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Effects of non-selective and size-selective fishing on perch populations in a small lake

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Retaining large individuals is considered intrinsic to sustainable fishing. In this nine-year study, we explored the effects of simulated recreational fishing on life-history traits of two perch (*Perca fluviatilis*) populations in a lake divided for experimental purposes into two sections. In each section, one of the two following fishing methods was used: non-selective and negatively size-selective i.e. large individuals released. Non-selective fishing rapidly decreased the average size and age of the spawning perch stock thus reducing the average size of spawned eggs. Both fishing procedures increased the share of females in the spawning population due to decreased age at maturity. The average age at maturity decreased more in females than in males. The reductions in the density and biomass of the populations and increase in the growth rate of perch were temporary but the effects on size and age structure persisted throughout the study period. The retention of large individuals can delay the adverse effects of fishing on populations, and enable reproduction of large females, thereby sustaining high genetic variability and better quality of offspring.

Introduction

Recreational fishing of inland waters has recently been suggested to jeopardize fish populations at a global scale (Allan *et al*. 2005, Lewin *et al*. 2006, Welcomme *et al*. 2010, Post 2013). However, the situation may be more alarming than suspected, since catches of recreational fishing are typically not reported which complicates the evaluation of the effects of fishing and hides possible historical declines of fish stocks (Post *et al*. 2002, Cooke and Cowx 2004). Besides fishing, numerous other anthropogenic pressures (e.g. eutrophication and hydro-morphological changes) affect fish populations in inland waters and make them more vulnerable to the effects of fishing (Allan *et al*. 2005). Especially large, piscivorous species, apex predators, are threatened, as their density is usually low, and population growth slower than that of smaller species at lower trophic levels (Allan *et al*. 2005).

Recreational fishing often targets large individuals (Lewin *et al*. 2006), and the decline of large individuals may have detrimental effects on the population status and furthermore on ecosystems. Birkeland and Dayton (2005) presented several arguments for retaining older/larger fish in populations, including higher amount and

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better quality of reproductive products, higher genetic diversity and, thus, better adaption to changing environment. Positively size-selective fishing and the resulting loss of large individuals decrease the amount and quality of offspring and may negatively affect the genetic properties of the population (Grift *et al*. 2003, Devine *et al*. 2012, Pukk *et al*. 2013, Kokkonen *et al*. 2015). The effects of fishing may be compensated in fish populations by increased growth rate, decreased age and/or size at maturity and increased fecundity (Brodeur *et al*. 2001). Eventually, size-selective fishing typically causes the decline of large individuals, which will have pronounced effects on the whole ecosystem, as documented in both freshwater (Allan *et al*. 2005) and marine environments (Pauly *et al*. 1998). In lake ecosystems of the boreal region, this may lead to expansion of cyprinid fishes which in turn may affect nutrient dynamics and enhance eutrophication processes (Olin *et al*. 2002).

In Finnish lakes, recreational fishing is very popular and comprises a major part (ca. 80%) of the total catch. There are 1.6 million recreational fishermen, equivalent to 30% of the whole population (source Natural Resources Institute Finland). The total catch of recreational fishing in freshwaters in 2014 was estimated to be 23 000 tonnes or on average 7 kg ha^{-1} (source Natural Resources Institute Finland). The most important species was perch (*Perca fluviatilis*) with the total catch of ca. 6600 tonnes, of which only 10% was released alive. Perch was caught using a variety of different gears: angling (54%), gillnets (28%) and traps (18%), and it can be assumed that gillnets and certain types of angling (trolling and cast by rod) select for large individuals (Lewin *et al*. 2006). Based on the intensity and size-selectiveness of recreational fishing, the local effects on perch demographic structure can be expected. Also for perch, it has been demonstrated that the amount and quality of offspring increase with female size, and positively size-selective fishing can reduce the amount and quality of reproductive products (Heyer *et al*. 2001, Olin *et al*. 2012). Globally, the species is one of the most important freshwater target species for human consumption (Craig 2000).

Experimental studies in natural environments give applicable results concerning the effects of fishing on wild populations (Underwood 1997, Brodeur *et al*. 2001). Such results are needed for sustainable use of fish resources. However, in only few studies the responses of fish populations to recreational fishing were studied experimentally in lakes (Goedde and Coble 1981, Mosindy *et al*. 1987, Nuhfer and Alexander 1994, Pierce *et al*. 1995).

In our nine-year study programme, we conducted a four-year intensive experimental fishing in an artificially-divided pristine lake. We aimed to explore the effects of simulated recreational fishing on life-history traits of two perch populations. We exposed one population to negatively size-selective fishing (large individuals were released) and the other to non-selective fishing (all length classes were targeted although their catchabilities may have differed). We examined responses in several traits including population abundance, biomass, age and size distribution, growth and production, fecundity and egg size, and average length and age of spawners. First, we hypothesized that non-selective fishing would rapidly decrease the number of large individuals since their catchability is higher as compared with that of small ones because of higher activity and longer swimming distances (Kurkilahti 1999). Second, the population retaining large individuals should show weaker responses in life history traits (i.e. lower reduction in population biomass and in average age and size) than the population subjected to fishing of all sizes of perch (Birkeland and Dayton 2005). Third, perch populations would partly compensate the effects of fishing by decreased age and size at maturity and subsequent increase in fecundity (Brodeur *et al*. 2001). Finally, loss of large individuals was suspected to adversely affect the quality (egg size) and amount (egg number) of reproductive products (Olin *et al*. 2012).

Material and methods

Study area

We conducted the study in Iso Valkjärvi (IVA) which is a small (3.8 ha), meso-humic and oligotrophic forest lake in southern Finland (Olin *et al*. 2010). The lake is nearly pristine, and all activities other than research are prohibited. In 1991, the lake was divided into two sections by a plastic wall because of a liming experiment that lasted until 1994 (Rask *et al*. 1996). During the liming experiment in 1992, the perch abundance was estimated to be ca. 1800 indiv. ha^{-1} in both sections (Rask *et al*. 1996). In 2005, we explored the lake to ensure that the effects of liming and acidification had subsided. In 2008, two scuba divers checked the plastic walls and no significant damages were reported. The areas (and mean depths) of the sections IVA_NS (NS = non-selective fishing) and IVA_SS (SS = size-selective fishing) were 1.6 ha (2.8 m) and 2.2 ha (3.8 m), respectively. The average total phosphorus concentration in surface water during the growing seasons (May–September) of the study years (2007–2012) was 14 μg l^{-1} in both sections. In the same period, the Secchi depth was 2.9 m in IVA_NS and 2.6 m in IVA_SS. Water colour during autumn turnover was lower in IVA_NS (49 mg Pt l^{-1}) than in IVA_SS (79 mg Pt l^{-1}). The average water temperature in surface water during growing seasons 2007–2012 (Table 1) was slightly higher in IVA_NS (17.0 °C) than in IVA_SS (16.8 °C). In both sections, the fish community consisted mainly of perch and pike (*Esox lucius*), but included also some stocked white fish (*Coregonus lavaretus*) and very few individuals of roach (*Rutilus rutilus*) (Olin *et al*. 2010). The estimated (Petersen) densities of ≥ 30-cm pike increased throughout the study period and were 10 (95%CL = 6–32) indiv. ha^{-1} in 2008–2009 and 10–14 (95%CL = 7–33) indiv. ha^{-1} in 2010–2012 in IVA_NS. The corresponding densities were much lower in IVA_SS: 2–4 (95%CL = 1–7) and 5–10 (95%CL = 5–223) indiv. ha^{-1}. The numbers of annually marked (and recaptured) pike in the years 2007–2012 ranged between 2 and 12 (2 and 9) and between 3 and 8 (1 and 4) in IVA_NS and IVA_SS, respectively.

