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Density and temperature dependent growth of pikeperch (Sander lucioperca) in the Archipelago Sea

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1 Paper title: Density and temperature dependent growth of pikeperch (*Sander lucioperca*) in the
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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 Thoreson,
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).

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2 Materials and methods

2.1 Study area

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

2.2 Fish sampling

The data were based on annual samples from commercial gillnet and trap net catches in the Archipelago Sea during the years 1991–2014. The number of individuals in year-classes (hereafter referred to as the year-class size) was obtained from pikeperch stock assessment (VPA) from Heikinheimo et al. (2014), updated with data from 2014 (Fig. 1). The year-class size was estimated using annual fisheries catch data Official Statistics of Finland (OSF) and virtual population analysis VPA (Pope’s cohort analysis, Hilborn and Walters, 1992) (Heikinheimo et al., 2014). In VPA, natural 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 age 1 (Heikinheimo et al., 2014). The natural mortality was assumed to remain constant over time in the studied years. See Heikinheimo et al. (2014) for a detailed description of the VPA. The research area covers ICES statistical squares of 49H1, 49H2, 50H1 in the Baltic Sea in Finland (Natural Resources Institute Finland, Luke); these samplings are partly connected to the EU Data Collection Framework.

Pikeperch samples were collected from commercial fishermen’s catches by the Natural Resources Institute Finland. The total length and weight of the fish were measured, and scales were taken from the standard area of the abdomen – on the side of the fish below the frontal part of the 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

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

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

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

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

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 (°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.

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4.2 Size-selective mortality and growth

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

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

Fisheries management should more strongly consider the evolutionary effects of fishing (Law and Grey, 1989; Conover and Munch, 2002; Jørgensen et al., 2007). This is important because parental 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.

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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

583

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.

586

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

587

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.
 598

599

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

602

603

604

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).