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The effects of age-at-maturation on the parameters of a biphasic Lester growth model in *Sander lucioperca*

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An accurate estimation of growth is crucial for any fish species that is a target in fishery. We applied a biphasic Lester model for pikeperch (*Sander lucioperca*) population that is a slow-growing one. In this model, age at maturity divide the growth into immature and matuire phases. Logistic regression models showed that both age and length were significant in males and females when using maturity as a dependent variable, and both of these variables differed between sexes. To estimate how the changes in used age at maturity affect the Lester model parameters, the effects of ages from 10% to 90% probability of maturity were analysed. The gonadosomatic index of males (max. 2%) and females (max. 8.6%) was used to select Lester models that also gave low estimates for the investments in reproduction (g). Low g values were found in the Lester models for ages from 60% to 90% probability of maturity in males, and from 30% to 70% in females.

Introduction

The somatic growth of fish can be classified into two distinctive phases: a pre-maturity phase in which all excess energy is used for somatic growth, and a post-maturity phase in which some or all excess energy is allocated for reproduction (Day & Taylor 1997). Lester *et al.* (2004) developed a growth model based on these two phases: the growth of immature fish can be estimated with a linear model, while the growth of mature fish follows that of the von Bertalanffy growth model. Compared with the von Bertalanffy model, the Lester model is a mechanistic growth model that allows the amount of energy invested in reproduction to be estimated. Moreover, Shuter *et al.* (2005) showed that this investment is also linked to other life history variables such as total mortality. However, when applying the Lester model, it is very important to assess the age at maturity correctly, because this divides the model into two categories.

The species studied by us is the slow-growing pikeperch (*Sander lucioperca*) in Sahajärvi, a lake in Finland (Vinni *et al.* 2009, Milardi *et al.* 2011). Olin *et al.* (2018) showed that the slow-growing female pikeperch matured at an older age but smaller size than the fast-growing ones. Aside from the growth rate, the first females matured three years earlier than the last ones (Olin *et al.* 2018). Thus, assigning one age at maturation to the entire population is not accurate, as it rarely fits all individuals (Lehtonen 1987, Raikova-Petrova & Živkov 1998, Lappalainen *et al.* 2003, Ruuhijärvi *et al.* 2005). This can be problematic when applying the biphasic Lester model. This model is usually estimated only for females (e.g. Shuter *et al.* 2005, Rennie & Venturelli 2015, Honsey *et al.* 2017) or for pooled sexes (Vainikka *et al.* 2017), while studies of male growth are rare (Enberg *et al.* 2008, Rennie *et al.* 2008).

The immature phase ends when the investment in reproduction begins. In pikeperch, the intense feeding period before the onset of the reproductive cycle, i.e. May–July, seems crucial for pikeperch to store enough energy to be able to start and complete their entire gametogenesis (Teletchea *et al.* 2009). Gonads mature during the late autumn or winter (Teletchea *et al.* 2009, M'Hetli *et al*. 2011, Fontaine *et al*. 2015) and spawning takes place the following spring (April to June, depending on the latitude) (Lappalainen *et al.* 2003). Hence, the investment in reproduction already started during the previous year, which should be taken into account when determining the age at maturity (Wilson *et al.* 2018).

Here, the main aim was to analyse the growth of pikeperch with the Lester model. Pikeperch in Sahajärvi is known to be an exceptionally slow-growing one (Milardi *et al*. 2011) compared with other pikeperch populations (Lappalainen & Malinen 2002). The fitting of Lester model requires information on age at maturity. Therefore, our first aim was to estimate age and length at maturation for each sex separately, and then for the pooled sexes. We were particularly interested in determining whether length is an important factor in the onset of maturation in males, as has been found for female pikeperch (Olin *et al.* 2018). If length is a significant factor in maturation, and not all pikeperch mature at the same age (Lehtonen 1987, Raikova-Petrova & Živkov 1998, Olin *et al.* 2018), we hypothesized that the mature pikeperch will be either longer or heavier than immature pikeperch of the same age. Our second aim was to evaluate how setting the age at maturity affects the parameters in the Lester model. This was done first by separating the sexes, and then by pooling all available data.

Material and methods

Pikeperch sampling, age determination and maturity

Pikeperch samples were collected with different types of gear in 2016 and 2017 from Sahajärvi, a lake in Finland. A seine was used to collect the samples for maturity estimations before the pikeperch spawning (May 2017), whereas the growth was estimated from samples collected with several types of gear, mainly gillnets (Table 1).

In the laboratory, pikeperch were measured (total length, TL, mm) and weighed (g), and 10–20 scales were taken from the area between the lateral line and pelvic fin. Scales were used in age determination and to back-calculate lengths. The age determinations were also compared with those based on the sagittae otoliths, especially in larger and older pikeperch. Otoliths were roasted with flame to coffee-brown and broken into two parts across the nucleus. Then the age was determined from otolith's broken surface (Tolonen *et al*. 1999). Since roughly half of

Table 1. Number of pikeperch (*n*) caught with different gear. Mesh sizes from knot to knot.

Gear	Dimensions	Period	*n*
Seine	Height 7 m, wing 150 m each with mesh size 10 mm and 6 mm in bag	May 2017	206
Nordic gillnet	Twelve 1.5 m × 2.5 m panels with mesh sizes of 5, 6.25, 8, 10, 12.5, 15.5, 19.5, 24, 29, 35, 43, and 55 mm	August 2017	148
Gillnet	Length 30 m, height 1.8 m, mesh sizes between 20 and 60 mm	July, September 2017	83
Gillnet, wire trap	Different types	June–November 2016, April–May 2017	23

the pikeperch were caught during the growing season, the back-calculated lengths at the end of the previous growing season were used in the growth models, i.e. only one back-calculated length per pikeperch was used. Length-at-age was back-calculated using the Fraser-Lee procedure (Bagenal & Tesch 1978). A value of 44 mm was used as the intercept (Ruuhijärvi *et al.* 1996).

Maturity was evaluated from the progonads of the pikeperch. Sex of the immature pikeperch (TL > 100 mm) was assessed from tissue slices on glass viewed under an optic microscope (Antila *et al.* 1988, Winkler *et al.* 1989, Hermelink *et al.* 2011). Mature individuals were sexed by dissection and direct observation of gonads. In mature or maturing females, the progonad is filled with maturing eggs; in males, the progonad shows no recognizable elements. The gonadosomatic indices (GSI = gonad weight/(total weight – gonad weight)) of both males and females were estimated from pikeperch caught in May (Table 1).

Statistical analyses

A *t*-test was used to compare mean lengths and weights between immature and mature pikeperch at the ages when some pikeperch were still immature and some mature. These analyses were done for each sex separately. Since the hypothesis was one-sided, i.e. mature pikeperch are either longer or heavier than the immature ones at the same age, we used a one-sided *t*-test. If the variances in the tested groups were equal, we used a pooled *t*-test; if they were unequal, a Satterthwaite *t*-test with the corresponding degrees of freedom was used instead (SAS 2015).