Removal fishing

To study the effects of non-selective (NS = non-selective, all size classes targeted) and negatively size selective (SS = large individuals, ≥ 16 cm not targeted) fishing on perch population traits, we conducted removal fishing during 2008–2011 in both sections of the lake. In IVA_NS, the target catch was half of the yearly estimated perch biomass and the fishing was aimed to be non-selective in terms of size (Table 2). In IVA_SS, half of the yearly estimated biomass of small perch was targeted for removal and large perch (≥ 16 cm) were released. The size limit was based on the average size when perch shift to piscivory in the local lakes (Estlander *et al*. 2010). We conducted removal fishing each year in May–June using wire traps (12 × 12 mm mesh, 5 × 80 cm opening) and gillnets (mesh sizes in bar length 10–55 mm in IVA_NS and 10–15 mm in IVA_SS, net size 1.8 × 30 m). The annual removal fishing efforts were 10–235 wire-trap days and 47–186 gillnet days in IVA_NS, and 56–438 wire-trap days and 65–146 gillnet days in IVA_SS. We first estimated the density, size structure and biomass of the spawning population and then started the

Table 1. Total phosphorus concentration (P_{tot}, μg l^{-1}), Secchi depth (m), and surface (0.5 m) water temperature (T, °C) in the Iso Valkjärvi sections where non-selective fishing (IVA_NS) and size-selective fishing (IVA_SS) were carried out during the study years. Values are average values during growing season (May–September). Number of samples or measurements (per year and lake side) was 6–8, 6–11 and 153 for P_{tot}, Secchi depth and T, respectively.

Year	P_{tot}		Secchi depth		T	
	IVA_NS	IVA_SS	IVA_NS	IVA_SS	IVA_NS	IVA_SS
2007	10	9	2.56	2.58	17.2	17.3
2008	13	12	2.81	2.70	16.4	15.3
2009	18	18	2.89	2.55	17.0	17.3
2010	19	22	2.76	2.14	17.6	17.3
2011	11	11	2.99	2.86	17.4	17.3
2012	16	15	2.96	2.82	16.4	16.3

removal fishing which was continued until the target catch was achieved or until perch activity ceased. The total length (TL, 1 cm size classes) and sex of each removed individual were determined; total weight of the catch per day and gear was recorded. A subsample (n = 1–88) for age and growth determination was taken on each day from the catch of both gear types.

Spawning stock density, biomass and length, age and sex structure

We estimated the density, biomass, size, age and sex structure of spawning perch stock (individuals > 7 cm) in spring 2007–2012 by marking and recapturing during two weeks after ice-break. Perch were caught with wire traps (same type as described above, 50–110 trap-days per section per year) and marked by fin clipping (tip of the right or left pelvic fin on alternate years); for more detailed methods *see* Olin *et al*. (2012). We used the Schnabel method (Seber 1982) to estimate the population size. The total number of annually marked (and recaptured) perch were 618–2220 (110–722) and 383–1885 (114–320) in IVA_NS and IVA_SS, respectively. From the mark–recapture catch, sex and TL (1 cm size classes) were determined. Sex distribution was expressed as female proportion (%) from total (unmarked) catch, and the between-year or between-section differences were analysed with Pearson's χ^2-test with Bonferroni correction. The length distributions were presented as number of unmarked individuals per wire trap (NPUE) of each size class, and the between-year or between-section differences were tested with the Kolmogorov-Smirnov test with Bonferroni correction. From the length distributions, the wire-trap NPUE of large (≥ 16 cm) individuals was calculated and the between-year and between-section differences were tested using ANOVA. Age structure was estimated by using the lake-section and year-specific age–length keys derived from the age samples of removal fishing, and the length distribution of mark and recapture catch.

Standard gillnet sampling

To obtain perch samples (relative abundance, and size and age structure) from a longer period, and to include young of the year (YOY) in sampling, we conducted standard gillnet test fishing (CEN 2005) three times per year in July–August in 2005–2013. The fishing effort was 6–8 Nordic multimesh gillnets per year per section and the soak time was ca. 12 h (overnight). The catch of each gillnet was counted and weighed, and the length (TL) of all individuals was measured. A subsample (n = 7–135) for age and growth determination was taken on each sampling day. The gillnet data were found to be severely skewed

Table 2. Target catches (kg ha^{-1}) and removal catches (kg ha^{-1} and indiv. ha^{-1}), and mean weight and length of perch in IVA_NS and IVA_SS during 2008–2011. In IVA_NS, all size classes were targeted whereas in IVA_SS ≥ 16 cm perch were released. Female (%) = percentage of female perch in removal catch.

	Target catch (kg ha^{-1})	Removal catch		Mean weight (g)	Mean length (cm)	Number of large (≥ 16 cm) fish removed (indiv. ha^{-1})	Female (%)
		(kg ha^{-1})	(indiv. ha^{-1})				
IVA_NS							
2008	17.0	18.6	621	30.0	13.4	145	26
2009	14.8	20.7	665	31.1	13.5	137	48
2010	18.2	10.2	937	10.9	9.7	20	40
2011	19.1	20.5	1471	13.9	10.8	38	46
IVA_SS							
2008	12.0	11.2	480	23.4	12.8	12	19
2009	4.1	8.3	317	26.2	13.2	32	38
2010	1.7	1.4	137	10.3	9.5	3	63
2011	15.7	17.3	2269	7.6	9.0	2	50

(positively skewed distribution with heteroscedasticity and overdispersion). Therefore, the between-year and between-lake-section differences in gillnet total NPUE (indiv. gillnet night^{-1}) and BPUE (g gillnet night^{-1}) were tested with a generalized mixed linear model. In the model, lake-section (IVA_NS, IVA_SS), year (2005–2013) and depth zone (littoral, pelagial surface, pelagial bottom) were fixed factors and fishing date (nested in year) was a random factor. The link function was *log* and the probability distribution was Poisson for NPUE and negative binomial for BPUE. We used the above tests also for the catch including NPUE of large perch (≥ 16 cm) only. Tukey-Kramer's test was used for pairwise comparisons.

Growth and production

The growth (annual length and weight increment) was determined from perch collected during spring removal fishing in 2008–2011 and late summer gillnetting in 2005–2013 (n = 1147 and 1006 in IVA_NS and IVA_SS, respectively). Perch used in ageing were measured for length (to the nearest mm) and weighed (to the nearest 0.1 g) and the yearly length-weight relationship was calculated for biomass and production estimates. The annual length increment of each fish was back-calculated from opercular bones using Monastyrsky's procedure (Bagenal and Tesch 1978). Large individuals (≥ 16 cm) were aged from otoliths. The differences between years and lake sections in the annual length increments of 1–7-year perch were tested with repeated ANOVA and Wald's statistics with Bonferroni correction in pairwise comparisons. The analysis included the fixed variables year, lake section, sex and individual, and back-calculated age was the repeated factor with compound symmetry as covariance structure (Horppila and Nyberg 1999). The density-dependence of length increment was analysed with ANCOVA including year and lake-section as fixed variables and gillnet NPUE as covariate (gillnet NPUE can be used as a density index in the lake, Olin *et al.* 2016). Age distributions were estimated by using age–length keys as described in Horppila *et al.* (2010). The between-year and between-section differences in the age distributions were tested with the Kolmogorov-Smirnov test with Bonferroni correction.

The annual perch production is the sum of the production for each length class (l) estimated by the following equation (Ricker 1975):

$$\text{Production} = \sum_{i=1}^{l} \frac{gB_0\left(e^{(g-Z)}-1\right)}{g-Z}, \qquad (1)$$

where g is the specific growth rate $[(\log_e W_2 - \log_e W_1)/(t_2 - t_1)]$, B_0 is the the estimated spring biomass, and Z is the instantaneous total mortality rate. Z was estimated as an yearly average of year-class specific mortality $Z_{\text{year-class}} = -\ln(N_{t+1}/N_t)$, where N is the wire trap CPUE of the year-class. When reasonable Z values could not be estimated, average Z for all years was used. For IVA_SS, Z was estimated separately for < 16 cm and larger perch due to the fishing procedure where larger perch were released.

Fecundity and egg size

For fecundity and egg-size estimates, we caught a sample of ripe female perch from both sections before and after three years of perch removal (IVA_NS n = 34 and 39, and IVA_SS n = 25 and 46 in 2008 and 2011, respectively). Gonads of those individuals were weighed, gonadosomatic index (GSI) calculated, and wet and dry (60 °C, 24 h) weights of a subsample of eggs (n = 50 per female) were measured. Total fecundity was calculated from gonad weight and average egg wet weight. The effects of lake section, year and female length (covariate) on GSI, total fecundity, and egg dry weight were tested with ANCOVA. To normalize variances, GSI was arcsine-transformed and total fecundity and egg dry weight were ln-transformed. The total amount of produced eggs (indiv. ha^{-1}), based on the density estimates, female size distribution and size specific total fecundity, was estimated for both sections and the years 2008 and 2011.

