

1 Paper title: Density and temperature dependent growth of pikeperch (*Sander lucioperca*) in the
2 Archipelago Sea

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16
17 Abstract - In the Archipelago Sea, pikeperch (*Sander lucioperca*) is an important species in both
18 commercial and recreational fisheries. Pikeperch is caught mainly with small mesh size gillnets,
19 and annual fishing mortality is high. The possible effects of such fisheries, as well as temperature
20 or density on pikeperch growth have not been studied earlier. The first hypothesis of this study
21 was that the effect of temperature on growth is positive and that of density is negative. The
22 second hypothesis was that size-selectivity of gillnets causes the fast-growing individuals to be
23 caught at younger ages than the slow-growing ones. The results showed that temperature had a
24 significant positive effect on growth, and this was greater than the negative effect of year-class
25 density, which was also significant. The gillnet selectivity caused a difference of up to 60 mm in
26 back-calculated lengths in the fully recruited age groups within the same year class, between
27 pikeperch caught at age 6+ and age 9+. Thus, the Rosa Lee phenomenon caused by gillnet size-
28 selectivity led to the removal of faster growing specimens from the population at younger ages.
29 This can potentially cause underestimation of real growth, and thus, poor fishery management.

30
31 Keywords: Density-dependence / management / fishing mortality / size-selective fishing / Baltic
32 Sea

33 1 Introduction

34 Pikeperch (*Sander lucioperca* (L.)) is a valuable species both in commercial and recreational
35 fisheries in the coastal waters of the Baltic Sea (Lehtonen et al., 1996; Saulamo and Thoresson,
36 2005; Heikinheimo et al., 2006). Pikeperch stocks have benefited from eutrophication and
37 increased temperatures during the recent decades (Lappalainen et al., 2002; Ådjers et al., 2006;
38 Heikinheimo et al., 2006). Indeed, the positive effects of temperature on year-class strengths and
39 growth of pikeperch are perceivable (Lappalainen et al., 2009). Temperature is critical for young-
40 of-the-year (Y-O-Y) pikeperch during the first summer, because juveniles must reach sizes that are
41 large enough to enable them to survive the first winter (Lappalainen et al., 2000; 2005a). A
42 negative relationship between growth, estimated as annual length increments, and year-class
43 strength has been found in pikeperch in the eastern Gulf of Finland, suggesting density-dependent
44 growth (Lappalainen et al., 2009). In general, density dependence commonly occurs early in life in
45 large habitats such as the marine environment, but it may also occur late in life – especially if the
46 habitable area is limited (Andersen et al., 2017; Zimmerman et al., 2018). As Lappalainen et al.
47 (2009) discussed, the negative effects of density on growth are easily masked by the strong
48 positive effects of temperature on growth (see also Lorenzen and Enberg, 2002). Therefore, the
49 possible effects of temperature on growth should be considered.

50

51 Size-selective fishing gear, for example gillnets, typically remove the faster-growing individuals
52 from the population at a higher rate than slower growing ones (Kraak et al., 2019); this process is
53 known as the “Rosa Lee’s phenomenon”. Such selective fishing can lead to a situation where the
54 remaining population becomes dominated by slower-growing individuals with an apparent
55 decreased mean growth rate (Kristiansen and Svåsand, 1998). If ignored, this phenomenon can
56 lead to errors in assessing the dynamics and status of fish stocks, causing a substantial bias in
57 management decisions (Kraak et al., 2019). Management strategies and decisions can be studied
58 for instance with size- and age-based models, which take into account the size-selectivity of the
59 estimated gear (e.g. Buijse et al., 1992; Machiels and Wijsman, 1996; Kraak et al., 2019).

60

61 In the Archipelago Sea, pikeperch is mostly fished with gillnets, which are strongly size-selective
62 gear (van Densen, 1987; Buijse et al., 1992). Such size-selectivity can often benefit fisheries
63 management (Zimmermann and Jørgensen, 2017). Small mesh-size gillnets of ≤ 45 mm bar length
64 are commonly used, but the minimum mesh-size regulations for gillnets only apply to some parts

65 of the Archipelago Sea. The fishing pressure is high in the area, with instantaneous fishing
66 mortality varying from about 1.0 to even 1.5 per year in fully recruited age groups of pikeperch
67 (Heikinheimo et al., 2006; 2014). For example, 43 mm gillnets catch pikeperch that are between 35
68 and 47 cm (on average, pikeperch are around 40 cm) (Heikinheimo et al., 2006). The legal
69 minimum landing size of pikeperch was 37 cm during the study period until the end of 2018, but is
70 currently 40 cm (total length; TL) for commercial fishermen having an annual revenue over 10 000
71 euro, and 42 cm TL for others.

72
73 Earlier studies have revealed that the growth of pikeperch is slow in the Archipelago Sea
74 compared with other coastal areas or lakes in Finland (Lehtonen, 1983; 1987; Heikinheimo et al.,
75 2006; Vainikka et al., 2017). Kokkonen et al. (2015) concluded that the strong fishing mortality
76 likely decreased the size and age at maturation of pikeperch in the Archipelago Sea. Even if earlier
77 maturation is linked to slower growth, there was no indication of a shift to slower growth in
78 pikeperch during the study period of 1980 to 2011. Instead, the condition factor had decreased.
79 According to Kokkonen et al. (2015), the simultaneous increase in water temperature may have
80 masked the effect of earlier maturation on growth.

81
82 In this study, we first estimated the effects of density and temperature on the annual length
83 increments of each pikeperch based on back-calculated lengths. Based on earlier studies from the
84 Baltic Sea (Lappalainen et al., 2009), we suggested that the effect of temperature on growth is
85 positive and that of density is negative. In the Baltic Sea, pikeperch live near the coast within the
86 archipelago areas (Lehtonen, 1983; Saulamo and Thoreson, 2005). As the year classes can be very
87 strong in warm summers (Lehtonen, 1983; Lappalainen et al., 2009), density-dependence in
88 growth can also be expected. Because pikeperch is mainly fished with gillnets, and the variation in
89 individual growth rates of pikeperch is high (Heikinheimo et al., 2006), it was hypothesized that
90 the size-selectivity of gillnets causes the fast-growing individuals to be caught at younger ages
91 than the slow-growing ones. Therefore, the growth of pikeperch observed based on sampling
92 could appear to be slow, when the actual growth based on their growth potential could be higher,
93 as has been shown for example in perch (*Perca fluviatilis*) (Machiels and Wijsman, 1996) and cod
94 (*Gadus morhua*) (Kristiansen and Svåsand, 1998). The effects of size-selectivity were analysed by
95 separately comparing average back-calculated lengths of pikeperch caught at age i and later at age
96 $i + 3$ years within the same year-class (Sinclair et al., 2002).

97

98 2 Materials and methods

99

100 2.1 Study area

101 The Archipelago Sea is a part of the Baltic Sea between the Gulf of Bothnia, the Gulf of Finland and
102 the Sea of Åland. The Archipelago Sea has a mosaic structure, including some 30 500 islands and
103 over 20 000 km shoreline (Bonsdorff et al., 1997). The average water depth in the Archipelago Sea
104 is only 23 m, and the deepest trench reaches 146 m (Leppäkoski et al., 1999). The average salinity
105 is 6–7 ‰ (Kullenberg, 1981), but is remarkably lower in areas close to river mouths. The duration
106 of the ice season varies from 130 to 200 days in the Bothnian Bay (north of the Archipelago Sea),
107 and from 80 to 100 days in the Gulf of Finland (east of the Archipelago Sea) (HELCOM, 2007).
108 Water temperatures range from 0 to 20°C, which can increase up to 25°C at the surface (HELCOM,
109 2007).