The age and length at maturity of pikeperch were estimated using logistic regression (SAS 2015). Maturity was estimated only for pikeperch caught in May just before the spawning (Table 1), because this is the best season to estimate maturity from gonads. These analyses started with pooled data to test whether the interaction between age and sex (male $n = 64$, female $n = 104$) is significant. Below are two examples of the logistic regression models used:

$$y = \frac{\exp(a + b \times \text{age})}{1 + \exp(a + b \times \text{age})}, \tag{1}$$

$$y = \frac{\exp(a + b \times \text{age} + c \times \text{length} + d \times \text{age} \times \text{sex})}{1 + \exp(a + b \times \text{age} + c \times \text{length} + d \times \text{age} \times \text{sex})}, \tag{2}$$

where y is maturity, expressed as 0 in immature and as 1 in mature pikeperch, age is in full years, length is the total length in mm, sex is a categorical variable, and a, b, c, and d are constants. In addition to the interaction between age and sex (Eq. 2), the interaction between length and sex was also analysed. Since both interactions (age × sex, or length × sex) were significant, sexes were also analysed separately. In these separate analyses, Firth's penalized likelihood approach was applied due to the separability and small sample size (Heinze 2006, SAS 2015). The use of logistic regression models enabled the probability of maturity to be estimated for those pikeperch whose maturity could not be determined based on sex, age, and length.

Logistic regression gives estimates of age or size at which a certain proportion of individuals are mature, which is different from maturation reaction norms (Barot *et al.* 2004). With the method used here, it is impossible to evaluate whether the observed maturation is the first in that individual's lifetime, or if it already matured in previous years (Barot *et al.* 2004).

Lester model

The Lester model was first fitted using data for males and females separately, and then using pooled data. This model describes immature growth with a linear model (Eq. 3), and mature growth as a von Bertalanffy (Eq. 4) curve:

$$l_t = h(t - t_1), \text{ when } t \leq T, \text{ and} \tag{3}$$

$$l_t = l_\infty(1 - \exp(-k(a - t_0))), \text{ when } t > T \tag{4}$$

where

$$l_\infty = \frac{3h}{g}, \tag{5}$$

$$k = \log\left(1 + \frac{g}{3}\right), \tag{6}$$

$$t_0 = \frac{\log\left(1-\left(\frac{g\left(T-t_1\right)}{3}\right)\right)}{\log\left(1+\frac{g}{3}\right)}, \quad (7)$$

where l_t is the length at age t, h is the juvenile growth rate (length per unit time), g is the investment in reproduction, t_1 is the hypothetical age at length 0, T is the last immature age, l_∞ is the asymptotic length, k is the von Bertalanffy (Brody) growth coefficient, and t_0 is the von Bertalanffy (adult) hypothetical age at length 0.

The Lester models were fitted using the R code that follows the one given in Wilson *et al.* (2018: appendix S1). In the R code, the analyses started by the division of data into immature and mature groups. Next, a linear growth model was fitted to the immature-pikeperch data (Eq. 3). This gave estimates for h and t_1. These two parameters were then used in fitting the growth for the mature group (Eqs. 5, 6 and 7). Because the age at maturity was known and estimated with logistic regression, only the investment in reproduction (g) was unknown (Eq. 5). The immature linear and mature growth joins at age T.

Generally, the age at 50% probability or maturity is chosen at the population level (Minte-Vera *et al.* 2016, Honsey *et al.* 2017). Here, the Lester models were fitted using age at 10% (A_{10}) to 90% (A_{90}) probability of maturity in T based on the logistic regressions first by sexes separately, and then for the pooled all data. Preliminary analyses showed that the selected age at maturity changes the Lester model parameters, and especially when the full age changes, for example from 4 to 5 years, because then the division of pikeperch into immature and mature groups also changes. In pikeperch, the investment in reproduction is already initiated during the previous year of the actual spawning, and the lower range (A_{10}–A_{40}) was selected to account for this. The use of lower range also reduces the risk of assigning mature pikeperch into the immature group, while the higher range (A_{60}–A_{90}) reduce the risk of assigning immature fish into the mature group. However, it was clear that the correct grouping into immature and mature groups based on one age at maturity was impossible, because there was no single age, which could be used to assign all the pikeperch to correct groups (Table 2).

Evaluation of fits of logistic regression and Lester models

The fits of logistic regression and Lester models were evaluated with Akaike's information criterion (AICc). AICc values can be used only in

Table 2. The number of immature and mature pikeperch by sexes in relation to length class and age in May 2017.

	Male		Female		Total n
	Immature (n = 39)	Mature (n = 25)	Immature (n = 75)	Mature (n = 29)	
Length class (TL, mm)					
100–150	6	–	13	–	19
151–200	13	–	23	–	36
201–250	9	–	15	–	24
251–300	9	10	16	4	39
301–350	2	11	8	10	31
351–400	–	3	–	10	13
401–450	–	1	–	5	6
Age (years)					
2	8	–	17	–	25
3	19	–	29	–	48
4	1	–	7	–	8
5	11	12	19	9	51
6	–	9	3	7	19
7	–	4	–	9	13
8	–	–	–	3	3
9	–	–	–	1	1

comparison between models that had the same data. AICc was calculated as:

$$\mathrm{AIC} = -2\log L + 2p, \tag{8}$$

$$\mathrm{AICc} = \frac{\mathrm{AIC} + 2p(p+1)}{(n-p-1)}, \tag{9}$$

where log$L$ is the log-likelihood, p is the number of parameters in the model, and n is the number of observations. Smaller AICc values indicate better fits. AICc values are not estimated in logistic models in which Firth's penalized likelihood approach is used (*see* https://cran.r-project.org/web/packages/brglm/index.html; Nagashima & Sato 2017).

In the Lester models, AICc values cannot be used to evaluate the fits over the whole range of age at maturity analysed here. Even though the same pikeperch data were divided into immature and mature groups (either males, females, or the pooled data), the groups were the same only when compared models and ages were within one full year; for example, when A_{30} = 4.64 years and A_{50} = 4.95 years as in males. If this was not the case, then the models between A_{50} and A_{60} (5.10 years) cannot be compared based on AICc values. Therefore, the Lester model fits and parameters were evaluated also using three independent estimates described below.

The first independent estimate was based on GSI values for males and females in May (Table 1) and the Lester model parameter g (Lester *et al*. 2004). GSI and g are not comparable directly, because the energy content per unit wet weight of gonad is typically higher than that of somatic tissue. According to Lester *et al*. (2004, and references therein), the energy ratio of gonad to soma on a wet weight basis varies between 1.24 and 2.0 in different fish species. They found the best match with the energy ratio value of 1.73 between gonads and soma, which was also used here for both sexes.

The mean GSI for the mature group in the pooled data was calculated in the following way: if sex was known, then the maximum GSI of that sex was used as an individual estimate, and if sex was unknown, then the mean value for both sexes was used.

The second estimate was based on the difference in lengths between calculated length with the linear immature growth model in the Lester model and that based on the logistic regression model where length was an independent variable (l_{diff}%). First, length at selected age at maturity was evaluated based on immature growth:

$$l_{A_x} = \mathrm{intercept} + h \times T, \tag{10}$$

where x is the selected percentage from 10% to 90%, T is the used age at maturity, and h is the corresponding growth rate (length per unit time) of immature pikeperch. The difference in lengths (l_{diff}%) between immature length (l_{A_x}) and logistic model was calculated as:

$$l_{\mathrm{diff}}\% = \frac{(l_{A_x} - l_x)}{l_{A_x}}, \tag{11}$$

where l_{A_x} is the length (TL, mm) from Eg. 10, l_x is the estimated length (TL, mm) at the age of used probability of maturity at A_x based on logistic regression, and x the selected percentage from 10% to 90%.

