1 # Density independent use of shallow riverine areas in juvenile

2 # Atlantic salmon

3

4

5

6 **Michael Puffer, Ole Kristian Berg, Frøydis Bolme Hamnes, Vidar Bentsen, Wouter Koch,**

7 **Ola Ugedal, Torbjørn Forseth, Jo Vegar Arnekleiv, and Sigurd Einum**

8

9

10 **Michael Puffer, Ole Kristian Berg, Frøydis Bolme Hamnes, Vidar Bentsen, Wouter Koch.**

11 Department of Biology, Norwegian University of Science and Technology (NTNU), Trondheim,

12 Norway.

13 **Ola Ugedal, Torbjørn Forseth.** Norwegian Institute for Nature Research (NINA), Trondheim,

14 Norway

15 **Jo Vegar Arnekleiv.** Department of Natural History, Norwegian University of Science and

16 Technology (NTNU), Trondheim, Norway

17 **Sigurd Einum.** Centre for Biodiversity Dynamics, Department of Biology, Norwegian

18 University of Science and Technology (NTNU), Trondheim, Norway

19 **Corresponding author: Ole K. Berg (email: ole.berg@bio.ntnu.no)**

Abstract:

21   Habitat use of aquatic organisms is essential to evaluate effects of many environmental

22 challenges like effects of hydro-power regulation, where stranding may occur under

23 hydropeaking (rapid dewatering of shallow river areas). Experimental studies as well as

24 observations from nature with juvenile Atlantic salmon (*Salmo salar*) show that the proportion of

25 the population that uses shallow depth was both independent of population density and

26 decreasing with fish size. Experiments were conducted both in the presence and in absence of

27 older fish, during day and night, and during all four seasons. Juvenile salmon from deep areas

28 may therefore distribute into the shallow areas even when fish density becomes reduced. Thus,

29 low density does not lead to reduced stranding risk and shallow areas may therefore function as a

30 sink in a within-generation source-sink dynamic under a repeated hydropeaking scenario. The

31 sink effect of rapid dewatering in shallow areas may be mitigated by e.g. seasonal and diurnal

32 regulation of hydropeaking activity, but dewatering may still result in extinction of weak

33 populations.

34

35 **Keywords:** habitat use, hydropeaking, intracohort competition, intercohort competition,

36 microhabitat use, stranding

Introduction

Habitat use (i.e. occurrence of an individual in a specific habitat with specific values of water velocity, substrate etc.) of fishes is crucial to determine their stranding risk in rivers where hydro-regulation activity may induce rapid variation in water level. Hydropower is an energy source with the potential to store energy (reservoirs) and this is believed to become more important in the future in order to balance the variation in wind and solar energy production. This benefit of hydropower comes at a cost for the riverine environment, degrading the physical, biological, recreational and economical values of the affected rivers (e.g. Pang et al. 2015). Hydropower production has considerable negative environmental effects, but due to action to mediate climate gas-emissions, hydropower is often considered as green and environmental friendly energy. Currently, more than 50% of the world's stream and river flow crosses one or more dams before reaching the oceans and this fraction could increase up to 90% by 2030 (Van Cappellen and Maavara 2016).

The results of river regulation are usually large-scale changes affecting biological organization levels from organisms to landscapes and involves changes in a multitude of topics from habitat use to general conservation biology or changes in nutrient load leading to profound community changes (Van Cappellen and Maavara 2016). In systems where rapid changes in water discharge, so-called hydropeaking, frequently occur due to fluctuating hydropower production, the effects of hydro-power production can be more pronounced (Irvine et al. 2015; Hauer et al. 2017). Hydropeaking causes a fraction of the riverbed to be dewatered, commonly referred to as the ramping zone with stranding of organisms and exposure to air in the ramping zone during low flow periods (e.g. Saltveit et al. 2001; Halleraker et al. 2003; Nagrodski et al. 2012). Riverine organisms are adapted to a variable environment, but hydropeaking is

60   unpredictable, since water level fluctuations and ramping speed exceed those occurring naturally