110

111 2.2 Fish sampling

112 The data were based on annual samples from commercial gillnet and trap net catches in the
113 Archipelago Sea during the years 1991–2014. The number of individuals in year-classes (hereafter
114 referred to as the year-class size) was obtained from pikeperch stock assessment (VPA) from
115 Heikinheimo et al. (2014), updated with data from 2014 (Fig. 1). The year-class size was estimated
116 using annual fisheries catch data Official Statistics of Finland (OSF) and virtual population analysis
117 VPA (Pope's cohort analysis, Hilborn and Walters, 1992) (Heikinheimo et al., 2014). In VPA, natural
118 mortality (M) was assumed to be 0.1 in the age groups ≥ 6 , 0.2 at ages 3–5, 0.3 at age 2, and 0.5 at
119 age 1 (Heikinheimo et al., 2014). The natural mortality was assumed to remain constant over time
120 in the studied years. See Heikinheimo et al. (2014) for a detailed description of the VPA. The
121 research area covers ICES statistical squares of 49H1, 49H2, 50H1 in the Baltic Sea in Finland
122 (Natural Resources Institute Finland, Luke); these samplings are partly connected to the EU Data
123 Collection Framework.

124

125 Pikeperch samples were collected from commercial fishermen's catches by the Natural Resources
126 Institute Finland. The total length and weight of the fish were measured, and scales were taken
127 from the standard area of the abdomen – on the side of the fish below the frontal part of the
128 posterior dorsal fin, below the lateral line. Age was determined from scales based on the annual

129 rings. The radius of scales and the distances of the annuli were measured with a microfilm viewer
130 from the polycarbonate impressions of scales. All the age determinations of pikeperch were done
131 by the same person. The lengths at earlier ages were back-calculated on the basis of the distances
132 of annual rings using Fraser and Lee's method (Bagenal and Tesch, 1978):

133

$$134 L_i = a + (L_c - a) * S_i / S_c,$$

135

136 where L_i is length at age i , L_c is the total length of the fish (mm), S_i is the distance between the
137 scale focus and annulus at age i , S_c is scale radius, and a is the intercept. For the intercept term a ,
138 44 mm was used as the length of pikeperch at scale formation (Ruuhijärvi et al., 1996). The total
139 number of analysed pikeperch was 24 375, of which 6 308 were caught with trap nets and 18 067
140 with gillnets.

141

142 2.3 Growth based on length increments

143 In the Archipelago Sea, pikeperch is mainly fished with gillnets in commercial fisheries, but trap
144 nets are also commonly used. However, because the differences between the mean length
145 increments of the pikeperch caught with trap nets and gillnets were small (Fig. 2), the data were
146 pooled in the following analysis.

147

148 A generalized linear model with log-normal errors and repeated measurements was used to study
149 the effects of age, temperature and density on the annual length increments of pikeperch. The
150 model was:

151

$$152 L_{inc\ y} = L_{y+1} - L_y,$$

$$153 L_{inc\ j, t, y} = \exp(\beta_0 + \beta_1 * A_j + \beta_2 * T_t + \beta_3 * S_{j, y}),$$

154

155 where L_{inc} is the annual length increment (mm), T is the temperature (water temperature sum
156 from the beginning of June to the end of September in year t), A is age j , and S is the number of
157 individuals in the year-class y at age j .

158

159 In the model, an individual fish was treated as a subject, and back-calculated length increments
160 were treated as repeated measurements, as recommended by Jones (2000). The model was fitted
161 using a SAS macro NLINMIX, which follows the PROC NLIN and PROC MIXED procedures. For the
162 covariance structure, the first-order autoregressive structure was used. Akaike's information
163 criterion (AIC, Akaike, 1974) was used to compare the different models. AIC is estimated as $2k -$
164 $2\ln(L)$, where k is the number of independently adjusted parameters, and L is the maximum value
165 of the likelihood function in the model. Thus, AIC measures the goodness of fit and penalises for
166 adding parameters to the model. The modelling approach was similar to that described by Dorn
167 (1992), but with the use of repeated measures. Lappalainen et al. (2005b; 2009) used a similar
168 growth model for pikeperch in lakes and in the Gulf of Finland.

169
170 In the growth analyses, daily mean water temperatures ($^{\circ}\text{C}$) from the first of June to the end of
171 September were summed together. Daily water temperature measurements were obtained from
172 the Finnish Environmental Institute. Water temperature was measured at 1 m depth in Ruissalo
173 Island between the years 1997–2008. The site is located in the south western coast of Finland,
174 near the city of Turku. For the periods when daily water measurements were not available (1980–
175 1996 and 2009–2013), a model by Kjellman et al. (2003) was used to estimate the daily water
176 temperature based on air temperature (see Kjellman et al., 2003; Pekcan-Hekim et al., 2011 for a
177 more detailed description of the model).

178
179 The year-class sizes of pikeperch varied substantially, and only the within-cohort density-
180 dependent effects were estimated. In preliminary analyses, year-class sizes and temperature sums
181 were log-transformed, because these gave smaller AIC-values when using log-transformed length
182 increments. We also standardized these three variables to mean 0 and to standard deviation 1 to
183 evaluate the effect sizes of each variable.

184
185 Only the main effects were analysed here based on preliminary analyses using variance inflation
186 factor (vif) to estimate possible multicollinearity among the main effects and their interactions.
187 Here, there are three possible two-way interactions: between temperature and age, between
188 temperature and stock size, and between age and stock size. When the annual length increments
189 were analysed with the interaction of temperature and age with the main effects of age, stock size
190 and temperature sum, vif was 4.6 for temperature and 17,819 for age, suggesting strong

191 multicollinearity. Similarly, when the interaction of temperature and stock size was analysed with
192 the main effects, vif was 187 for temperature and 15,534 for stock size. In the model with
193 interaction between age and stock size with the main effects, vif was 122.6 for age and 96.0 for
194 the interaction. In the model with only the main effects, vif was 1.0 for temperature, 2.1 for stock
195 size and for 2.1 for age, suggesting low multicollinearity. Therefore, only the main effects were
196 studied here.

197

198 2.4 Size-selective mortality

199 The presence, direction and magnitude of size-selective mortality in pikeperch were analysed with
200 the separate analyses of variances (ANOVA) for the mean back-calculated lengths for each pair of
201 ages (Sinclair et al., 2002). The analyses tested for differences in length-at-age i between fish
202 caught at age i and $i + 3$ in the same year-class y . Therefore, the comparison was always done
203 between lengths at the same age within the same year-class. The null hypothesis was that in the
204 absence of selection for growth, there should be no differences between back-calculated lengths
205 for a given age regardless of the age at which pikeperch were caught within an individual cohort. It
206 was presumed that a three year gap was enough to detect possible differences in length-at-age
207 due to size-selective fishing with gillnets.

208

209 The model was:

210

$$211 L_{i,t,y} = \beta_0 + \beta_1 X + \beta_2 Y + \epsilon,$$

212

213 where $L_{i,t,y}$ is the mean back-calculated length at age i of a fish caught in year t of year-class y , X is
214 the age, and Y is the year-class. The age of capture was i for the younger age in the pair and $i + 3$
215 for the older age. Statistical analyses were performed with SPSS® (version 24) and SAS (version
216 9.4).