The third estimate was the percentage of pikeperch assigned into correct group based on their observed maturity in May. Thus, when pikeperch were divided into immature or mature group based on their age, the percentage of pikeperch that were in the correct group was calculated as:

$$\mathrm{Corr}\% = ((n_{\mathrm{C\_imm}} + n_{\mathrm{C\_mat}})/(n_{\mathrm{C\_imm}} + n_{\mathrm{C\_mat}} + n_{\mathrm{W\_imm}} + n_{\mathrm{W\_mat}})) \times 100, \tag{12}$$

where n_{C} is the number of pikeperch in the correct group, n_{W} is the number of pikeperch in the wrong group, imm = immature group, and mat = mature group.

The observed estimate of GSI was used as the first criterion to select a group of Lester models with similar g value. After this, the AICc values were used, and if there were no differences in AICc values, then l_{diff}% and Corr% were applied.

Results

Maturity and GSI

In Sahajärvi, the youngest mature pikeperch were 5 years old; all 7-year-old and older pikeperch were mature in May 2017 (Table 2). Significant differences (one-sided *t*-test) were found in mean lengths and weights between immature and mature pikeperch at ages 5 and 6 (Table 3). As hypothesized, the mature pikeperch were longer (mean 19 mm and 38 mm for males and females, respectively) and heavier (57 g and 107 g for males and females, respectively) than the immature ones at age 5. These differences were much greater in females at age 6; this could not be tested in males, as there were no immature males at age 6 (Table 3).

Age and length at maturation differed between sexes when sex was used as a categorical variable in logistic regressions (models 1–4, e.g. length × sex M; Table 4). Models fitted for length

Table 3. Mean lengths (TL, mm) and weights (g) of male and female pikeperch at age 5 and 6 in relation to maturity in May 2017 in Sahajärvi. Minimum and maximum lengths and weights are in parentheses, and *p* values are from one-sided *t*-test. Var = variance between groups, eq. = equal variances, uneq. = unequal variances, df = degree of freedom.

Sex	Age	Size	Immature	*n*	Mature	*n*	Var	df	*p*
Male	5	length	280 (250–320)	11	299 (256–342)	12	eq.	21	0.034
Male	5	weight	175 (122–266)	11	232 (136–367)	12	eq.	21	0.014
Male	6	length	–	–	342 (291–401)	11	–	–	–
Male	6	weight	–	–	371 (187–648)	11	–	–	–
Female	5	length	282 (234–332)	19	320 (291–385)	9	eq.	26	0.002
Female	5	weight	185 (93–308)	19	292 (178–500)	9	uneq.	10.5	0.007
Female	6	length	303 (272–322)	3	362 (302–427)	7	eq.	8	0.035
Female	6	weight	230 (173–282)	3	446 (226–760)	7	eq.	8	0.043

Table 4. Model parameters in logistic regressions using maturity (0 = immature, 1 = mature) as the dependent variable, and age and length as the independent variables. In models 1–4, sex is a categorical variable (M = male, F = female). SE = standard error. Immature males *n* = 39, mature males *n* = 25, immature females *n* = 75, mature females *n* = 29.

Model	Sex	Variable	Parameter estimate	SE	X^2	$p > X^2$	AICc
1	M & F	Intercept	–16.83	3.22	27.39	< 0.001	84.4
		length	0.057	0.11	27.52	< 0.001	
		length × sex M	0.003	0.01	7.48	0.006	
2	M & F	Intercept	–13.95	2.98	21.96	< 0.001	88.8
		age	2.71	0.58	21.75	< 0.001	
		age × sex M	0.12	0.05	4.70	0.030	
3	M & F	Intercept	–21.70	4.65	21.74	< 0.001	73.5
		age	1.57	0.60	6.77	0.009	
		length	0.046	0.13	12.00	< 0.001	
		length × sex M	0.003	0.01	6.63	0.010	
4	M & F	Intercept	–22.09	4.78	21.40	< 0.001	73.0
		age	1.67	0.61	7.44	0.006	
		length	0.045	0.13	11.72	< 0.001	
		age × sex M	0.18	0.07	7.00	0.008	
5	M & F	Intercept	–19.53	4.13	22.40	< 0.001	79.1
		age	1.62	0.58	7.69	0.006	
		length	0.037	0.11	10.77	0.001	
6	M & F	Intercept	–13.40	2.84	22.35	< 0.001	91.7
		age	2.59	0.55	21.79	< 0.001	
7	M & F	Intercept	–14.76	2.65	31.01	< 0.001	91.0
		length	0.050	0.09	30.75	< 0.001	

showed better fits than age based on the variable X^2 and AICc values in logistic regressions (model 1 *vs*. 2, model 6 *vs*. 7; Table 4). When males and females were analysed separately using only age or length, both of these variables were significant independent variables (models 8, 9, 11, 12; Table 5). Males were both shorter and younger at maturation than females (Fig. 1). The calculated values for A_{50} and L_{50} were 5.0 years (95%CI (confidence interval) = 3.6–7.2 years) and 279 mm (95%CL = 205–360 mm TL) in males (models 8 and 9; Table 4), and 5.4 years (95%CI = 3.7–6.3 years) and 310 mm TL (95%CI = 240–380 mm TL) in females (models 11 and 12; Table 5). In females, both age and length were significant in the same logistic regression model (model 13; Table 5 and Fig. 2), whereas this was not the case in males (model 10; Table 5).

The mean GSI of males was 0.004 (or 0.4%) (SD = 0.004, min–max = 0.001–0.020) in May. There was no linear relationship between weight and GSI in males ($r^2 = 0.01$, $p > 0.05$, df = 30). The mean weight of mature males was 277.5 g (SD = 122.5, min–max = 115–648). In females, the mean GSI was 0.054 (SD = 0.023, min–max = 0.010–0.086) and the mean weight of mature females was 420.8 g (SD = 207.8, min–max = 178–936). GSI increased towards heavier females (GSI = 0.023 + 7.38E-5 × body weight (g); $r^2 = 0.43$, $p < 0.001$, df = 29) (Fig. 3).

Growth based on the Lester model

Males and females

The observed maximum GSI was 0.02 in males and when multiplied by 1.73, the calculated estimate of g was 0.035, suggesting low investments in reproduction in males. The models between A_{60} and A_{90} gave smaller investments in reproduction (g = 0.20–0.24) than those of A_{10} to A_{50} in which high values of g were observed (0.31–0.38) (Table 6). Within the models from A_{60} to A_{90}, AICc values were almost identical and l_{diff}% was the lowest with A_{80} (Fig. 4 and Table 6).

In females, different ages at maturity divided the data into three groups of models (A_{10}–A_{20}, A_{30}–A_{70}, and A_{80}–A_{90}; Table 6). The maximum observed GSI in females was 0.086 and when multiplied by 1.73, the direct calculated estimate for g was 0.15, suggesting low investments in reproduction also in females. The models between A_{30} and A_{70} gave the lowest g values, and within these models, the lowest AICc was found for A_{70} (Fig. 5a), while the lowest g and l_{diff}% was for A_{30} (Fig. 5c).