Results

Perch removal catches

The realised (and target) removal catches were

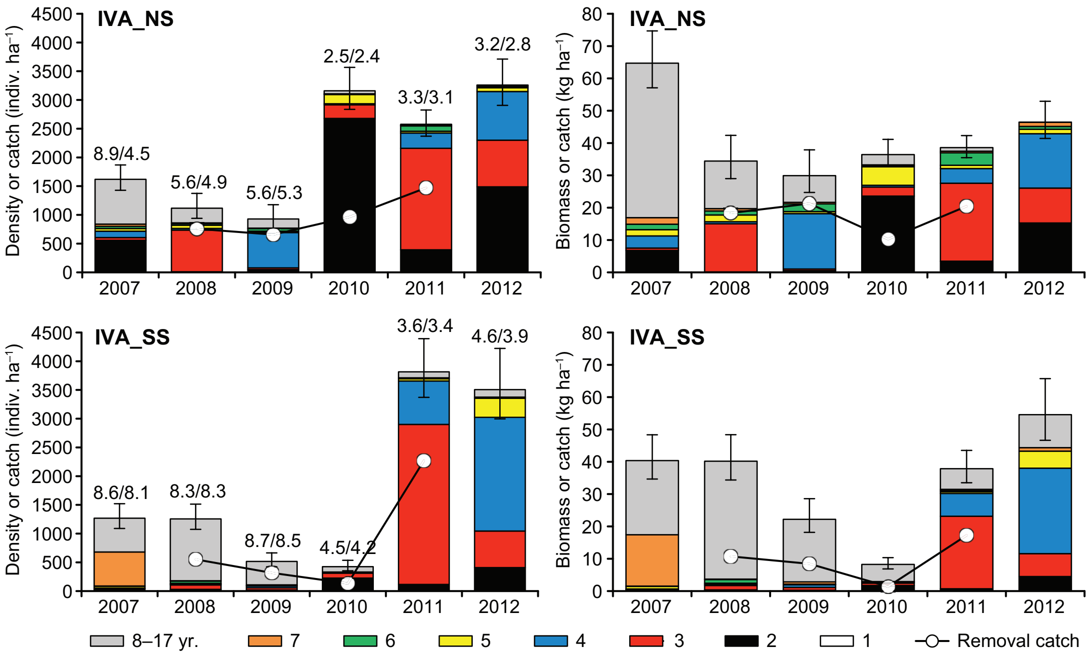

Fig. 1. Estimated total densities and biomasses (with 95%CLs) of perch populations in the lake sections IVA_NS and IVA_SS in spring 2007–2012. Colours indicate the shares of 1–7-year age groups. Older age groups (8–17 years, grey) are pooled. Average age (years) of female/male spawners is shown above the bars in the left-hand-side plots. Removal catches (indiv. ha^{-1}) are also shown.

10–21 (15–19) kg ha^{-1} yr^{-1} in IVA_NS and 1–17 (2–16) kg ha^{-1} yr^{-1} in IVA_SS (Table 2). The cumulative removal catch in 2008–2011 was 70 and 38 kg ha^{-1} in IVA_NS and IVA_SS, respectively. The catches in numbers of perch removed were 621–1471 indiv. ha^{-1} in IVA_NS and 137–2269 ha^{-1} in IVA_SS. The target catch was attained or exceeded in IVA_NS in all years except in 2010 when the strong year-class 2008 entered the spawning population and we could reach only 56% of the target catch before perch spring activity ceased and removal catches collapsed. In IVA_SS, the target catch was attained fairly well, and in 2009 even exceeded by 108%. The mean weight of perch in removal catch was 23–31 g in 2008 and 2009 but decreased after that to less than half of the original values in both sections of IVA (Table 2). The release of large (≥ 16 cm) individuals from the removal catch of IVA_SS succeeded quite well as the yearly removed amount was 3–70 large individuals (0.1%–10% of the total catch). In IVA_NS, the removal catch of large individuals was 31–228 individuals per year (2%–23% of the total catch). The removal catch of large individuals decreased clearly in both sections along the study period (Table 2). More males than females were removed in every year except in 2010 and 2011 in IVA_SS. The share of females in the removal catch increased 2–3 fold in both sections after 2008.

Biomass and density of perch

In both lake sections, the estimated (Schnabel) density and the biomass of the perch spawning population decreased in the first spring (2009) after the onset of removal fishing in 2008 (Fig. 1 and Tables 3–4). Unexpectedly, the estimated reductions in density and biomass were clearly steeper in IVA_SS, where target catches were lower and almost all of ≥ 16 cm perch were released (Table 2). In IVA_NS, a strong increase in the estimated perch density occurred in 2010, when 2-year-old perch (year-class 2008) entered the spawning population. The density and biomass remained high thereafter despite the intensive fishing, since strong year-classes were produced also in 2009 and 2010 (Table 3). In IVA_SS, both perch biomass and density reached their minima in 2010, because the strong year-class 2008 grew much slower in IVA_SS than in IVA_NS and most of the year-class did not reach maturity until 2011, when density and biomass of the spawning population considerably increased in IVA_SS (Table 4). Intensive fishing in 2011 (Fig. 1) reduced the densities of the year-classes 2007 and 2008; however in the next year (2012), the total densities remained unaffected because of the year-classes 2009 and 2010 contributing to the catches.

Both the catch in weight (Generalized mixed linear model, main effect of year: $F_{7,79} = 2.80$, $p = 0.028$) and the catch in numbers (Generalized mixed linear model, main effect of year: $F_{7,79} = 2.82$, $p = 0.026$) in gillnets reflected the perch removal and production of strong year classes (Fig. 2). In both sections, gillnet NPUE (Tukey-Kramer: $p = 0.099$ for IVA_NS and $p = 0.004$ for IVA_SS) and especially BPUE (Tukey-Kramer: $p = 0.018$ for IVA_NS and $p = 0.002$ for IVA_SS) responded to the first perch removal and collapsed in 2008 as compared with the previous year. In 2009, when the individuals of the strong year-class 2008 were large enough to be efficiently caught by gillnets, NPUE and BPUE of perch increased again (but significantly only in IVA_NS in NPUE, Tukey-Kramer: $p = 0.045$). In 2011, the gillnet catches decreased for a second time after another intensive spring removal (Table 2), but returned quickly to the pre-fishing levels in 2012–2013. The gillnet catches were higher in IVA_NS than in IVA_SS throughout the study period (statistically significantly in 2006, 2008 and 2012 in NPUE, Tukey-Kramer: $p = 0.042$, 0.024 and 0.008, respectively, and in 2012 in BPUE, Tukey-Kramer: $p = 0.077$).

Age, size and sex distributions of perch

The perch fishing and the following response in

Table 3. The density (indiv. ha^{-1}) and biomass (kg ha^{-1}) estimates of different perch year-classes (2003–2011, year-classes 1990–2002 are pooled) and total population (with 95%CL) in IVA_NS in 2007–2012.

Year-class	2007	2008	2009	2010	2011	2012
Density						
2011						1
2010					1	1487
2009					392	812
2008				2679	1766	848
2007			50	236	265	64
2006		10	29	20	31	21
2005	557	727	615	160	93	25
2004	48	28	22	9	9	0
2003	111	54	47	4	0	0
1990–2002	903	297	166	52	19	1
Total	1619	1116	929	3160	2577	3259
	(1428–1868)	(940–1374)	(767–1177)	(2836–3567)	(2369–2825)	(2905–3712)
Biomass						
2011						< 1
2010					< 1	15
2009					3	11
2008				24	24	17
2007			1	3	5	1
2006		< 1	< 1	1	1	1
2005	7	15	17	6	4	1
2004	1	1	1	< 1	< 1	0
2003	4	2	2	< 1	0	0
1990–2002	53	17	9	3	1	< 1
Total	65	34	30	36	39	46
	(57–75)	(29–42)	(25–38)	(33–41)	(35–42)	(41–53)