217

218 3 Results

219 3.1 Length increments

220 The evaluation of different models with only one of the main effects showed that age was the
221 most important independent variable to describe the variation in log-transformed length
222 increments based on AIC-values (Tab. 1). The next important variable was the year-class size,

223 which performed better than temperature. In the two variable models, the best fit was found with
224 age and temperature, while the three variable model gave the smallest AIC-values. In this model,
225 the effects of age and year-class size were negative on the length increments of pikeperch, while
226 the effect of temperature was positive (Tab. 2). Residuals showed no clear deviations, so the
227 model 1 fitted quite well to the length increments (Fig. 3). In the same length increment model, in
228 which all the three independent variables were standardized to mean 0 and to standard deviation
229 1, the biggest effect size was in age (-0.084), then temperature (0.036), and the lowest effect size
230 was in density (-0.004). The first order autocorrelation between subsequent length increments
231 was -0.014.

232

233 3.2 Size-selective mortality

234 The comparisons of back-calculated lengths showed that the mean lengths were significantly
235 larger at ages 3 up to 7 years than in individuals caught 3 years later within the same year-class
236 (Tab. 3). On average, the difference was up to 60 mm in fully recruited age groups. These
237 differences became smaller in the comparisons between older pikeperch, for example between 6
238 and 9 year-old or 7 and 10 year-old individuals (Tab. 3), because even these 6 or 7 year-old
239 pikeperch have been subjected to selective fishing for several years.

240

241 Based on the back-calculated lengths, growth appears to stop at a length of 400 mm (Fig. 4).
242 Nevertheless, if the mean annual length increments (Fig. 2) are summed up, for example at the
243 age of 10, the average length of a pikeperch should be 490 mm, rather than 400 mm suggested by
244 back-calculated lengths. This is clearly seen from Figure 5, which is a "graphical summary" of the
245 results presented in Table 3. Following the high fishing pressure, the older age groups mainly
246 consist of the slow growing individuals, leading to the impression of truncated growth in these age
247 groups. This phenomenon is also seen in the trap net data, which shows that the increasing
248 proportion of slow growers towards older age groups is not only due to selective gillnet fishing,
249 but is actually present in the population.

250

251 4 Discussion

252

253 4.1 Pikeperch growth

254 The results showed that the year-class size of pikeperch had a negative effect on annual length
255 increments, while the effect of water temperature was positive. The negative effects of year-class
256 size on annual length increments suggest density-dependency in pikeperch growth in the
257 Archipelago Sea. Usually, density dependence is stronger in recruitment than in somatic growth,
258 although it can be present in both (Zimmermann et al., 2018). For example, in the Baltic Sea, the
259 selective fishing of cod led to density dependent growth (Svedäng and Hornborg, 2014). The
260 authors suggested that this was related to lower mortality of intermediate sized cod, partly
261 because of lower catchability when the size selectivity was increased, and partly because of
262 lowered predation from larger sized cod as their numbers declined. Here, the observed growth
263 patterns for pikeperch are similar to those found in some lakes (Lappalainen et al., 2005b) and in
264 the eastern Gulf of Finland (Lappalainen et al., 2009). Similar to the study by Lappalainen et al.
265 (2009), the year-class effect in the Archipelago Sea was weaker than the effect of temperature.
266 Notably, the positive effects of temperature on growth only apply if the temperature is less than
267 the optimum, and if food availability is sufficient (Morgan, 2018). Thus, extrapolating the effects of
268 temperature beyond the observed temperature range can be misleading.

269

270 The different growth trajectory for the first year compared with the later years suggests that age-
271 dependent sub-models might be worth considering for pikeperch. The same applies to density-
272 dependence as well; age groups could be pooled to include different density-dependent
273 mechanisms at different ages. Nevertheless, this is challenging due to the complex mechanisms of
274 density-dependence (e.g. Rose et al., 2001), which could act both within and between age groups.
275 For example, adults can compete with all adult age groups for food, whereas Y-O-Y compete for
276 food within their own age groups but can also be subjected to cannibalism from the older age
277 groups. This, in turn, can improve the growth of those individuals that survive from the predation,
278 because it reduces the density of the year class and consequently lowers competition for food. In
279 our model, the density-dependence was included only through the competition within the age
280 group. This was a rather strong simplification considering the above-mentioned processes, hence
281 using a biologically more realistic model could theoretically lead to stronger density-dependence
282 in growth.

283

284 4.2 Size-selective mortality and growth

285 High fishing effort and selective fishing have been shown to select for slower growth and earlier
286 maturation (Kristiansen and Svåsand, 1998; Law, 2000; Heikinheimo et al., 2006). The difference in
287 back-calculated lengths at the same ages between pikeperch caught three years apart was up to
288 60 mm in fully recruited age groups, indicating very strong size selection for pikeperch in the
289 Archipelago Sea. Gillnets are the main gear used in fisheries, and since the fishing pressure is high,
290 up to 80% of the catchable stock is removed annually (Heikinheimo et al., 2014). Thus, the
291 individuals that first reach the size at which they are vulnerable to fishing will be largely removed
292 from the population, while the proportion of slow growers correspondingly increases in the
293 population (Heikinheimo et al., 2006). The slower an individual grows, the longer it will be able to
294 escape from fishing (in the case where fishing is size-selective and the smaller individuals are not
295 exploited), which favours the slow growth in evolutionary terms (Law, 2007). It can be argued that
296 the slow growers are dominant in the older age groups in the Archipelago Sea.

297

298 The approach of protecting immature fish from fishing and instead targeting the larger ones has
299 been the cornerstone in fisheries management and scientific advice for decades (Garcia et al.,
300 2012). The theory behind this strategy is based on optimizing the yield per recruit function to
301 maximize the yield in weight by searching for the optimal size/age of first capture and fishing
302 mortality (Beverton and Holt, 1957). Protection of immature fish and implementing a policy where
303 fish are allowed to spawn at least once has proven to minimize the risk of severe recruitment
304 overfishing and stock collapses (Myers and Mertz, 1998). These targets, i.e. protecting smaller and
305 younger fish, mean larger size at recruitment for fishing. This is typically done by using different
306 minimum mesh size regulations and/or minimum size limits for caught fish. Recently, concerns
307 over the impacts of this selective fishing on fisheries have increased (e.g. Law, 2000; Conover and
308 Munch, 2002; Zhou et al., 2010; Laugen et al., 2014; Heino et al., 2015). Selectively removing
309 larger and older fish favours life history traits related to slower growth, as well as earlier age and
310 smaller size at maturity (Law, 2000; Conover and Munch, 2002; Ottersen et al., 2006).