61   (Poff et al. 1997). The ramping zone may therefore represent a potential hazard for organisms

62   that prefer shallow areas. In the case of rivers, shallow and slow-flowing shorelines may be used

63   and even preferred by certain species and life stages, and individuals are able to respond to

64   natural gradual decreases in flow by moving out to more central areas. Both intra- and

65   interspecific competition and fish predation may be lowered in shallow areas, and enemy-free

66   space may make shallow areas preferable, especially for the smallest fry (e.g. Heggenes &

67   Borgstrøm 1991). However, under hydropeaking, these shallow areas may become of low

68   quality due to high risk of stranding and mortality during rapid declines in flow. Thus,

69   hydropeaking causes a mismatch between the environmental clues they usually use for selecting

70   habitat and the actual habitat quality (Donovan and Thompson 2001; Kokko and Sutherland

71   2001; Schlaepfer et al. 2002; Hale and Swearer 2016). Increased use of renewable energy, more

72   open energy markets, increased transmission capacities and more variable patterns of energy use,

73   all lead to more demands for market-oriented regulation of hydropower production (Harby &

74   Noack 2013), and hydropeaking has become increasingly common in rivers in Europe and North

75   America. While there are no international overview of the extent of hydropeaking practices, in

76   Austria alone it has been estimated that 800 km of river stretches are affected (Melcher et al.

77   2016).

78   The effects of hydropeaking on organisms in regulated rivers can be divided into two

79   different problem areas: habitat-specific parameters, especially depth, which determine the

80   dewatering risk for a given organism and then the factors which determine mortality of stranded

81   organisms (e.g. Bradford 1997; Sauterleute et al. 2016; Puffer et al. 2017). For fish, stranding

82   may result in high mortality. The present paper, however, deals with the first of these processes:

83   assessing factors which determine the use of shallow areas, which are the areas with higher

84   stranding risk. One fish taxon that has received much attention with regards to the issue of

85   hydropeaking in temperate areas is salmonids, and in particular Atlantic salmon (*Salmo salar*).

86   Habitat use in juvenile Atlantic salmon is influenced by body size, time of day, season, predation

87   risk, food and shelter availability, and is extensively described in the literature (e.g. Heggenes et

88   al. 1999; Armstrong et al. 2003; Berg et al., 2014; Puffer et al. 2015). In general, they may be

89   found over the whole range of available depths, including the shallow shorelines that become

90   dewatered during hydropeaking. However, the "efficiency" of the shallow shorelines as a trap

91   (Hale and Swearer 2016), and hence the population-level effect of hydropeaking induced

92   mortality, will be highly influenced by the extent to which this occupancy is density-dependent.

93   There are three possible scenarios in terms of occupancy of the ramping zone:

94   1) it is negatively density-dependent, i.e. the proportion of fish in the ramping zone increases

95   with decreasing population density

96   2) it is density-independent, i.e. the proportion of the population in the ramping zone is

97   independent of population density

98   3) it is positively density-dependent, i.e. the proportion of fish in the ramping zone increases with

99   increasing population density.

100   If the use of the ramping zone is negatively density-dependent (scenario 1), it would act as a

101   hazard zone or trap for juvenile Atlantic salmon, with the population-level effect increasing with

102   decreasing population density. Scenario 1 may then efficiently drive populations to extinction,

103   particularly in combination with other negative environmental factors. For scenario 2 there is no

104   feedback between population density and negative effects of hydropeaking, and a more constant

105   population-level effect is predicted. Finally, under scenario 3 the negative effect of hydropeaking

106   is expected to decrease with decreasing population density, making it of less concern in terms of

107   population persistence.

108   The present study provides both extensive experimental and observational data on

109   Atlantic salmon habitat use that enables us to distinguish between the three density-dependent

110   scenarios outlined above. The focal habitat dimension investigated was water depth. Experiments

111   were conducted in four artificial outdoor-streams. To increase the generality of our findings these

112   experiments were conducted both in the presence and absence of older fish, during day and

113   night, and during all four seasons. The experimental results were complemented and verified

114   with observational data on wild juvenile Atlantic salmon depth use in three Norwegian rivers.