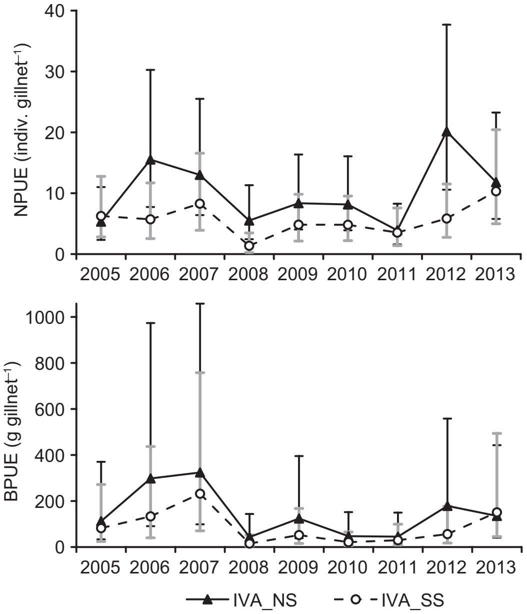

Fig. 2. Perch gillnet NPUE (indiv. gillnet^{-1}) and BPUE (g gillnet^{-1}) in the lake sections IVA_NS and IVA_SS. Error bars denote 95% confidence limits.

reproduction clearly changed the age structure of spawning population in both sections of the lake (Fig. 1). Before the start of the perch fishing in 2007–2008, the perch populations consisted mainly of > 3-year-old perch in both lake sections. In IVA_SS, where only small perch were targeted, the spawner average age increased in the first year (2009) after the removal fishing (Kolmogorov-Smirnov: $D_{303,207} = 0.459$, $p < 0.001$). In the second year after the onset of removal fishing (2010), the age distribution became clearly more dominated by young spawners (2–3 years old) as compared with that in both sections in the previous year (Kolmogorov-Smirnov: $D_{207,402} = 0.633$, $p < 0.001$ and $D_{266,335} = 0.855$, $p < 0.001$, in IVA_SS and IVA_NS, respectively), and the age structure remained young thereafter. A massive recruitment of 2-year-old perch of the year-class 2008 into the spawning stock appeared in 2010 in IVA_NS (Figs. 1 and 3). In IVA_SS, perch growth was slower and the majority of the strong year-class 2008 recruited to the spawn-

Table 4. The density (indiv. ha^{-1}) and biomass (kg ha^{-1}) estimates of different perch year-classes (2003–2011, year-classes 1990–2002 are pooled) and total population (with 95%CL) in IVA_SS in 2007–2012.

Year-class	2007	2008	2009	2010	2011	2012
Density						
2011						
2010					< 1	409
2009				< 1	115	635
2008				227	2785	1979
2007			19	85	754	332
2006		31	37	13	39	0
2005	40	76	32	6	11	19
2004	7	14	1	1	5	14
2003	7	15	4	0	0	0
1990–2002	1215	1121	422	93	104	117
Total	1269	1256	516	425	3815	3505
	(1089–1520)	(1074–1513)	(421–664)	(353–535)	(3371–4393)	(2996–4223)
Biomass						
2011						
2010					< 1	4
2009				< 1	< 1	7
2008				2	22	26
2007			< 1	1	7	5
2006		< 1	1	< 1	< 1	0
2005	< 1	1	1	< 1	< 1	1
2004	< 1	< 1	< 1	< 1	< 1	1
2003	< 1	< 1	< 1	0	0	0
1990–2002	40	38	20	5	6	9
Total	40	40	22	8	37	55
	(35–48)	(34–48)	(18–29)	(7–10)	(33–43)	(47–66)

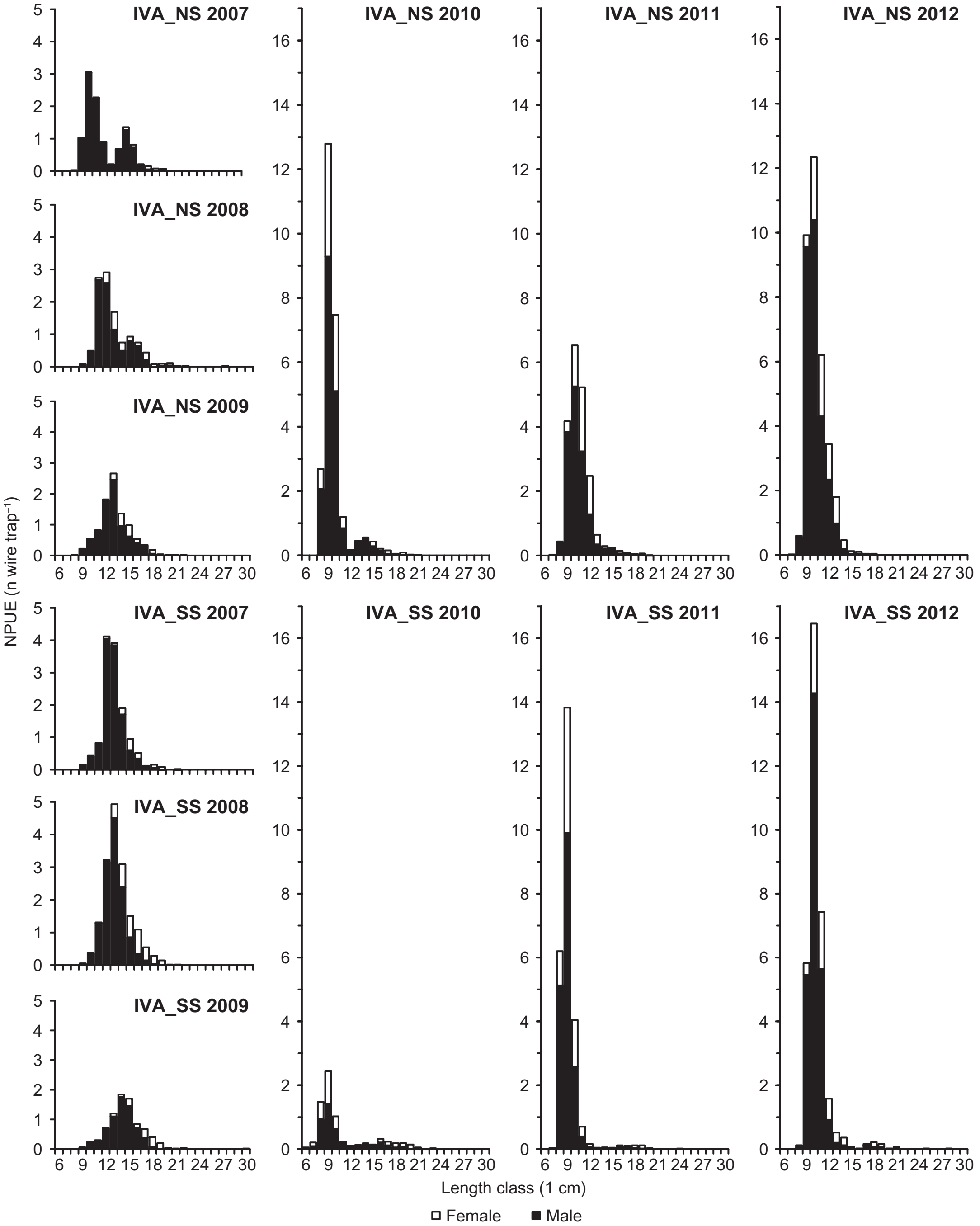

Fig. 3. Length frequency distributions of male (black columns) and female (white columns) perch in wire trap catch (indiv. wire trap^{-1}) during spawning period in IVA_NS and IVA_SS.

ing population in 2011 which resulted in the highest density estimate recorded in the study. Two spawning 1-year-old perch were caught, both from IVA_NS, in 2011 (male) and 2012 (female).