311

312 Fisheries management should more strongly consider the evolutionary effects of fishing (Law and
313 Grey, 1989; Conover and Munch, 2002; Jørgensen et al., 2007). This is important because parental
314 size is correlated with larval performance in many fish species, including pikeperch, and larger

315 individuals produce larger eggs and more viable offspring (Chambers and Leggett, 1996;
316 Marteinsdottir and Steinarsson, 1998; Berkeley et al., 2004; Kamler, 2005; Olin et al., 2018). Using
317 both minimum and maximum size limits have been offered as one solution to minimizing these
318 effects. Vainikka et al. (2017) simulated the effect of such management strategy for inland
319 pikeperch populations. For heavily exploited populations, this strategy was not effective enough to
320 ensure the stability of yields and minimal evolutionary effect. Their results suggested that fishing
321 mortality rates should be restricted to relatively low levels to minimize the risks of the undesirable
322 evolutionary effects of fishing. In the Archipelago Sea, the current fishing pressure is high enough
323 to generate a similar result. The main issue in the area is the excessive fishing, which imposes
324 strong selection for earlier maturation (Law and Grey, 1989; De Roos et al., 2006; Andersen et al.,
325 2007; Jørgensen et al., 2007). Distributing harvesting with moderate mortality across the species,
326 stocks, and sizes in an ecosystem in proportion to their natural productivity is recommended to
327 more effectively prevent the adverse ecological effects of fishing, while simultaneously supporting
328 sustainable fisheries (Garcia et al., 2012). Such approach would improve the sustainability of
329 pikeperch fisheries in the Archipelago Sea.

330

331 The survival of pikeperch Y-O-Y during their first winter is strongly size selective, i.e. the first year
332 of life selects for fast growth, because those individuals that grow fast enough during their first
333 summer are more likely to survive over their first winter (Lappalainen et al., 2000; 2005a). Such
334 mortality can be expected to counteract the selective effects of fishing (Vainikka and Hyvärinen,
335 2012). This raises the question: could this selection for fast growth in the young of the year act as
336 a buffer for selection for slow growth later in life, or is the fishery-induced selection for slow
337 growth heritable to a degree that is strong enough to threaten the growth potential of the Y-O-Ys?
338 If so, the excessive selective fishing could cause a serious threat to reproduction in the long term.
339 This should be studied in more detail in the future.

340

341 The commercial catch samples may not give the true impression of pikeperch growth in the
342 Archipelago Sea. Notably, there is large individual variation in growth rates. Nevertheless, the fast-
343 growing pikeperch will largely be removed from the population as soon as they reach the allowed
344 catchable size. In older age groups, the length-at-age data is biased towards slow growth, and
345 these data should not be used directly for example in Y/R-analyses. The situation is similar to that
346 described by Kristiansen and Svåsand (1998) for cod. In order to avoid such problems, length-

347 based modelling was recommended by Kraak et al. (2019). There are different possibilities to
348 estimate the true growth potential of the older age groups of pikeperch. First, there is large
349 individual variation in pikeperch growth rates, and the growth potential can be simulated by
350 extrapolating the growth estimates of young age groups based on trap net samples. Secondly,
351 observed length differences due to gillnet selectivity can be used to estimate more realistic growth
352 also for the older age groups of pikeperch.

353

354 To conclude, the effect of temperature was positive on growth while that of density was negative,
355 similar to what has been found in other pikeperch populations in the northern Baltic Sea.
356 However, because of size-selective fishing, the growth suggested by the data is probably not
357 providing an accurate picture of the real growth potential in the Archipelago Sea. Thus, the
358 assessment of the population production should be based on the true growth potential, where the
359 effect of size selection by gillnets on growth has been excluded. We strongly encourage further
360 studies on the growth and interaction between the fisheries and population dynamics of
361 pikeperch in the Baltic coastal areas.

362

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364 References

365

366 Ådjers K, Appelberg M, Eschbaum R, Lappalainen A, Minde A, Repecka R, Thoresson G. 2006.
367 Trends in coastal fish stocks of the Baltic Sea. *Boreal Env Res* 11: 13-25.

368

369 Akaike H. 1974. A new look at the statistical model identification. *IEEE Transactions on Automatic*
370 *Control* 19: 716–723.

371

372 Andersen KH, Farnsworth KD, Thygesen UH, Beyer JE. 2007. The evolutionary pressure from fishing
373 on size at maturation of Baltic cod. *Ecol Modell* 204: 246-252.

374

375 Andersen KH, Jacobsen NS, Jansen T, Beyer JE. 2017. When in life does density dependence occur
376 in fish populations? *Fish Fish* 18: 656-667.

377

378 Bagenal TB, Tesch FW. 1978. Age and growth. In: Bagenal T. (Ed.), Methods for Assessment of Fish
379 Production in Fresh Waters. Blackwell, Oxford. pp. 101–136.
380

381 Berkeley SA, Chapman C, Sogard SM. 2004. Maternal age as a determinant of larval growth and
382 survival in a marine fish, *Sebastes melanops*. Ecology 85: 1258–1264.
383

384 Beverton RJH, Holt SJ. 1957. On the dynamics of exploited fish populations. Ministry of
385 Agriculture and Fisheries. Fish Investigat 19, 533 p.
386

387 Bonsdorff E, Blomqvist EM, Mattila J, Norkko A. 1997. Long-term changes and coastal
388 eutrophication. Examples from the Åland Islands and the Archipelago Sea, northern Baltic Sea.
389 Oceanologica Acta 20: 319–329.
390

391 Buijse AD, Pet JS, van Densen WL, Machiels MA, Rabbinge R. 1992. A size-and age-structured
392 simulation model for evaluating management strategies in a multispecies gill net fishery. Fish Res
393 13: 95–117.
394

395 Chambers RC, Leggett WC. 1996. Maternal influences on variation in egg sizes in temperate
396 marine fishes. Am Zool 36: 180–196.
397

398 Conover DO, Munch SB. 2002. Sustaining fisheries yields over evolutionary time scales. Science
399 297: 94–96.
400

401 Dorn MW. 1992. Detecting environmental covariates of Pacific whiting *Merluccius productus*
402 growth using a growth-increment regression model. Fish Bull 90: 260–275.
403

404 Garcia S, Kolding MJ, Rice J, Rochet M-J, Zhou S, Arimoto T, Beyer JE, Borges L, Bundy A, Dunn D,
405 Fulton EA, Hall M, Heino M, Law R, Makino M, Rijnsdorp AD, Simard F, Smith ADM. 2012.
406 Reconsidering the consequences of selective fisheries. Science 335: 1045–1047.
407

408 Heikinheimo O, Setälä J, Saarni K, Raitaniemi J. 2006. Impacts of mesh-size regulation of gillnets on
409 the pikeperch fisheries in the Archipelago Sea, Finland. Fish Res 77: 192–199.

410
411 Heikinheimo O, Pekcan-Hekim Z, Raitaniemi J. 2014. Spawning stock–recruitment relationship in
412 pikeperch *Sander lucioperca* (L.) in the Baltic Sea, with temperature as an environmental effect.
413 *Fish Res* 155: 1–9.
414
415 Heino M, Pauli BD, Dieckmann U. 2015. Fisheries-induced evolution. *Annu Rev Ecol Evol Syst* 46:
416 461-480.
417
418 HELCOM, 2007. Climate change in the Baltic Sea Area. HELCOM Thematic Assessment 2007. Baltic
419 Sea Environmental Proceedings No. 111.
420
421 Hilborn R, Walters CJ. 1992. Quantitative fisheries stock assessment: choice, dynamics and
422 uncertainty. Chapman and Hall, New York. 570 p.
423
424 Jones CM. 2000. Fitting growth curves to retrospective size-at age data. *Fish Res* 46: 123–129.
425
426 Jørgensen C, Enberg K, Dunlop ES, Arlinghaus R, Boukal DS, Brander K, Ernande B, Gårdmark A,
427 Johnston F, Matsumura S, Pardoe H, Raab K, Silva A, Vainikka A, Dieckmann U, Heino M, Rijnsdorp
428 AD. 2007. Managing evolving fish stocks. *Science* 318: 1247–1248.
429
430 Kamler E. 2005. Parent–egg–progeny relationships in teleost fishes: an energetics perspective. *Rev*
431 *Fish Biol Fish* 15: 399–421.
432
433 Kjellman J, Lappalainen J, Urho L, Hudd R. 2003. Early determination of perch and pikeperch
434 recruitment in the northern Baltic Sea. *Hydrobiologia* 495: 181–191.
435
436 Kokkonen E, Vainikka A, Heikinheimo O. 2015. Probabilistic maturation reaction norm trends
437 reveal decreased size and age at maturation in an intensively harvested stock of pikeperch *Sander*
438 *lucioperca*. *Fish Res* 167: 1–12.
439
440 Kullenberg G. 1981. Physical oceanography. In: Voipio A. (ed.), *The Baltic Sea*. Elsevier
441 *Oceanography series No. 30*. Elsevier Scientific Publishing Company, Amsterdam. pp. 135–181.