Pooled data

Different ages at maturity divided the pikeperch

Table 5. Logistic regression results with maturity as the dependent variable, and age and length as independent variables, separately for each sex. Firth's penalized likelihood approach was used in all models. SE = standard error. Immature males n = 39, mature males n = 25, immature females n = 75, mature females n = 29.

Model	Sex	Variable	Parameter estimate	SE	X^2	$p > X^2$
8	Male	Intercept	–13.56	5.18	6.85	0.009
		age	2.74	1.03	7.14	0.008
9	Male	Intercept	–13.22	3.70	12.77	< 0.001
		length	0.047	0.13	12.69	< 0.001
10	Male	Intercept	–16.38	5.70	8.25	0.004
		age	1.48	0.98	2.29	0.130
		length	0.032	0.18	3.23	0.072
11	Female	Intercept	–11.22	2.60	18.65	< 0.001
		age	2.07	0.50	17.46	< 0.001
12	Female	Intercept	–16.08	3.83	17.59	< 0.001
		length	0.052	0.13	17.24	< 0.001
13	Female	Intercept	–18.79	4.77	15.49	< 0.001
		age	1.04	0.50	4.29	0.038
		length	0.042	0.15	8.41	0.004

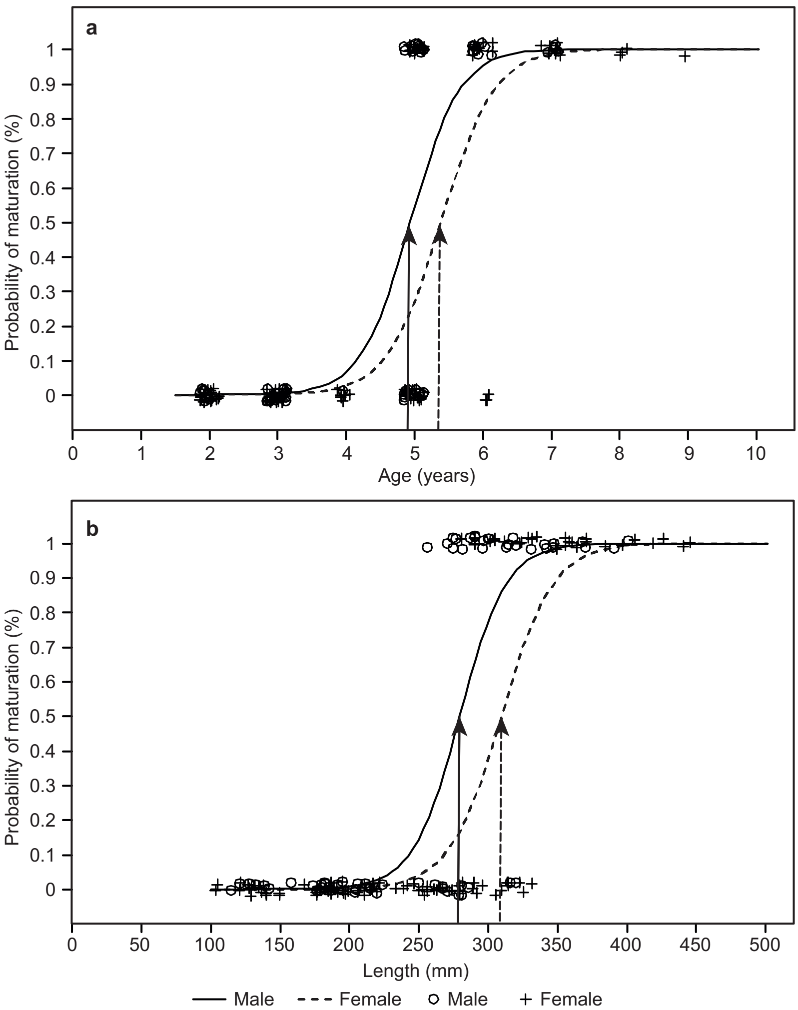

Fig. 1. Probability of maturity in relation to (**a**) age and (**b**) length. Arrows indicate age and length at 50% probability of maturity.

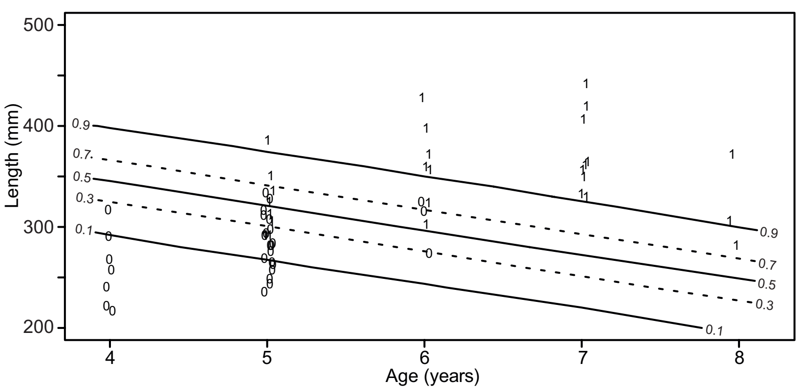

Fig. 2. Isopleths (0.1–0.9) of the probability of maturity in females in relation to age and length (model 13; Table 5). 0 = immature female in May, 1 = mature female in May. Note that age markers are jittered.

into three groups of the same data in both immature and mature groups. These were from A_{10} to A_{30}, from A_{40} to A_{80}, and A_{90} (Table 7). The mean GSI was calculated for the pikeperch in the mature group by using the observed maximum GSI values of 0.086 for females, 0.020 for males, and 0.053 for pikeperch with unknown sex. The calculated mean GSI was 0.050 in

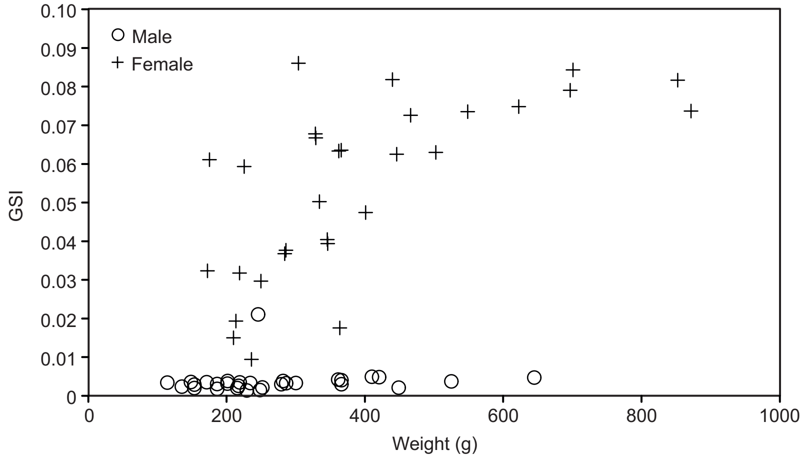

Fig. 3. Gonadosomatic index (GSI) in relation to weight (g) without gonads in females (open circles) and in males (pluses) in May.