The size-structure of spawning perch stock responded clearly to removal fishing (Fig. 3). After the dominance of 11–14 cm fish in 2007–2009, size classes < 10 cm were the most abun-

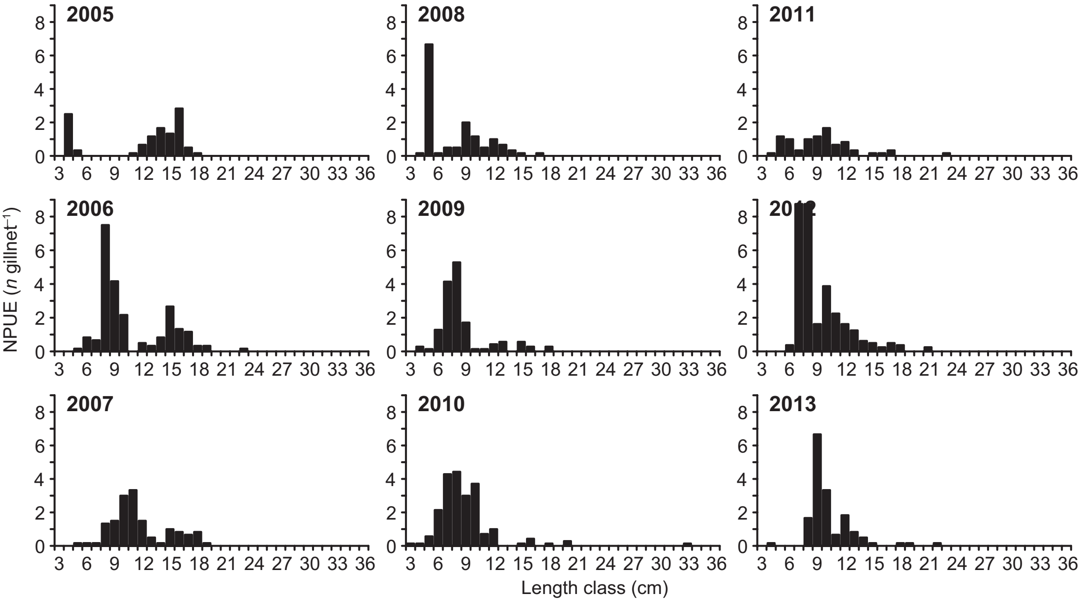

Fig. 4. Length frequency distributions of perch in gillnet catches during late summers in 2005–2013 in IVA_NS.

dant in both sections in 2010 (Kolmogorov-Smirnov: $D_{415,552} = 0.690, p < 0.001$ and $D_{479,2026} = 0.791$, $p < 0.001$, in IVA_SS and IVA_NS, respectively). NPUE of large (≥ 16 cm) perch differed significantly between the basins and among the years (ANOVA: $F_{11,439} = 7.58$, $p < 0.001$). In IVA_NS, NPUE of large (≥ 16 cm) perch in wire traps decreased in 2010–2012 to one tenth of the original value during the study period (3.0 *vs*. 0.3–0.4 indiv. wire trap^{-1}, Tukey: $p < 0.002$). In IVA_SS, NPUE of large perch was initially (in 2007) lower than in IVA_NS (3.0 *vs*. 1.6 indiv. wire trap^{-1}, Tukey: $p = 0.003$), but increased in 2008–2009 to the same level (3.3–3.9 indiv. wire trap^{-1}) until it decreased in 2010–2012 to 0.6–1.3 indiv. wire trap^{-1} (Tukey: $p < 0.017$). Spawning small males (6–8 cm) and females (7–8 cm) were caught first time in 2010–2011 in both sections, which indicated decreased size at maturation.

In 2008 when the perch removal started, the size distributions in the late summer gillnet catches in IVA_NS changed clearly towards younger size classes as compared with the previous year's size distribution (Fig. 4) (Kolmogorov-Smirnov: $D_{92,84} = 0.503$, $p < 0.001$) but in IVA_SS this change was not significant (Fig. 5). In IVA_NS, the strong year-class 2008 (4–5 cm) appeared in the gillnet catch already during the same summer, but in IVA_SS, it did not recruit to gillnet catch until 2009 (peak in 6–7 cm size classes). The intensive perch removal in spring 2011 flattened the size distribution in the gillnet catch in the following summer in IVA_SS (Kolmogorov-Smirnov: $D_{127,54} = 0.463, p < 0.001$). In IVA_NS, the strong year-class 2010 recruited to the gillnet catch in 2012 which was seen as the peak in 7–8 cm size classes (Kolmogorov-Smirnov: $D_{55,248} = 0.242$, $p = 0.010$). In IVA_SS, other strong year-classes seemed not to be developed and there were no significant changes in the size distributions. NPUE (indiv. gillnet night^{-1}) of large individuals (≥ 16 cm) in IVA_NS decreased clearly from 3.0 in 2007 to 1.1 in 2008 (Generalized mixed linear model, main effect of year: $F_{8,95} = 4.08$, $p = 0.005$, Tukey-Kramer's test for pairwise comparisons: $p = 0.003$) but after that the increase was statistically insignificant. In IVA_SS, a significant decrease in NPUE of large perch was recorded during the study period (linear regression: $F_{1,7} = 29.989$, slope = –0.074, $r^2 = 0.811$, $p = 0.001$).

The percentage of females in wire trap catch of spawning time in May was < 10% in 2007 in both lake sections (Fig. 6). In 2008–2009,

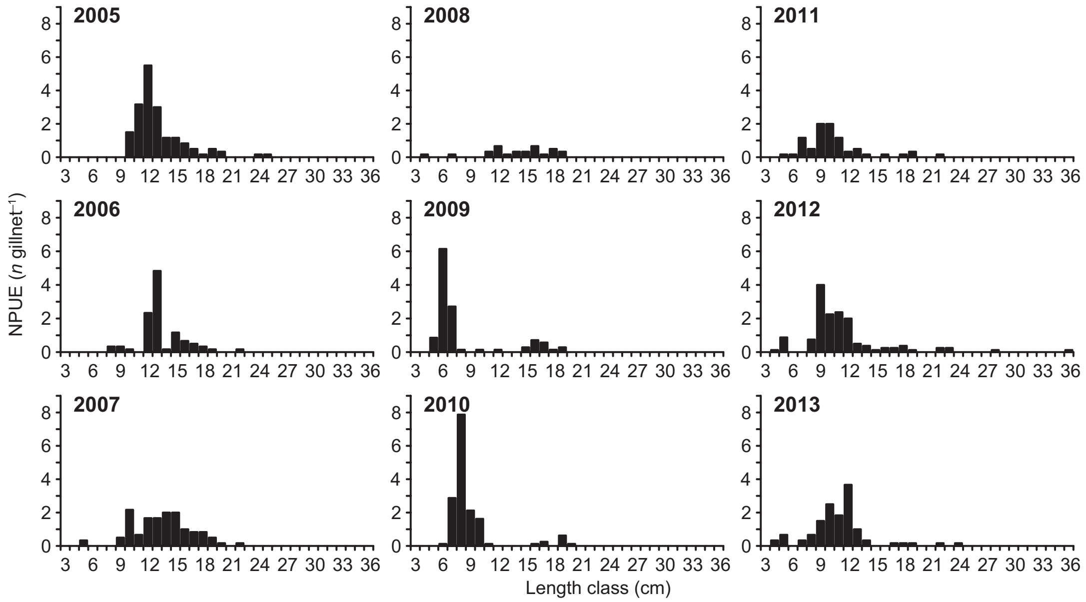

Fig. 5. Length frequency distributions of perch in gillnet catches during late summers in 2005–2013 in IVA_SS.

the corresponding percentages were 14%–18% in IVA_NS and 18%–21% in IVA_SS. In 2010, the percentage of females increased sharply from the previous year in both lake sections and was 28.3% in IVA_NS (Pearson's χ^2_1 = 39.381, $p < 0.001$) and 41.3% IVA_SS (Pearson's χ^2_1 = 58.096, $p < 0.001$). The subsequent decrease resulted in the female proportion of ca. 20% in both sections in 2012 (Pearson's χ^2_1 = 34.038, $p < 0.001$ and χ^2_1 = 55.937, $p < 0.001$ for IVA_NS and IVA_SS, respectively). The highest female proportions in 2010 coincided with the high number of small (< 10 cm), mature females in the trap catches (26.7% and 40.4% of the total catches in IVA_NS and IVA_SS, respectively). Thereafter, the share of < 10 cm females decreased drastically in both sections, to the level of 5% in 2012. The female percentage in gillnet catches was clearly higher than that in wire trap catches (Fig. 6).

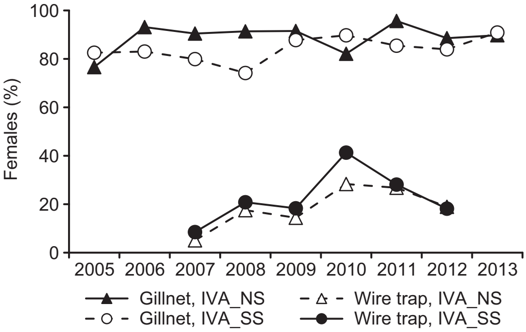

Fig. 6. Female percentages (in total number of perch individuals caught) in gillnets and wire traps in IVA_NS and IVA_SS.