442
443 Kraak SB, Haase S, Minto C, Santos, J. 2019. The Rosa Lee phenomenon and its consequences for
444 fisheries advice on changes in fishing mortality or gear selectivity. ICES J Mar Sci 76: 2179-2192.
445
446 Kristiansen TS, Svåsand, T. 1998. Effect of size-selective mortality on growth of coastal cod
447 illustrated by tagging data and an individual-based growth and mortality model. J Fish Biol 52: 688-
448 705.
449
450 Lappalainen A, Söderkultalahti P, Wiik T. 2002. Changes in the commercial fishery for pikeperch
451 (*Stizostedion lucioperca*) on the Finnish coast from 1980 to 1999 – Consequences of environmental
452 and economic factors. Arch Fish Mar Res 49: 199–212.
453
454 Lappalainen J, Erm V, Kjellman J, Lehtonen H. 2000. Size-dependent winter mortality of age-0
455 pikeperch (*Stizostedion lucioperca*) in Pärnu Bay, the Baltic Sea. Can J Fish Aquat Sci 57: 451–458.
456
457 Lappalainen J, Vinni M, Kjellman J. 2005a. Diet, condition and mortality of pikeperch (*Sander*
458 *lucioperca*) during their first winter. In: Repka S. (Ed.), Lake Hiidenvesi – studies on a clay-turbid
459 and eutrophic multi-basin lake. Adv Limnol 59: 207–217.
460
461 Lappalainen J, Malinen T, Rahikainen M, Vinni M, Nyberg K, Ruuhijärvi J, Salminen M. 2005b.
462 Temperature dependent growth and yields of pikeperch in Finnish lakes. Fish Manage Ecol 12: 27–
463 35.
464
465 Lappalainen J, Milardi M, Nyberg K, Venäläinen A. 2009. Effects of water temperature on year-
466 class strengths and growth patterns of pikeperch (*Sander lucioperca* (L.)) in the brackish Baltic Sea.
467 Aquat Ecol 43: 181–191.
468
469 Laugen AT, Engelhard GH, Whitlock R, Arlinghaus R, Dankel DJ, Dunlop ES, Eikeset AM, Enberg K,
470 Jørgensen C, Matsumura S, Nusslé S, Urbach D, Baulier L, Boukal DS, Ernande B, Johnston FD,
471 Mollet F, Pardoe H, Therkildsen NO, Uusi-Heikkilä S, Vainikka A, Heino M, Rijnsdorp AD,
472 Dieckmann U. 2014. Evolutionary impact assessment: accounting for evolutionary consequences
473 of fishing in an ecosystem approach to fisheries management. Fish Fish 15: 65-96.

474
475 Law R. 2000. Fishing, selection, and phenotypic evolution. *ICES J Mar Sci* 57: 659–668.
476
477 Law R. 2007. Fisheries-induced evolution: present status and future directions. *Mar Ecol Progr Ser*
478 335: 271–278.
479
480 Law R, Grey DR. 1989. Evolution of yields from populations with age-specific cropping. *Evol Ecol* 3:
481 343–359.
482
483 Lehtonen H. 1983. Stocks of pike-perch (*Stizostedion lucioperca* L.) and their management in the
484 Archipelago Sea and the Gulf of Finland. *Finn Fish Res* 5: 1–16.
485
486 Lehtonen H. 1987. Selection of minimum size limit for pike-perch (*Stizostedion lucioperca*) in the
487 coastal waters of Finland, 1985. *Proc V Congr Europ Ichthyol, Stockholm*, pp. 351–355.
488
489 Lehtonen H, Hansson S, Winkler H. 1996. Biology and exploitation of pikeperch *Stizostedion*
490 *lucioperca* (L.), in the Baltic Sea area. *Ann Zool Fenn* 33: 525–535.
491
492 Leppäkoski E, Helminen H, Hänninen J, Tallqvist M. 1999. Aquatic biodiversity under
493 anthropogenic stress: an insight from the Archipelago Sea (SW Finland). *Biodiv Conserv* 8: 55–70.
494
495 Lorenzen K, Enberg, K. 2002. Density-dependent growth as a key mechanism in the regulation of
496 fish populations: evidence from among-population comparisons. *Proc Royal Soc Lond B: Biological*
497 *Sciences* 269: 49–54.
498
499 Machiels MA, Wijsman J. 1996. Size-selective mortality in an exploited perch population and the
500 reconstruction of potential growth. *Ann Zool Fenn* 33: 397-401.
501
502 Marteinsdottir G, Steinarsson A. 1998. Maternal influence on the size and viability of cod (*Gadus*
503 *morhua* L.) eggs and larvae. *J Fish Biol* 52: 1241–1258.
504

505 Morgan MJ. 2018. Understanding biology to improve advice for fisheries management. *ICES J Mar*
506 *Sci* 75: 923–931.

507

508 Myers RA, Mertz G. 1998. The limits of exploitation: a precautionary approach. *Ecol Appl* 8(sp1):
509 S165-S169.

510

511 Official Statistics of Finland (OSF): Commercial Marine Fishery [e-publication]. Helsinki: Natural
512 Resources Institute Finland. Access method: http://www.stat.fi/til/akmer/index_en.html

513

514 Ottersen G, Hjermann DØ, Stenseth NC. 2006. Changes in spawning stock structure strengthen the
515 link between climate and recruitment in a heavily fished cod (*Gadus morhua*) stock. *Fish Oceanogr*
516 15: 230–243.

517

518 Olin M, Vainikka A, Roikonen T, Ruuhijärvi J, Huuskonen H, Kotakorpi M, Vesala S, Ala-Opas P,
519 Tiainen J, Nurminen L, Lehtonen H. 2018. Trait-related variation in the reproductive characteristics
520 of female pikeperch (*Sander lucioperca*). *Fish Manage Ecol* 25: 220-232.

521

522 Pekcan-Hekim Z, Urho L, Auvinen H, Heikinheimo O, Lappalainen J, Raitaniemi J, Söderkultalahti P.
523 2011. Climate warming and pikeperch year-class catches in the Northern Baltic Sea. *Ambio* 40:
524 447–456.

525

526 De Roos AM, Boukal DS, Persson L. 2006. Evolutionary regime shifts in age and size at maturation
527 of exploited fish stocks. *Proc Royal Soc London B: Biological Sciences* 273: 1873-1880.