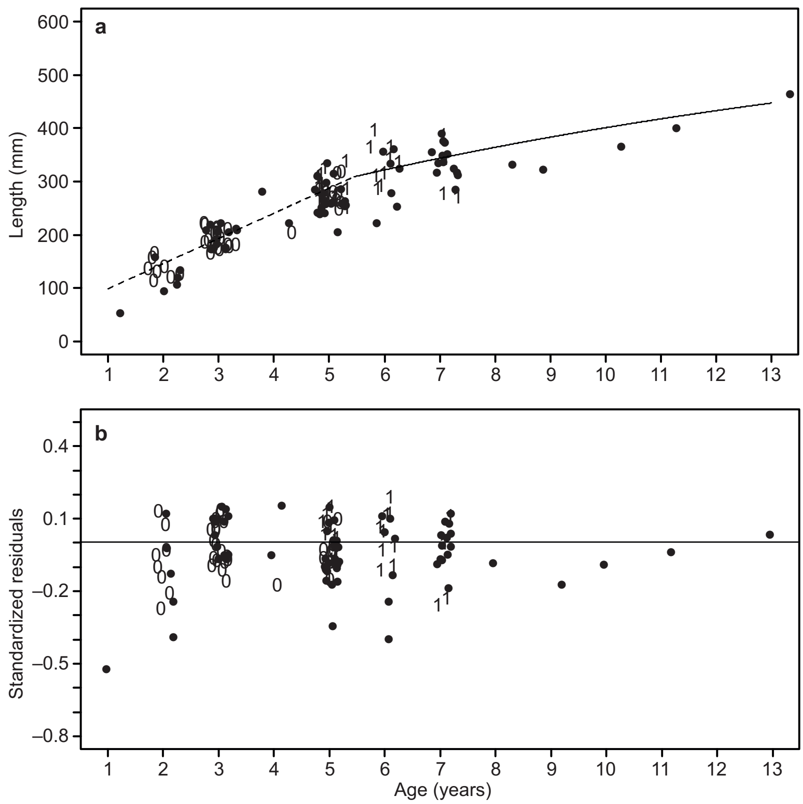

Fig. 4. Lester model fit in age at 80% probability of maturity for males in Sahajärvi. Immature growth is marked with a broken line; mature growth with a solid line. (**a**) Age at 80% probability is 5.45 years, asymptotic length is 643 mm TL, and investment in reproduction (*g*) is 0.22. (**b**) Corresponding standardized residuals from Lester model **a**. 0 = immature male, 1 = mature male, • = male pikeperch with unknown maturity. Note that age markers are jittered.

mature pikeperch in models from A_{10} to A_{30}, 0.057 in A_{40} to A_{80}, and 0.059 in A_{90}. When these mean GSI values were multiplied with 1.73, the estimated values for g were all close to 0.10. The lowest g values were found in Lester models from A_{40} to A_{80} (g = 0.16–0.20). Within these, the lowest AICc and l_{diff}% values, and the highest Corr% were with A_{80} (Fig. 6).

Comparisons of Lester models

Differences between the length at age estimates in those Lester models that gave small investments in reproduction and the observed mean lengths at age were small (Table 8). In males, the Lester model using A_{80} gave length estimates that were between –7 and 9 mm TL of the observed

Table 6. Lester model parameters (h, t_1, g, and l_∞) for different ages at probability (A_x, from 10% to 90%) of maturity (T) for males and females. In all growth models, parameters h and g were significant. If T was 4.36, then pikeperch that were ≤ 4 years old and ≥ 5 years old were grouped into immature fish and mature fish, respectively. n_1 = the total number of pikeperch in the group, n_2 = the number of pikeperch in the correct group, and n_3 = the number of pikeperch in the incorrect group based on maturity in May 2017. l_{diff}% = length difference at age T between lengths based on linear model (intercept and h) and that based on the logistic regression model; in males, l_x (*see* Eq. 11) was calculated with model 9 (Table 5), and in females with model 12 (Table 5). AICc values can be compared only between the models that have the same data. CI = confidence interval.

	A_x	T	Immature							Mature				
			Intercept	h (95%CI)	t_1 (95%CI)	n_1, n_2, n_3	r^2	l_{diff}%	AICc	g (95%CI)	l_∞	n_1, n_2, n_3	AICc	Corr%
Male	10	4.15	18.5	59.8 (32.0–87.7)	–0.31 (–10.17–9.55)	50, 28, 0	0.75	12.8	449	0.31 (0.28–0.35)	575	83, 25, 11	822	89.4
	20	4.44	18.5	59.8 (32.0–87.7)	–0.31 (–10.17–9.55)	50, 28, 0	0.75	12.5	449	0.34 (0.30–0.38)	530	83, 25, 11	827	89.4
	30	4.64	18.5	59.8 (32.0–87.7)	–0.31 (–10.17–9.55)	50, 28, 0	0.75	11.9	449	0.36 (0.31–0.40)	503	83, 25, 11	834	89.4
	40	4.80	18.5	59.8 (32.0–87.7)	–0.31 (–10.17–9.55)	50, 28, 0	0.75	11.6	449	0.37 (0.32–0.42)	486	83, 25, 11	842	89.4
	50	4.95	18.5	59.8 (32.0–87.7)	–0.31 (–10.17–9.55)	50, 28, 0	0.75	5.8	449	0.38 (0.32–0.44)	474	83, 25, 11	852	89.4
	60	5.10	51.3	47.3 (30.8–63.7)	–1.09 (–5.20–3.03)	95, 39, 12	0.85	1.7	881	0.20 (0.15–0.25)	719	38, 13, 0	393	88.5
	70	5.26	51.3	47.3 (30.8–63.7)	–1.09 (–5.20–3.03)	95, 39, 12	0.85	1.0	881	0.21 (0.15–0.26)	683	38, 13, 0	393	88.5
	80	5.45	51.3	47.3 (30.8–63.7)	–1.09 (–5.20–3.03)	95, 39, 12	0.85	0.3	881	0.22 (0.16–0.28)	643	38, 13, 0	392	88.5
	90	5.75	51.3	47.3 (30.8–63.7)	–1.09 (–5.20–3.03)	95, 39, 12	0.85	–0.7	881	0.24 (0.18–0.31)	584	38, 13, 0	392	88.5
Female	10	4.36	17.3	60.6 (40.8–80.4)	–0.28 (–7.00–6.43)	96, 53, 0	0.77	4.9	879	0.28 (0.23–0.32)	656	95, 29, 22	987	78.8
	20	4.75	17.3	60.6 (40.8–80.4)	–0.28 (–7.00–6.43)	96, 53, 0	0.77	7.2	879	0.31 (0.26–0.36)	583	95, 29, 22	992	78.8
	30	5.02	44.3	50.4 (35.1–65.6)	–0.88 (–5.00–3.2)	139, 72, 9	0.81	1.2	1327	0.17 (0.11–0.23)	893	52, 20, 3	555	88.5
	40	5.23	44.3	50.4 (35.1–65.6)	–0.88 (–5.00–3.2)	139, 72, 9	0.81	1.8	1327	0.19 (0.13–0.25)	814	52, 20, 3	554	88.5
	50	5.42	44.3	50.4 (35.1–65.6)	–0.88 (–5.00–3.2)	139, 72, 9	0.81	2.3	1327	0.20 (0.14–0.27)	743	52, 20, 3	553	88.5
	60	5.62	44.3	50.4 (35.1–65.6)	–0.88 (–5.00–3.2)	139, 72, 9	0.81	2.9	1327	0.23 (0.15–0.30)	671	52, 20, 3	551	88.5
	70	5.83	44.3	50.4 (35.1–65.6)	–0.88 (–5.00–3.2)	139, 72, 9	0.81	3.5	1327	0.25 (0.17–0.33)	599	52, 20, 3	550	88.5
	80	6.09	42.9	50.8 (36.6–64.9)	–0.84 (–4.36–2.67)	157, 75, 13	0.84	4.5	1517	0.30 (0.21–0.40)	508	34, 13, 0	365	87.5
	90	6.49	42.9	50.8 (36.6–64.9)	–0.84 (–4.36–2.67)	157, 75, 13	0.84	5.5	1517	0.38 (0.25–0.50)	405	34, 13, 0	366	87.5