Perch growth and production

Perch growth was slow in Iso Valkjärvi (Fig. 7) and slower in IVA_SS than in IVA_NS (repeated measures ANOVA main effect of lake section: $\chi^2_{1,53142}$ = 10.55, $p = 0.001$. On average, 1-, 3-, 5- and 7-year-old perch were 5.9, 11.7, 14.8 and 15.8 cm long (TL) in IVA_NS, and 5.4, 9.9, 11.8, and 11.9 cm long (TL) in IVA_SS (Bonferroni: $p < 0.001$, in all cases). Females grew faster than males in both sections (Bonferroni: $p < 0.001$, in both cases). The growth rate of the year-class 2005 increased in 2012 in IVA_NS and in 2011–2012 in IVA SS as compared with the growth of this year-class in five previous years (Bonferroni: $p < 0.001$, in all cases). Instead, the average length of the year-class 2007 stopped increasing in both basins and was not higher in 2012 as compared with that in 2011 (Bonfer-

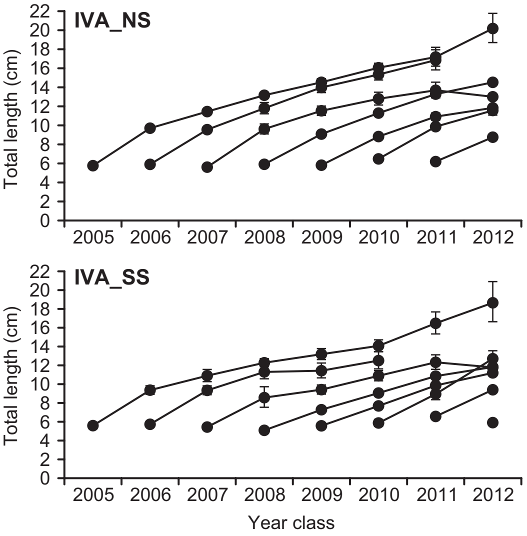

Fig. 7. Growth of perch year-classes 2005–2012 in IVA_NS and IVA_SS. Error bars are 95% confidence limits.

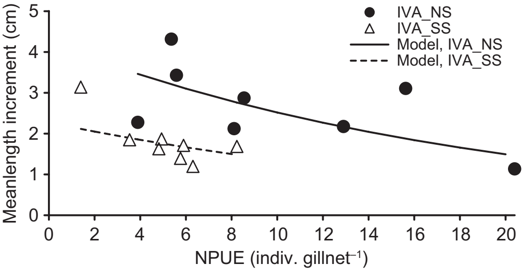

Fig. 8. Average length increment of perch in IVA_NS and IVA_SS in relation to perch density expressed as gillnet NPUE (indiv. gillnet^{-1}) in late summer. The length increments are age-group-weighted (ages 1–7 years) values during the whole growth season. The curves represent the ANCOVA model estimates.

roni: $p > 0.010$, in all cases) indicating that the fast growing individuals of this year-class were removed in fishing. In the years when perch density was low according to gillnet NPUE, the average length increment of all age classes was relatively high (ANCOVA effect of NPUE: $F_{1,13} = 9.41$, $p = 0.009$) indicating density-dependent growth (Fig. 8). Thus, perch growth responded positively when removal fishing was intensive enough to decrease the perch density in the lake. The responses of different age groups to density changes were not significantly different.

The perch production first decreased but then increased substantially in both sections after the start of the perch removal (Table 5). In IVA_NS, the perch production was initially higher, and its decrease was slighter and recovery faster than in IVA_SS. The production per biomass (*P*/*B*) increased especially in IVA_NS during the last years of the study (Table 5). On average *P*/*B* was higher in IVA_NS than in IVA_SS. The total mortality in IVA_NS increased after perch fishing started (Table 5).

Fecundity, egg size and egg production

GSI in female perch was 6.6%–29.6% (mean = 18.6%). GSI was not dependent on female length and there were no significant between-year or between-section differences. The relation between total fecundity and female length differed significantly among the years but not between the lake sections (ANCOVA effect of length × year: $F_{1,135} = 8.58$, $p = 0.004$; length × lake section: $F_{1,135} = 3.49$, $p = 0.064$). According to this model, fecundity in smaller size classes (< 12 cm in IVA_SS, and < 16 cm in IVA_NS) was higher in 2008 than in 2011, whereas the corresponding fecundity in larger size classes increased and was higher in 2011 than in 2008 (Fig. 9). When comparing the lake sections, smaller perch (< 17 cm in 2008 and < 10 cm in 2011) had higher fecundity in IVA_NS, whereas fecundity in the larger size classes was higher in IVA_SS.

Egg dry weight increased with female length (ANCOVA effect of female length: $F_{1,135} = 26.72$, $p < 0.001$; Fig. 9). Egg dry weight of 16 cm females was on average 27% greater than that of 10 cm females. The relation between female length and egg dry weight was significantly different among the years (ANCOVA main effect of year: $F_{1,135} = 22.89$, $p < 0.001$) and between the lake sections (ANCOVA main effect of lake section: $F_{1,135} = 11.02$, $p = 0.001$). In 2008, eggs were on average 23% heavier in relation to female length than in 2011. In IVA_SS, egg weight in relation to female length was on average 14% greater than in IVA_NS. In 2011 in IVA_SS, small females seemed to produce heavier eggs than large ones, but this difference was not significant.

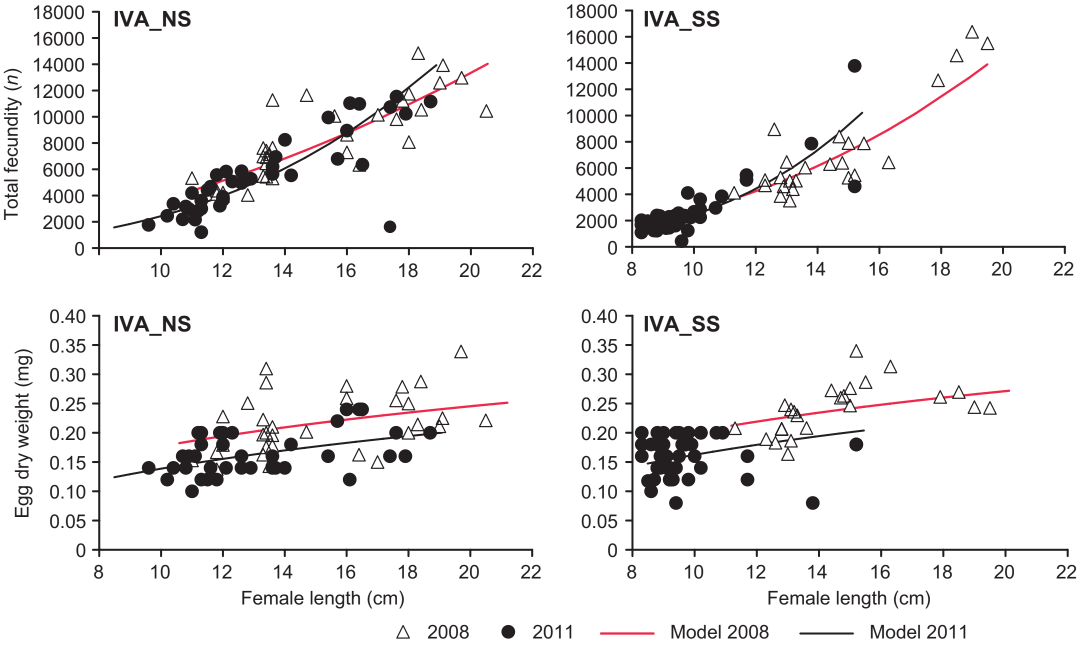

Fig. 9. Total fecundity and egg dry weight in relation to the length of female perch in IVA_NS and IVA_SS in the years 2008 and 2011. The curves represent the ANCOVA model estimates.

Because of the responses in perch densities, size structure, fecundity and egg dry weight, the estimated total amount and average size of produced eggs changed from 2008 to 2011 (Fig. 10). The total amount of produced eggs increased by 14% and 9% in IVA_NS and IVA_SS, respec-

Table 5. Yearly production rates (P, kg ha^{-1}), production per biomass values (P/B), instantaneous total mortality (Z), annual survival (S), annual mortality rate (A) and harvest rate of the estimated spring density (H) estimated of perch populations in the two lake sections in 2007–2012. For IVA_SS, Z, S, A and H were estimated separately for < 16 cm and ≥ 16 cm perch due to the fishing procedure. Z could not be estimated for all years.