528

529 Rose KA, Cowan JH, Jr, Winemiller KO, Myers RA, Hilborn R. 2001. Compensatory density
530 dependence in fish populations: importance, controversy, understanding and prognosis. *Fish Fish*
531 2: 293–327.

532

533 Ruuhijärvi J, Salminen M, Nurmio T. 1996. Releases of pikeperch (*Stizostedion lucioperca* (L.))
534 fingerlings in lakes with no established pikeperch stock. *Ann Zool Fenn* 33: 553–567.

535

536 Saulamo K, Thoresson G. 2005. Management of pike-perch migrating over management areas in a
537 Baltic archipelago Area. *Ambio* 34: 118–122.

538

539 Sinclair AF, Swain DP, Hanson JM. 2002. Measuring changes in the direction and magnitude of size-
540 selective mortality in a commercial fish population. *Can J Fish Aquat Sci* 59: 361–371.

541

542 Svedäng H, Hornborg S. 2014. Selective fishing induces density-dependent growth. *Nature*
543 *communications* 5: 1-6.

544

545 Vainikka A, Hyvärinen P. 2012. Ecologically and evolutionarily sustainable fishing of the pikeperch
546 *Sander lucioperca*: Lake Oulujärvi as an example. *Fish Res* 113: 8–20.

547

548 Vainikka A, Olin M, Ruuhijärvi J, Huuskonen H, Eronen R, Hyvärinen P. 2017. Model-based
549 evaluation of the management of pikeperch (*Sander lucioperca*) stocks using minimum and
550 maximum size limits. *Boreal Env Res* 22: 187-212.

551

552 Van Densen WLT. 1987. Gillnet selectivity to pikeperch, *Stizostedion lucioperca* (L.), and perch,
553 *Perca fluviatilis* L., caught mainly wedged. *Aquacult Fish Manag* 18: 95-106.

554

555 Zhou S, Smith AD, Punt AE, Richardson AJ, Gibbs M, Fulton EA, Pascoe S, Bulman C, Bayliss P,
556 Sainsbury K. 2010. Ecosystem-based fisheries management requires a change to the selective
557 fishing philosophy. *Proc Nat Acad Sci* 107: 9485-9489.

558

559 Zimmermann F, Jørgensen C. 2017. Taking animal breeding into the wild: Regulation of fishing gear
560 can make fish stocks evolve higher productivity. *Mar Ecol Progr Ser* 563: 185-195.

561

562 Zimmermann F, Ricard D, Heino M. 2018. Density regulation in Northeast Atlantic fish populations:
563 Density dependence is stronger in recruitment than in somatic growth. *J Anim Ecol* 87: 672-681.

564

565 Tables

566

567 Table 1. AICs from different models used to estimate length increments of pikeperch (log-
568 transformed) based on age, temperature sum, and size of the year-class. The best fitting model
569 with the smallest AICs was the model using all three variables. All models included intercepts, and
570 temperature sum and year-class size were log-transformed. Total number of increment
571 observations and individuals was 136 649 and 24 375, respectively.

572

573

Model	AIC
Age	149 267
Temperature sum	188 081
Year-class size	177 263
Age, temperature sum	130 280
Age, year-class size	149 273
Age, temperature sum, year-class size	130 204

574

575

576 Table 2. The parameter values and test statistics for the effects of age (age in years 1-10),
577 temperature sum (calculated based on daily mean water temperature (°C) from 1st of June to end
578 of September in each year) and year-class size (number of pikeperch) on length increments of
579 pikeperch. Temperature sums, year-class sizes and length increments were log-transformed.

580

581

Parameter	Parameter value	Std. Error	t	P
Intercept	-3.099	0.0325	--	--
Age	-0.043	0.0002	-199.53	<0.001
Temperature sum	0.616	0.0043	144.57	<0.001
Year-class size	-0.004	0.0004	-9.79	<0.001

582

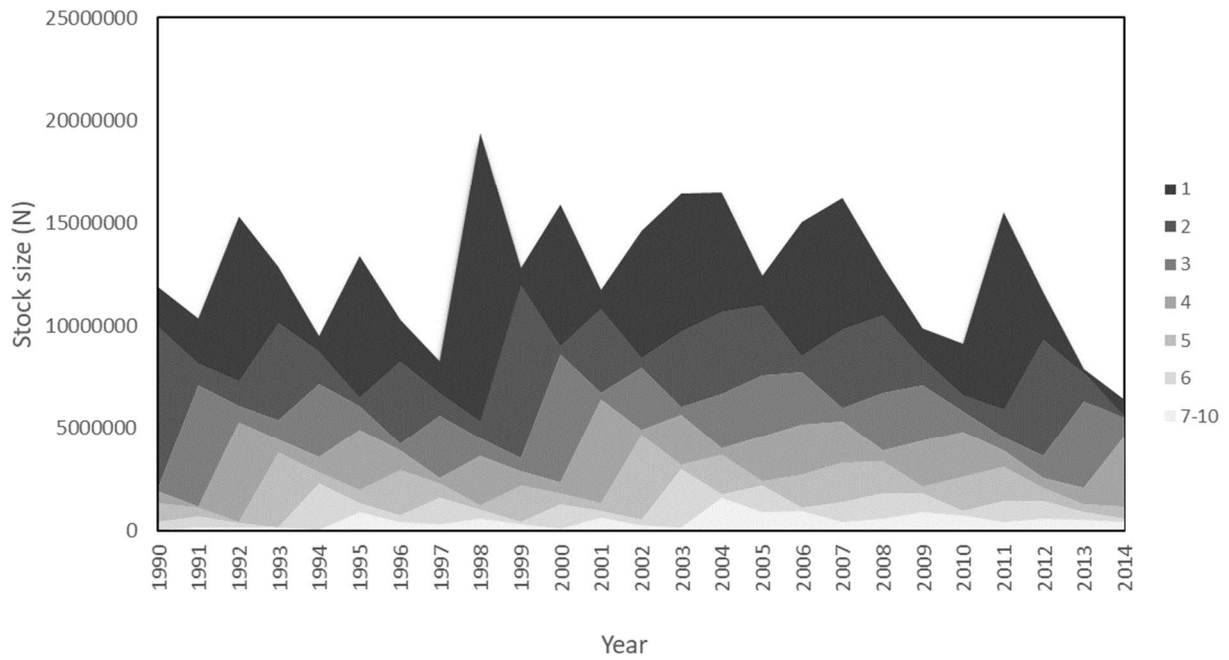
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584 Table 3. ANOVA statistics and average differences in mean back-calculated lengths (mm) at age i between pikeperch caught at age i or i + 3. R²
 585 is the adjusted R squared; * significance P<0.05; ** P<0.01.