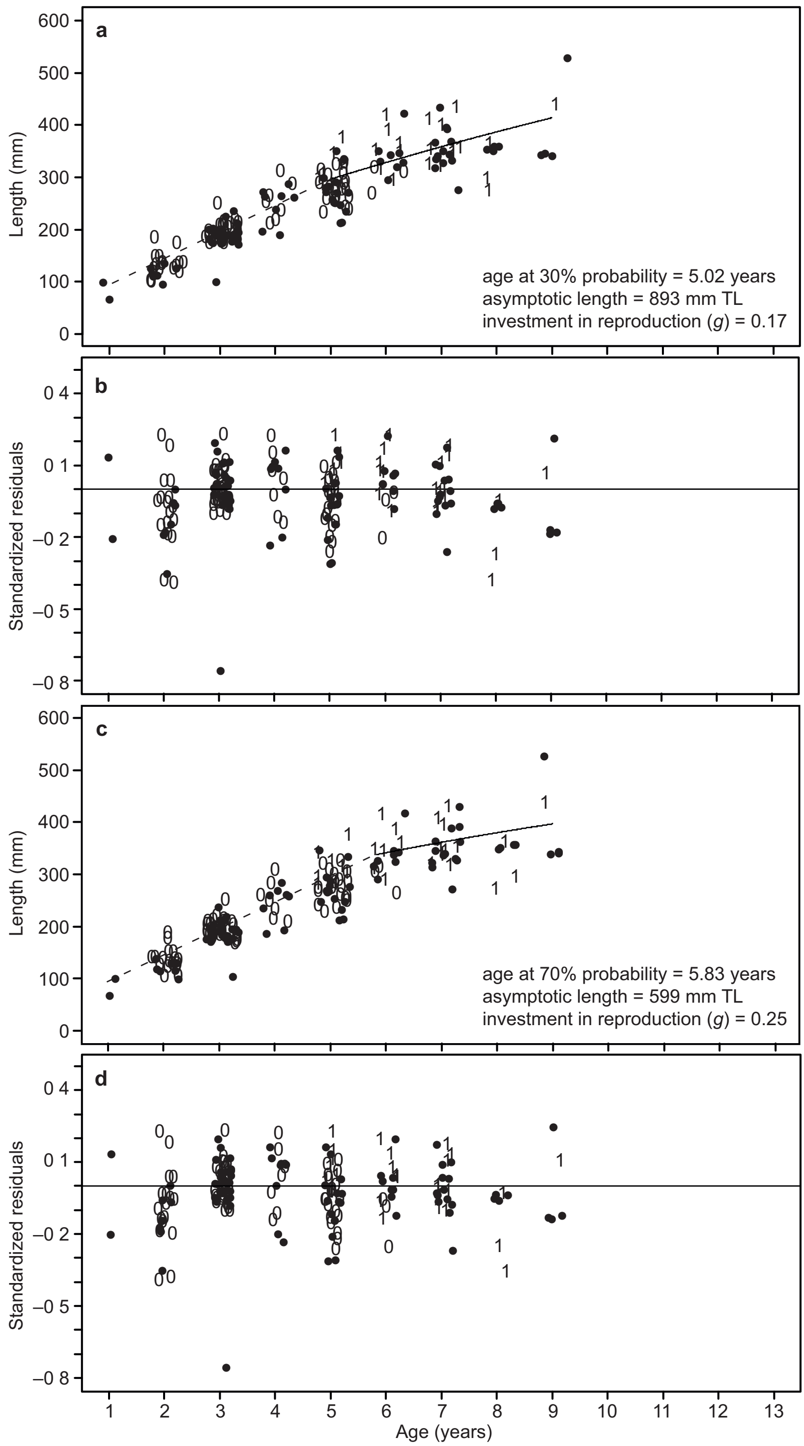

Fig. 5. Lester model fits in age at (**a**) 30% and (**c**) 70% probability of maturity for females; dashed line = immature growth, solid line = mature growth with a solid line. (**b**) Standardized residuals from Lester model in **a**. (**d**) Standardized residuals from Lester model in **c**. 0 = immature female, 1 = mature female, • = female pikeperch with unknown maturity status. Note that age markers are jittered.

mean lengths at ages between 2 and 7 years (n > 9, Table 8). In females, the length estimates for A_{70} were between –13 and 10 mm of observed mean lengths at ages between 2 and 7 years, while in the pooled data, the A_{80} gave length estimates that were between –14 and 13 mm

Table 7. Lester model parameters (h, t_1, g, and l_∞) for different ages at maturity (T) (from 10% to 90%) in pooled data. All linear growth models were highly significant (h and r^2) as were the investments in reproduction (g) in the non-linear part. If T was 4.36, then pikeperch that were ≤ 4 years old and ≥ 5 years old were grouped into immature and mature fish, respectively. n_1 = the total number of pikeperch in the group, n_2 = the number of pikeperch in the correct group, and n_3 = the number of pikeperch in the wrong group based on maturity in May 2017. l_{diff}% = length difference at age T between lengths based on linear model (intercept and h) and that based on the logistic regression model; l_x (*see* Eq. 11) was calculated in pooled pikeperch data with model 7 (Table 5). AICc values can be compared only between the models that have the same data. CI = confidence interval.

A_x	T	Immature							Mature				
		Intercept	h (95% CI)	t_1 (95%CI)	n_1, n_2, n_3	r^2	l_{diff}%	AICc	g (95%CI)	l_∞	n_1, n_2, n_3	AICc	Corr%
10	4.33	10.2	62.6 (52.1–73.1)	−0.16 (−4.08–3.75)	213, 94, 0	0.82	10.2	1916	0.29 (0.26–0.31)	651	207, 54, 33	2144	68.3
20	4.64	10.2	62.6 (52.1–73.1)	−0.16 (−4.08–3.75)	213, 94, 0	0.82	10.7	1916	0.31 (0.28–0.34)	609	207, 54, 33	2161	68.3
30	4.85	10.2	62.6 (52.1–73.1)	−0.16 (−4.08–3.75)	213, 94, 0	0.82	11.0	1916	0.32 (0.29–0.35)	587	207, 54, 33	2180	68.3
40	5.02	37.3	51.1 (43.1–59.1)	−0.73 (−2.95–1.42)	315, 124, 21	0.87	1.84	2948	0.16 (0.13–0.19)	950	105, 33, 3	1124	76.9
50	5.18	37.3	51.1 (43.1–59.1)	−0.73 (−2.95–1.42)	315, 124, 21	0.87	1.80	2948	0.17 (0.14–0.20)	907	105, 33, 3	1122	76.9
60	5.34	37.3	51.1 (43.1–59.1)	−0.73 (−2.95–1.42)	315, 124, 21	0.87	1.77	2948	0.18 (0.14–0.21)	865	105, 33, 3	1121	76.9
70	5.51	37.3	51.1 (43.1–59.1)	−0.73 (−2.95–1.42)	315, 124, 21	0.87	1.66	2948	0.19 (0.15–0.24)	821	105, 33, 3	1121	76.9
80	5.71	37.3	51.1 (43.1–59.1)	−0.73 (−2.95–1.42)	315, 124, 21	0.87	1.45	2948	0.20 (0.16–0.24)	773	105, 33, 3	1120	76.9
90	6.03	37.1	51.2 (43.1–59.2)	−0.73 (−2.77–1.32)	352, 127, 37	0.87	1.46	3364	0.22 (0.17–0.279)	702	68, 17, 0	733	64.4

of observed lengths between 1 and 8 years (Table 8).