	2007	2008	2009	2010	2011	2012
IVA_NS						
P	13.08	12.84	8.54	24.96	16.66	19.22
P/B	0.20	0.37	0.29	0.68	0.43	0.41
Z	0.62	0.57	0.90	0.37	1.39	–
S	0.54	0.57	0.41	0.69	0.25	–
A	0.46	0.43	0.59	0.31	0.75	–
H	–	0.56	0.72	0.30	0.57	–
IVA_SS						
P	7.03	10.05	3.46	1.99	19.66	22.33
P/B	0.17	0.25	0.16	0.24	0.52	0.41
$Z_{<16\text{ cm}}$	–	1.00	0.61	–	0.67	–
$Z_{\geq 16\text{ cm}}$	–	0.84	0.65	0.97	–	–
$S_{<16\text{ cm}}$	–	0.37	0.54	–	0.51	–
$S_{\geq 16\text{ cm}}$	–	0.43	0.52	0.38	–	–
$A_{<16\text{ cm}}$	–	0.63	0.46	–	0.49	–
$A_{\geq 16\text{ cm}}$	–	0.57	0.48	0.62	–	–
$H_{<16\text{ cm}}$	–	0.49	0.95	0.38	0.61	–
$H_{\geq 16\text{ cm}}$	–	0.05	0.20	0.06	0.02	–

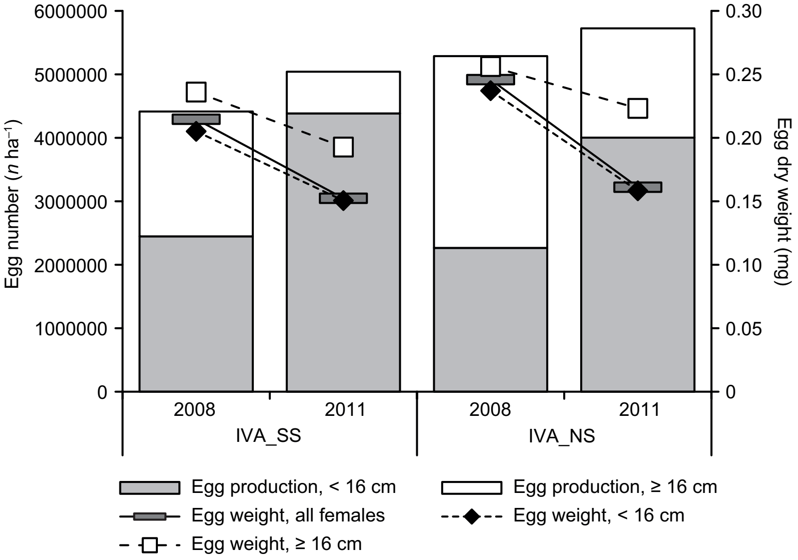

Fig. 10. Total number and average dry weight of perch eggs produced in IVA_NS and IVA_SS in the years 2008 and 2011.

tively. In IVA_NS in 2008, 44% of the eggs were produced by large individuals, in 2011 only 13%. In IVA_SS, the share of eggs produced by large individuals decreased less than in IVA_NS, from 57% in 2008 to 30% in 2011. Because of both smaller amount of large females and decreased egg weight in relation to female size, the average dry weight of eggs decreased from 2008 to 2011 by 29% and 34% in IVA_NS and IVA_SS, respectively. In 2011, the average sizes of eggs were still 5% (all females) and 14% (large females) greater in IVA_SS than in IVA_NS.

Discussion

The results of our study support earlier observations that intensive fishing can cause pronounced changes in the life-history traits of the harvested population (Brodeur *et al.* 2001, Paukert & Willis 2001, Olsen *et al.* 2004, Pukk *et al.* 2013, Kokkonen *et al.* 2015). As hypothesized, non-selective fishing resulted in a rapid decrease in the average size and age of the spawning perch stock. This could be seen in the removal catches, in the mark and recapture estimates and in the gillnet catches. As expected, we found decreased size at maturity and some indication of younger age at maturity. The fishing affected the sex structure of the perch stock as it resulted in an increased proportion of females. In the section where large individuals were not targeted (IVA_SS), the aforementioned responses appeared later and not as strongly as had been hypothesized. As we assumed, the average size of spawned eggs decreased especially in the section where also large individuals were targeted (IVA_NS). We observed the expected increase in fecundity only in large females. Contrary to what was expected, the total amount of spawned eggs did not decrease because the number of mature females increased considerably. The changes in the total abundance of perch were only temporary and both the density and biomass increased in two years to a level higher than before fishing.

Perch compensated the removal very efficiently, and a strong year-class was produced already in the same year the effective fishing started. This is most likely due to decreased juvenile mortality because of lower predation and competition. A large part of the adult population spawned before being removed and likely there were no significant reductions in the amount of eggs produced in the first removal spring. Reduced cannibalism and intra-specific competition due to the adult removal probably reduced the juvenile mortality and enabled the production of a strong year-class. Cannibalism may have been more important factor in juvenile mortality than piscivory by pike, because the density of pike increased in both lake sections during the study period without suppressing small perch density. In perch, juvenile mortality due to cannibalism can be high in small lakes with few fish species and cannibalism can regulate the year-class strength (Persson *et al.* 2000). However, the observed differences in pike density might have contributed to the differences in responses between the lake sections. The estimated, relatively low pike density and subsequent predation may have partly enabled the formation of a dense, slow-growing year-class 2008 in IVA_SS, whereas in IVA_NS pike predation may have reduced the strength of the year-class 2008 enabling fast growth and early maturation. In the later years in IVA_NS, the strong year-class 2008 retained high egg production, and this, and reduced cannibalism due to low number of piscivorous perch, resulted in other strong year-classes in the later years despite the increased intra-cohort food competition and pike density. The initially-higher pike density and predation in IVA_NS may have caused the reduction in old perch abundance from 2007 to 2008 before the removal fishing, but the higher pike predation did not prevent perch abundance from reaching as high a level as in IVA_SS after the perch removal started. The strong year class in 2008 was not related to high water temperature as the year 2008 was colder than average (Table 1).

One important factor in increased fry production was the observed decreased age at maturation in females, which enabled effective reproduction even though the number of large females decreased. Before the removal fishing in 2007–2008, the perch abundance estimates were quite comparable to the estimates prior to the collapse in 1992 in the same lake (1800 indiv. ha^{-1} in both sections; *see* Rask *et al.* 1996) which can be regarded as a stable-state density in the lake. The earlier documented collapse of perch population (> 95%) in 1992 in IVA_NS (Rask *et al.* 1996) did not result in similar immediate compensation by fry production probably due to stronger loss of spawning stock. Documented collapses of perch stocks due to fishing alone are rare and likely the species is quite tolerant to exploitation due to low size and age at maturity and plasticity in environmental requirements (Craig 2000). Despite this, Pukk *et al.* (2013) showed that when (commercial) fishing is very intensive, this alone can cause collapse of the perch population. Often, the observed decline of exploited perch stock is related to changes in environment, e.g. eutrophication (Nilsson *et al.* 2004, Eckmann *et al.* 2006). In this study, the removal decreased the perch population only in the first year, but after that the abundances increased to a higher levels than before fishing or in the early 1990s (Rask *et al.* 1996). The high water temperature in 2010 in IVA_NS may have also contributed to the increased perch abundance. In the other years of perch removal or in IVA_SS, the water temperatures were not higher after than before the removal fishing and the observed increase in perch abundance was most likely not related to temperature.

Although the perch population abundance seems to tolerate quite well fishing-induced changes, many exploited perch populations have shown similar responses in size and age structure as in this study, thus indicating vulnerability to growth overfishing (i.e. fish are harvested at a smaller size than the optimum that would produce the maximum yield per recruit). In Matsalu Bay, Estonia, the mean age and length of perch population decreased considerably during the intensive exploitation in 1991–1999 (Pukk *et al.* 2013). Intensive recreational ice fishing decreased the amount of large perch in Äimäjärvi, a lake in Finland, after the perch stock had recovered from fish kills (Ruuhijärvi *et al.* 2010). The perch growth was slower and mean size smaller in the moderately exploited Finnish *versus* the weakly fished Russian part of Karjalan Pyhäjärvi (Auvinen 1987). In Finnish lakes Koitere and Kolovesi, the mean size of perch increased considerably after fishery regulation (Auvinen *et al.* 2004, 2005). It seems that large and old perch individuals are more vulnerable to (Kurkilahti 1999) or targeted by fishing (Lewin *et al.* 2006) and thus the typical response to fishing is decreased mean size and age. In this study, the decrease in the mean size was very steep in IVA_NS even though large perch were not specifically targeted. This might indicate high vulnerability of large individuals to fishing due to high activity and long swimming distances (Kurkilahti 1999). However, the abundance of large individuals decreased also in IVA_SS , probably because of decreased recruitment to large size classes. Intensive fishing of < 16 cm perch apparently decreased the amount of recruits reaching 16 cm length, as only slight growth response was observed.