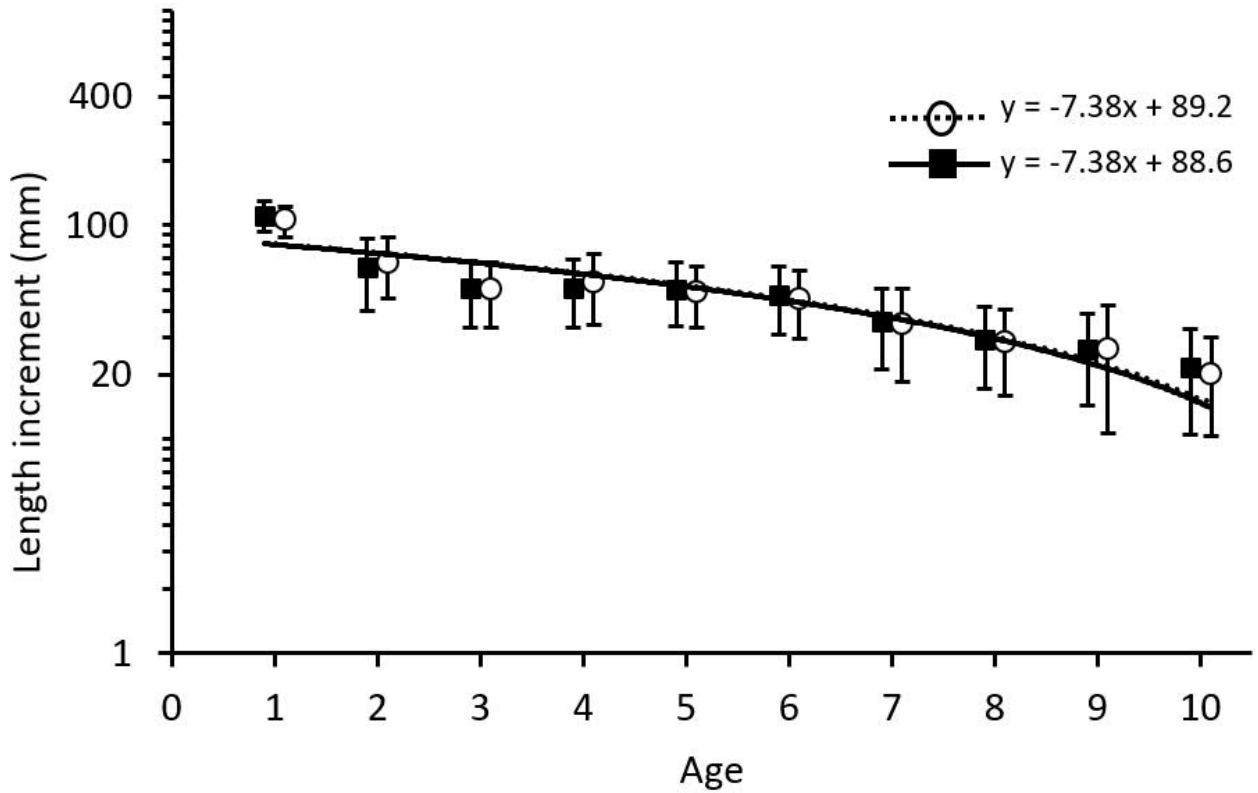
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Gear	Back-calculated length at age (i)	Age of capture	Year-classes	N	R ²	Year-class df and F	Age df and F	Average difference in length at age (i) (mm)
Both	2	2+ and 5+	1997–1998, 2000–2009	5123	0.39	11; 292.5**	1; 38.7**	-5.18
Both	3	3+ and 6+	1996–2008	5941	0.11	12; 54.2**	1; 75.8**	8.40
Both	4	4+ and 7+	1995–2007	5725	0.44	12; 57.7**	1; 2511.5**	44.73
Both	5	5+ and 8+	1994–2006	7556	0.39	12; 26.7**	1; 3870.3**	57.68
Both	6	6+ and 9+	1993–2005	6091	0.24	12; 11.5**	1; 1674.8**	58.24
Both	7	7+ and 10+	1991–1992, 1995, 1997–2004	3441	0.18	10; 27.2**	1; 369.6**	47.45
Gillnet	2	2+ and 5+	1997–1998, 2000–2009	3746	0.43	11; 251.1**	1; 49.7**	-7.13
Gillnet	3	3+ and 6+	1996–2008	4712	0.12	12; 49.6**	1; 45.5**	7.47
Gillnet	4	4+ and 7+	1995–2007	4448	0.43	12; 47.5**	1; 1961.9**	45.27
Gillnet	5	5+ and 8+	1994–2006	5124	0.42	12; 23.6**	1; 3315.4**	59.49
Gillnet	6	6+ and 9+	1993–2005	4636	0.33	12; 10.1**	1; 1924.8**	63.43
Gillnet	7	7+ and 10+	1991–1992, 1995, 1997–2004	2748	0.24	10; 23.0**	1; 494.6**	54.11
Trap net	2	2+ and 5+	1997–1998, 2000–2009	1377	0.26	11; 43.4**	1; 0.2	-0.63
Trap net	3	3+ and 6+	1996–2008	1229	0.15	12; 11.7**	1; 46.5**	13.34
Trap net	4	4+ and 7+	1995–2007	1277	0.53	12; 11.1**	1; 690.3**	49.92
Trap net	5	5+ and 8+	1994–2006	2432	0.37	12; 18.8**	1; 572.8**	58.60
Trap net	6	6+ and 9+	1993–2005	1455	0.17	12; 13.1**	1; 74.2**	34.20
Trap net	7	7+ and 10+	1997, 1999–2002, 2004	438	0.14	5; 11.5**	1; 3.6*	14.38

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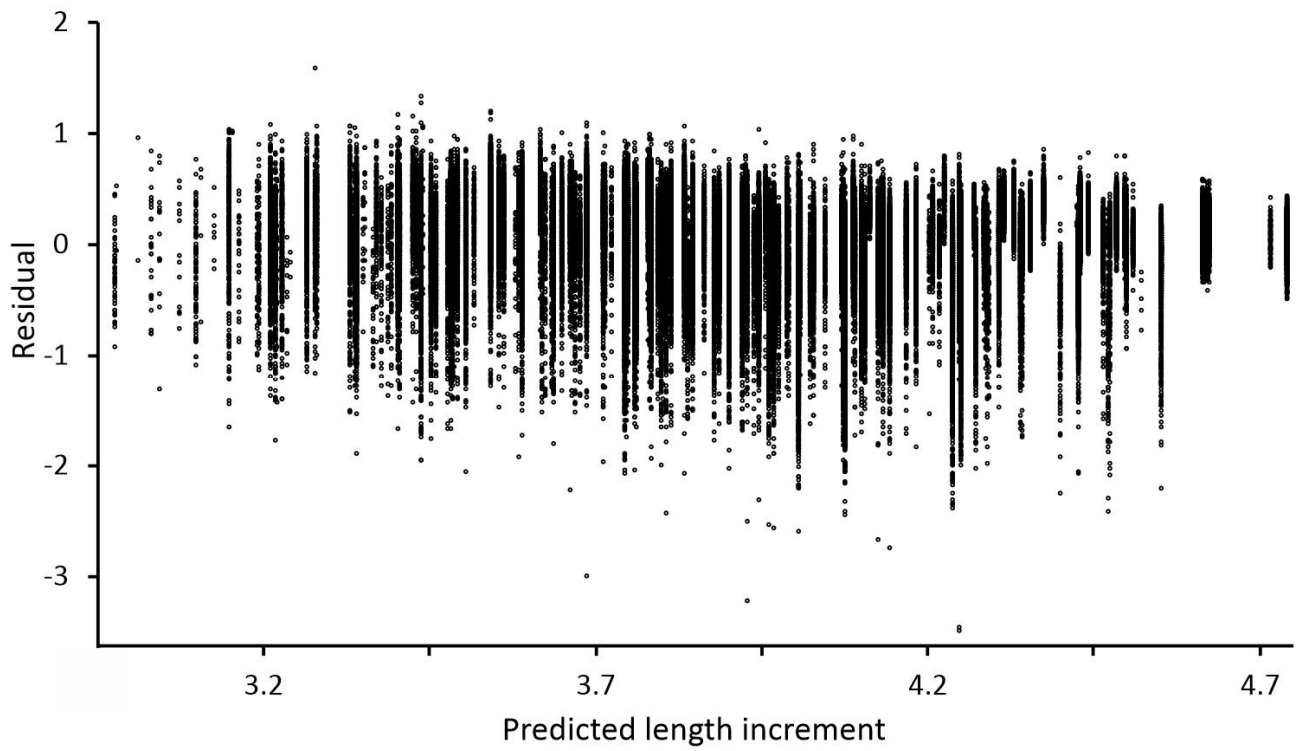
589
590 Fig. 1. Stock sizes (N) of age groups 1–10 of pikeperch by year based on the VPA. Age groups 7–10
591 have been combined. The year-classes appear as ridges and valleys.
592



