL (Pierce *et al*. 1995), it can be considered an acceptable trade-off towards more sustainable fishing and diverse size distribution. Recreational fisheries in developed countries are often motivated by diverse leisure-related factors, e.g. the challenge of the catch, rather than simply maximizing biomass yield of the fishery (Arlinghaus 2006, Pierce 2010). Maintaining pike stock by HSL regulation requires catch-and-release practice for valuable large fish, which requires a certain skill level from the angler in order to minimize post-release mortality, injuries by hooking and handling and other sublethal alterations in physiology and behaviour (Cooke and Schramm 2007, Klefoth *et al*. 2008). According to our experience gained in this study as well as that of others (Tomcko 1997, Arlinghaus *et al*. 2008, Klefoth *et al*. 2008, Koski 2009, Stålhammar *et al*. 2014), pike is relatively resistant to catch and release fishing by angling with typically less than 5% mortality, which enables management of pike fisheries by HSL regulation. Furthermore, it has to be noted that our handling procedure, which included length and weight measurements, scale sampling, fin-clipping and tagging, was rougher than normal catch and release fishing.

Future challenges and conclusions

To ensure sustainable use of pike stocks in the long-term, it is important to increase our under-

standing of the ecological effects of pike fishing, and to manage pike fishing in a way which minimizes the harmful effect of fishing. Such knowledge will help preserving vital pike populations and their role in ecosystems, as well as socio-economic benefits of high-quality pike fisheries. Although the popularity of recreational fishing is expected to decrease in developed countries in the forthcoming years (FAO 2012), the pressure by recreational fishing on fish stocks may not decrease as there has been a rapid development in fishing techniques and fishing gear (Radonski 2002, Cooke and Cowx 2006). Managing pike fisheries in a sustainable manner is particularly important in the context of other human-induced impacts such as climate change, eutrophication and changes in hydro-morphological conditions, which may affect pike populations and increase their vulnerability to the negative effects of fishing (Allan *et al*. 2005, Lehtonen *et al*. 2009). To overcome the challenges pike stocks are increasingly facing today, while acknowledging the popularity of pike in recreational fishing and its high ecological importance and socio-economical value, it is imperative to develop sustainable fishing practices. In order to achieve this, fisheries stakeholders should be more active in implementing ambitious, even experimental methods to protect large pike, as also suggested by Carlson (2016).

To conclude, our study emphasizes the high potential of HSL regulation for conserving large fish, which is an essential feature in sustainable pike fishing. HSL proved to be better than MLL for maintaining a diverse population size and age structure. As per fisheries management, to maintain pike population vitality and natural ecosystem functioning, or to develop high-quality pike fishing (presence of trophy fish), regulation of pike fishing by HSL is advised. However, if fishing pressure on pike is considerable, also other fisheries regulation methods may be required.

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