The Lester models showed small differences in lengths at age between A_{10} and A_{90} (Fig. 7). The maximum difference in Lester models that gave low investments in reproduction was 17 mm TL (in females between A_{30} and A_{70} at

Table 8. Length at age based on Lester models compared with observed mean lengths at age in males, females and pooled data. Age at maturity (T) is based on the selected models (*see* Tables 6 and 7). Lengths at age 1–5 and 6–9 are for immature and mature growth, respectively. SE = standard error. All lengths are in mm TL.

Age	T (males)				Mean length	SE	n
	5.10	5.26	5.45	5.75			
1	99	99	99	99	65	–	1
2	146	146	146	146	137	5.5	13
3	193	193	193	193	200	3.3	33
4	240	240	240	240	245	26.1	3
5	288	288	288	288	286	4.0	45
6	316	319	322	328	329	11.2	16
7	341	342	344	347	346	9.0	17
8	364	364	364	365	345	–	1
9	386	385	383	381	335	–	1

Age	T (females)					Mean length	SE	n
	5.02	5.23	5.42	5.62	5.83			
1	95	95	95	95	95	96	16.1	2
2	145	145	145	145	145	135	3.9	24
3	195	195	195	195	195	200	2.8	55
4	246	246	246	246	246	259	9.0	15
5	296	296	296	296	296	291	5.4	43
6	328	330	333	337	341	350	9.8	18
7	358	359	359	360	361	369	8.3	22
8	387	385	384	382	380	348	14.6	7
9	414	410	406	402	397	413	36.7	5

Age	T (pooled data)					Mean length	SE	n
	5.02	5.18	5.34	5.51	5.71			
1	88	88	88	88	88	82	7.3	13
2	139	139	139	139	139	132	2.0	83
3	191	191	191	191	191	201	2.0	98
4	242	242	242	242	242	256	8.0	19
5	293	293	293	293	293	287	3.0	102
6	327	328	331	333	337	345	7.6	37
7	358	359	360	362	364	362	6.7	40
8	389	389	389	389	390	377	13.8	13
9	417	416	415	414	413	400	32.7	6

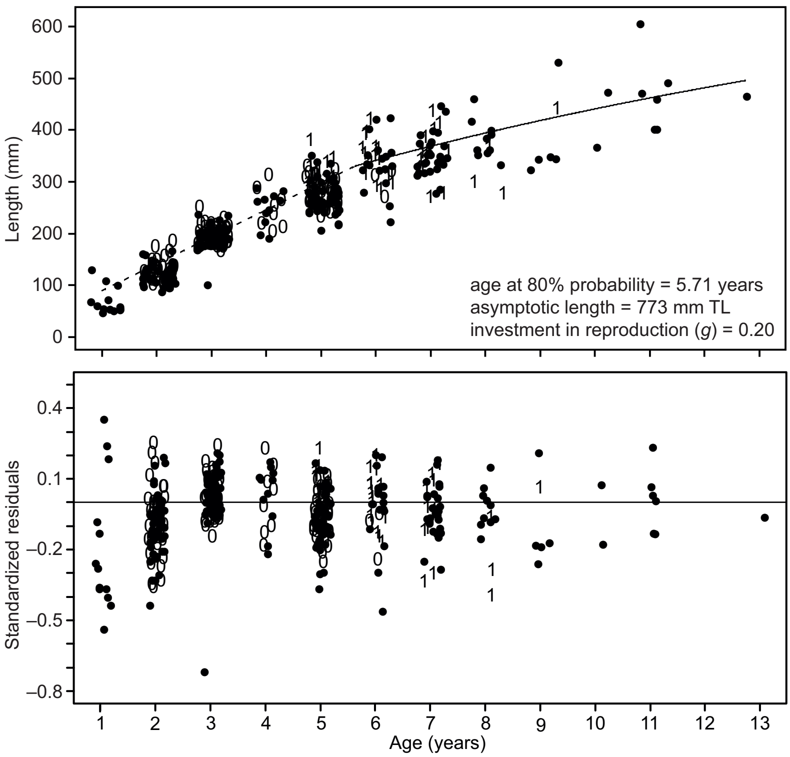

Fig. 6. (**a**) Lester model fits in age at 80% probability of maturity for pooled pikeperch, and (**b**) standardized residuals from Lester model. Dashed line = immature growth, solid line = mature growth 0 = immature male or female, 1 = mature male or female, • = pikeperch with unknown maturity status. Note that age markers are jittered.

age 6; Table 8). However, the differences in asymptotic lengths were much larger in Lester models that gave low investments in reproduction. In males, the asymptotic lengths were between 719 mm and 584 mm TL in models from A_{60} to A_{90}, between 893 mm and 599 mm TL in A_{30} to A_{70} in females, and between 950 and 773 mm TL in A_{40} to A_{80} in the pooled data, respectively (Tables 6 and 7).

Discussion

The results showed that the onset of maturation in pikeperch depends on both age and length, and that these differed significantly between the sexes. The observed GSI values for both sexes were low, and these were used to select the Lester models that also gave low values of investments in reproduction (g). Low investments were found in Lester models in which the age at maturity varied between 5 and 6 years. In these models, the differences in mean lengths at age between different models were small, and were also small when compared with the observed mean lengths at age.

In Sahajärvi, the age at maturity was spread over two years, which seems typical for pikeperch in other lakes in Finland as well as in southern Europe (Raikova-Petrova & Živkov 1998, Lappalainen *et al.* 2003, Ruuhijärvi *et al.* 2005, Olin *et al.* 2018). In Sahajärvi, the estimated age at 50% probability of maturity of female pikeperch (5.4 years) was within the range that has been shown for six other lakes in Finland (4.2–6.9 years) (Olin *et al.* 2018). On the other hand, the length at 50% probability of maturity was smaller (male 279 mm TL, female 310 mm TL) than in other Finnish lakes (male 340–360 mm TL, female 403–460 mm TL) (Lehtonen & Miina 1988, Olin *et al.* 2018). In Sahajärvi, females at maturation were both older and longer than males at maturation, which seems to be typical for the *Sander* and *Perca* species (Scott & Crossman 1973, Raikova-Petrova & Živkov 1998, Rennie *et al.* 2008, Venturelli *et al.* 2010, Olin *et al.* 2018). In Europe, the age at maturity in both sexes of pikeperch was from