593

594 Fig. 2. Average back-calculated length increments (mm, ± 1 SD, log-scale) of pikeperch in relation
 595 to age, in gillnets (black squares) and in trap nets (open circles). The lines indicate linear regression
 596 between length increments and age. Markers are shifted (-0.1 years for gillnets and +0.1 for trap
 597 nets) for comparison. Note the log-scale of the y-axis.

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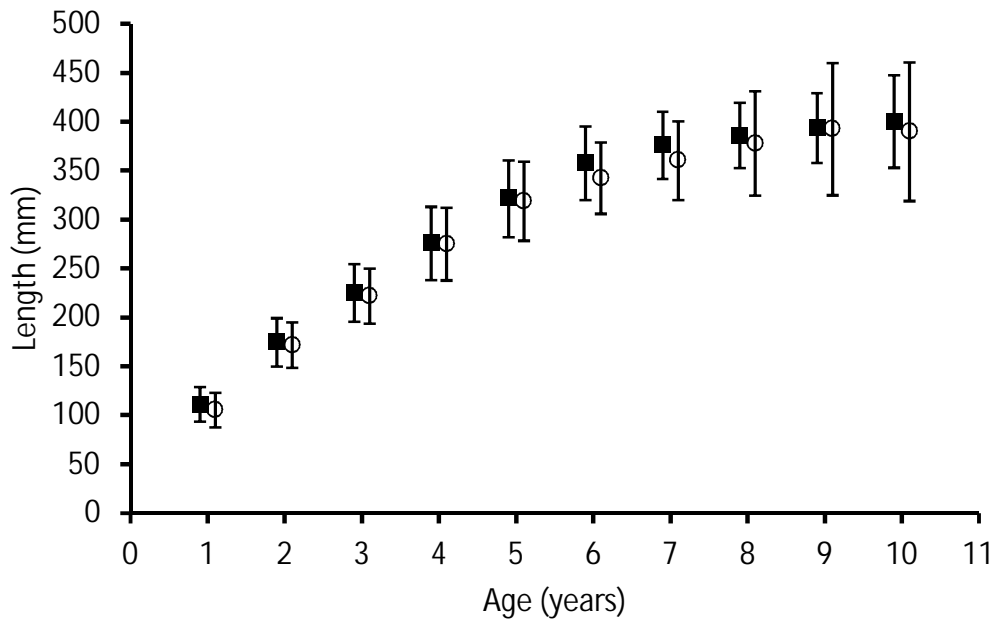


599

600 Fig. 3. Residuals from growth model in relation to predicted length increments (mm TL; log-
601 transformed).

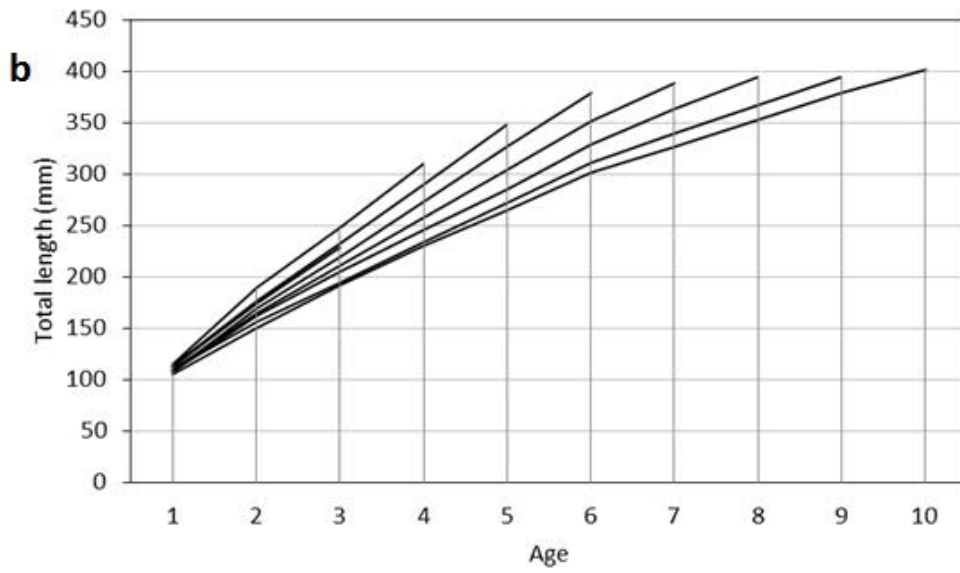
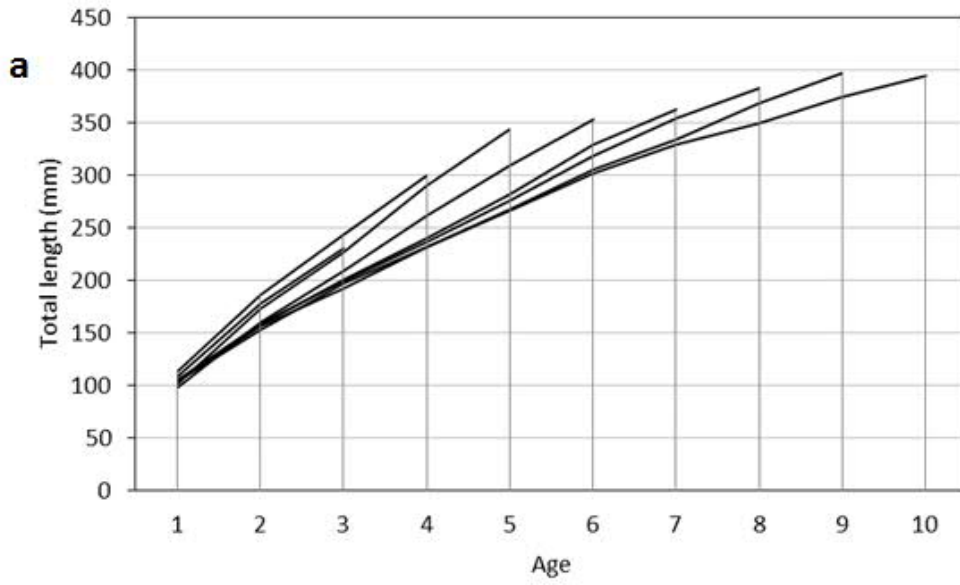
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605 Fig. 4. Back-calculated lengths (± 1 SD) of pikeperch in gillnets (black squares) and in trap nets
606 (open circles). Markers are shifted (-0.1 years for gillnets and +0.1 for trap nets) for comparison.



607
 608 Fig. 5. Mean back-calculated lengths (mm) of pikeperch caught at different ages with trap nets (a)
 609 and gillnets (b).