We observed a clear decrease in size at maturation and, in IVA_NS, some evidence of lowered age at maturation in both males and females. Pukk *et al*. (2013) found the reduction in age at sexual maturity only in males in Matsalu Bay, Estonia, whereas in our study, females responded even stronger than males. This may be due to the harsher oligotrophic environment in our study lake than in the Baltic Sea, forcing females to allocate resources in reproduction at the earlier age (Stearns and Crandall 1984). Females and males often confront different selective pressures regarding the trade-off between growth and reproduction, therefore the consequences of changes in environmental conditions can be different for males and females (Rennie *et al*. 2008). Environmental stress affects the activity and growth of perch females more than of males (Horppila *et al*. 2011, Estlander and Nurminen 2014), and thus response in the timing of maturity can differ between sexes. Our results indicate that fisheries-induced response in perch maturation size and age can be very rapid, appearing even in two years after the onset of fishing. This might make the species vulnerable to fishing-induced evolution (Kokkonen *et al*. 2015).

The observed increase in the proportion of females both in spawning population and in late summer gillnet catches was understandable, as the majority of the removal catch were males. This was due to the higher activity of male perch during spawning (Craig 2000) resulting in higher catchability in the passive gears that we used. Another explanation for the increase of relative abundance of females is that in the first strong year-class (2008), produced in the year when fishing started, females maturated at the same time as males, not a year later as in the years before the fishing. This was seen as the steep increase in the female proportion in the wire-trap catch in 2010 and reduction thereafter, when removal catch started to include more females. The earlier maturation of females can be seen as a response to released resources, or predation threat, or population reaction to sudden catastrophic collapse (Stearns and Crandall 1984), and is one likely reason for the quick recovery of perch populations in this study. However, there seemed to be a trade-off in earlier maturation as young females were reproducing with relatively low nutritive state which can be seen in decreased egg dry weight in relation to size. Water temperature in the preceding year may also affect positively the ability of a female to invest in spawning but the water temperature in 2007 was not higher than average, and the relatively high water temperature in 2010 should have increased maternal investment but the opposite occurred. Therefore, removal fishing was the most likely reason for the observed changes in maternal investment. We are not aware that this kind of fishing-related decrease in the quality of reproductive products within a size-class has been documented earlier. Some studies have, however, indicated that decrease in average size of spawners can result in decreased quality of reproductive products (Heyer *et al*. 2001, Olin *et al*. 2012). In several fish species, recreational fishing is found to be selective towards large females (Lewin *et al*. 2006) and this kind of harvesting may have strong and long-lasting effect on targeted populations.

Perch production eventually clearly exceeded fishing pressure in IVA_NS and was at the same level as removal catch in IVA_SS. The increased production was rather due to increased abundance than faster growth rate as also observed by Horppila *et al*. (2010) in the lakes in the same region. According to the increased P/B ratio, perch stock almost doubled its capacity to renew population biomass in IVA_NS, indicating good ability to withstand exploitation (Charnov 1993), which partly explained the quick recovery of perch population densities. In both lake sections, the P/B ratio was initially lower than the value reported for yellow perch (0.53, Randall and Minns 2000) but after the removal fishing in IVA_NS, the P/B ratio reached a considerably higher level (0.7). Based on these results, the P/B ratio in perch populations of oligotrophic lakes is rather low in pristine conditions but it does not mean that those populations are vulnerable to catastrophic events.

The growth of older perch increased in one year-class (2005) but decreased in another (2007). This might be due to the increased food resources (perch fry) that favoured individual growth in the older year-class with larger individuals which had better ability to utilize fish fry as compared with the individuals of the younger year-class (Persson *et al*. 2000). The reason for the observed decrease in average length in the year-class 2007 in later years might be explained by growth-selective fishing that first removed the faster growing individuals, while the remaining individuals could not utilize the increased resources for faster growth. Growth-selective fishing will most probably have evolutionary effects on the targeted fish population in the long term (Kokkonen *et al*. 2015). The growth of perch was density-dependent in both lake sections and thus the growth was faster in the years fishing was effective enough to reduce the perch density. Density-dependent growth was also found by Rask *et al*. (1996) in the same lake. However, as the perch density increased in both lake sections after the short decline, the growth response of perch to fishing was temporary and in the latest year perch growth was slower than before the fishing in IVA_NS. The perch population collapse (> 95%) in 1992 in the same lake (in the section IVA_NS) induced much stronger growth response (Rask *et al*. 1996) which was related to increased availability of macroinvertebrate food and resulted in a 5-cm increase in the mean length of the remaining perch, to > 20 cm, in summer 1993. However, differences in food resources did not explain the observed difference in growth rate between the lake sections in the present study. The growth of perch in IVA_SS was clearly slower than in IVA_NS during the whole study period despite the lower perch density. Before the start of fishing, the estimated biomass of zooplankton and macroinvertebrates were higher in IVA_SS, thus differences in available food resources do not explain the pro-fishing growth-differences (L. Nurminen unpubl. data). After 3 years of removal fishing, the macroinvertebrate biomass was higher in IVA_NS than in IVA_SS thus indicating higher food resources for perch. Decreased time spent on feeding due to predation risk is also a possible reason for slower growth of small perch, since large perch were more abundant in IVA_SS (Estlander and Nurminen 2014). Contrary, pike density was much lower in IVA_SS as compared with the other lake section, but as stated before for mortality of small perch, pike predation may be a less important factor than cannibalism. Since perch growth is temperature-dependent (Rask *et al*. 2014), one explanation for the growth differences could be the difference in average temperature between the lake sections: IVA_SS was slightly colder than IVA_NS. Genetic differences can also play a role, as the population in IVA_NS collapsed in 1992 (Rask *et al*. 1996) and the individuals that remained may have been a phenotype characterised by fast growth rate (Pukk *et al*. 2013). Whatever the determining factor for the between-lake-section difference in the growth is, the initial faster growth rate in IVA_NS partly enabled the observed earlier recovery of perch abundance after removal fishing started.

Our experimental fishing was not intensive enough to cause recruitment overfishing, which should result in < 35% of spawning potential ratio (population fecundity in the exploited circumstances in relation to the un-exploited circumstances; *see* Goodyear 1993). The reduced egg production due to a decrease in numbers of large individuals was overcompensated by increased density of young spawners. In addition, the fecundity of large individuals increased. This was probably due to increased food resources (perch fry) for large individuals enabling higher energy allocation to reproduction. The observed reduced dry weight of eggs in relation to female size may be due to the trade-off between egg quality and egg number. In the situation of increased mortality and reduced interspecific competition, the number of offspring is more important than their quality (Engen *et al*. 2014). Our study revealed that unselective fishing can rapidly change the perch population structure towards small size classes thus decreasing the share of large reproducers and the average size of eggs produced and probably decreasing genetic variability in the offspring.

In conclusion, this study suggests several compensation mechanisms that pristine perch populations have against sudden and strong fishing pressure: reduced size and age at maturation, increased share of females in the spawning stock, higher growth rate when fish density drops, reduced cannibalism when large individuals are scarce, and higher fecundity of large individuals. These mechanisms explain the fast recovery of perch populations despite the intensive fishing. The important mechanism reducing long-term population renewal ability was the decreased quality and variety of produced eggs due to a decrease in numbers of large females. This might induce evolutionary changes in the long term, reducing the population ability to withstand intensive fishing. The supposed growth-selectivity of fishing which should decrease the share of fast-growing individuals in the targeted population, is another factor that might eventually have evolutionary consequences. When exploiting perch stocks, the demographic structure of populations has to be retained to ensure the existence and reproduction of large females and large genetic variability. According to this study, maximum length limit for perch does not prevent a decrease in average size due to growth overfishing, if fishing pressure is high. However, it delays the truncation in size distribution and enables the reproduction of large females thereby sustaining high genetic variability and better quality of offspring. For sustainability, management with length-limitation should always be accompanied by restrictions in catch rates if angler density is high in relation to the stock size.

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