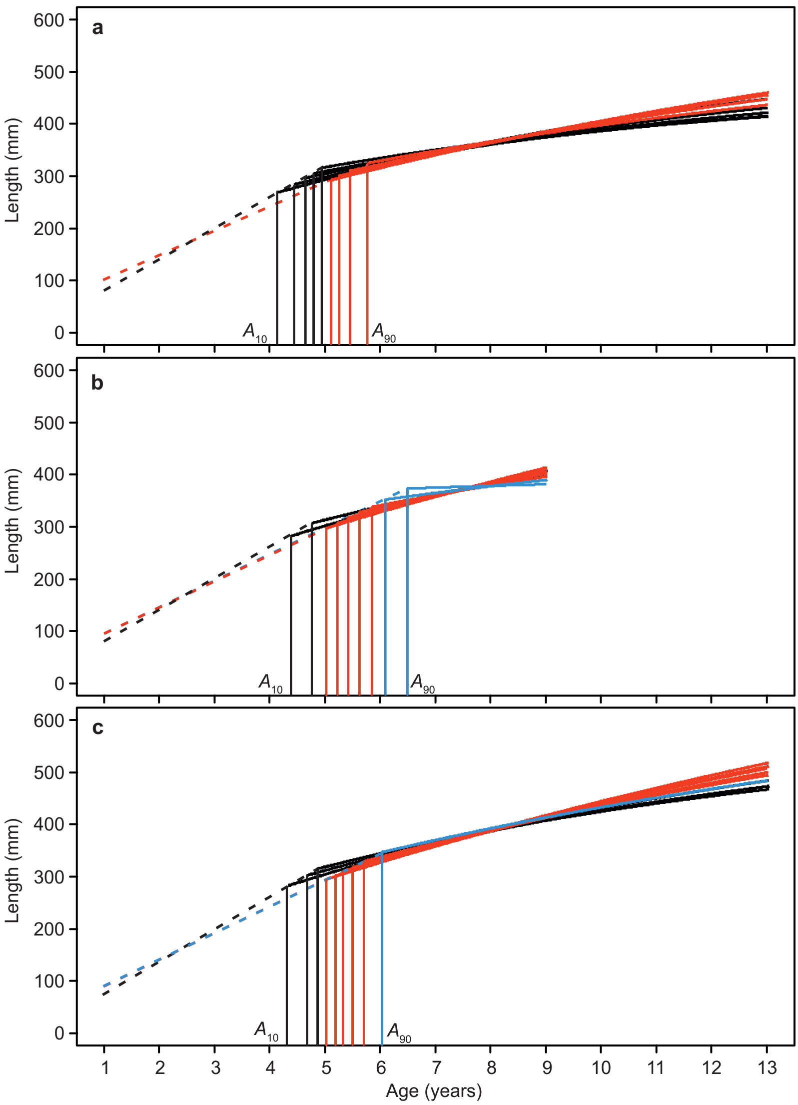

Fig. 7. Pikeperch growth based on Lester models in (**a**) males, (**b**) females and (**c**) pooled data with different age at probability of maturity (A_{10}–A_{90}). Horizontal lines indicate ages from 10% to 90% probabilities of maturity.

1 to 9 years, while the maximum age at maturity in females was 10 years. In southern Europe, where the growth of pikeperch was more rapid, the age at maturity was lower than in pikeperch that were closer to the northern distribution range (Raikova-Petrova & Živkov 1998). Similarly, in another *Sander* species, walleye (*Sander vitreus*), the growth was faster and the age at maturity was lower in warmer than in colder lakes (Venturelli *et al.* 2010).

In Sahajärvi, pikeperch growth was slow (Milardi *et al*. 2011), which is probably the reason for the observed smaller length at 50% probability of maturity than in other studies (Lehtonen & Miina 1988, Olin *et al.* 2018). In perch (*Perca fluviatilis*), the age at maturity was similar between populations showing normal and stunted growth, but the length at maturity was smaller in populations showing stunted growth (Heibo *et al.* 2005). The reasons for the slow growth of pikeperch in Sahajärvi are not known, but the abundance of small pikeperch has been very high (Milardi *et al*. 2011). Notably, a large part of the diet was non-piscine, which is uncharacteristic for the typically piscivorous pikeperch (Vinni *et al*. 2009, Milardi *et al*. 2011). Venturelli *et al*. (2010) showed that in populations of walleye that have experienced dramatic changes in abundances, there was an increase in the immature growth rate when the abundance was lower.

The best Lester models were selected based on the observed GSI in May and investments in reproduction (*g*). GSI values were low for both sexes in Sahajärvi, which have been observed also in other pikeperch populations, and were low when compared for example with perch (Uysal *et al*. 2006, M'Hetli *et al*. 2011, Fontaine *et al.* 2015). Therefore, the Lester models that gave low *g* values were selected. The lowest *g* values in Lester models were found with age at maturity from 5.10 to 5.75 years in males, and from 5.02 to 5.83 years in females. In these models, the investments in reproduction ranged from 0.20 to 0.24 in males, and from 0.17 to 0.25 in females. In the pooled data, the lowest *g* values between 0.16 and 0.20 were found for age at maturity between 5.02 and 5.71 years. Vainikka *et al.* (2017) showed similar *g* values, between 0.16 and 0.24, for the sex-pooled pikeperch data from six lakes in Finland.

The energy ratio value used here was based on that of females in the original articles reviewed by Lester *et al*. (2004). There are only few energy ratio estimates available for males. In yellow perch (*Perca flavescens*) males, the ratio value was 0.85 (the energy density of testes to the energy density of the whole fish (Rennie 2003)), and in salmon (*Salmo salar*) males 1.00 (Jonsson *et al*. 1991). Therefore, the used energy ratio of 1.73 could be too high for males, but this had no effects on the selection of the best Lester models, because the lowest *g* value was 0.20 in males. Notably, additional costs in reproduction come from guarding the eggs of pikeperch males in the nest after spawning. This behaviour ceases when the larvae are hatched (Lappalainen *et al.* 2003).

Fitting the Lester model requires knowledge of the age at maturity. Here, the best results were obtained with age at maturity between 5.45 and 5.83 years or with A_{70} in both males and females, and with A_{80} in the pooled data. The greatest hindrance for estimating the growth of mature fish was that the number of large and old pikeperch were low in our data (Minte-Vera *et al.* 2016). The lack of such data affects the estimation of the parameter that is probably the most interesting and has the highest importance (investment in reproduction), and affects the estimation of the asymptotic lengths.

The low number of old and large pikeperch in Sahajärvi is due to gillnet fishing. In many lakes in Finland, including Sahajärvi, recreational fishermen can use gillnets after purchasing required fishing permits. The minimum allowed mesh size of gillnets is 60 mm (knot to knot), while the minimum legal size limit of pikeperch is 420 mm TL. Gillnet fishing was suggested to be the cause for the low number of pikeperch larger than 420 mm in the lake (Milardi *et al.* 2011). The same was noted here, as the number of large (> 420 mm TL) was also low, which makes it difficult to estimate the growth of mature pikeperch. However, the growth of immature, juvenile pikeperch can be estimated more reliably, because the number of immature fish is generally high enough, and their abundance is not directly related to fishing that targets mature fish. Here, the best estimates of the immature growth rate per year was 47.3 mm TL in males, 50.4 mm TL in females, and 51.1 mm TL in the pooled data. These values are lower than estimated based on the Lester model in other Finnish lakes (55.6–97.1 mm TL) (Vainikka *et al.* 2017).

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