115

Materials and methods

Experimental study: Study site and experimental design

118   Experiments were performed at the Norwegian Institute for Nature Research (NINA)

119   Station, Ims (south-western Norway, 58° 54' N, 5° 57' E). Four outdoor arenas (i.e. round,

120   concrete pools) were used in the experiments with water originating from a nearby lake, which

121   entered each arena through an individual adjustable water inlet. Each arena comprised a curved

122   stream divided by mesh screens (Fig. 1; Appendix Fig. A4-A7) into three sections, each about 10

123   m^2, and constant water flow (for details about the arenas, see: Berg et al. 2014). About 50% of

124   each section was covered with white plastic foil above the water surface to provide overhead

125   shade. Differences in water depth between the outer and inner walls of the streams were created

126   by a sloped gravel streambed, creating a shallow area on the inner side and a deep area on the

127   outer side of the curved stream. To determine depth use at the end of a trial, the shallow (mean

128   depth 18 cm; range 2–31cm) and deep areas (mean depth 31; range 15–44 cm) of the sections

129   were separated by remotely lowering/releasing screens (i.e. "trapdoors") placed longitudinally

130   above the stream. When the trap doors were released, they separated the shallow from the deep

131   area to ensure the correct determination of fish distributed into shallow/deep area (for further

132   details see: Berg et al. 2014). A pilot study was conducted to determine the time required to

133   obtain a stable depth use distribution for each trial. After sampling at different trial durations, a

134   minimum of 20 hours was chosen as no further change in depth use distribution occurred later.

135

Experimental study: Experimental fish and procedures

137   The juvenile Atlantic salmon were hatched from eggs originating from the local River

138   Imsa once a year during spring and reared at the research station. Fish used in our experiments

139   were thus hatched in spring and then used throughout the four different seasons, which explains

140   the increase in body size in our figures (spring: min. 22 mm – winter: max. 150 mm).

141   Experiments were repeated in all seasons (spring, summer, autumn, winter). Young-of-the-year

142   (YOY) were stocked at either low (one YOY m^{-2}) or high (three YOY m^{-2}) density into each

143   section, and this was done both in the presence and absence of two overyearling (i.e. > 1 year

144   old) individuals (for details see: Table 1). Our overyearlings were 1+ salmon, hatched and kept

145   at the same facility under the same conditions, but of course in larger tanks because of their size.

146   The chosen YOY densities were within the range of densities found in wild populations of YOY

147   salmonids (Grant and Imre 2005). Experimental fish were only used once.

148   For autumn and winter experiments, both day- and night-time trials were performed,

149   whereas only daytime trials were performed during spring and summer as our experimental

150   facility's northward geographical position precludes dark nights in spring and summer. Thus, the

151   combination of these different factors resulted in different **treatments** in the different seasons,

152 i.e. the spring experiments comprised only low vs. high density (= two treatments and no

153 overyearling due to the large difference in size between overyearling and YOY with risk of

154 predation (e.g. Kennedy and Strange 1980)), whereas the autumn experiments comprised

155 combinations of low vs. high density, with vs. without overyearling, and day vs. night (= eight

156 treatments). Recapture of fish was done by portable electrofishing gear after lowering (releasing)

157 the screens which separated the shallow and deep part. Electrofishing thus only function as a

158 mean of enumeration of fish. Depth use was determined by counting the number of YOY

159 recovered in shallow versus deep areas in each section, and the body length (fork length, ± 1

160 mm) of each individual was measured. When performing night trials, the arenas were stocked at

161 02:00 am, and fished again at 00:00 the next night when it already had been completely dark for

162 about three hours.

163   The summer experiment lasted from 14. – 29. June 2010, the autumn experiment from

164 31. August – 17. September 2010, the winter experiment from 8. – 23. February 2011, and the

165 spring experiment from 7. – 13. May 2011. The experimental depth use study was based on a

166 total number of 609 experimental replicates (Table 1), pilot studies excluded.

167

168 **Experimental study: Statistics**

169   All statistical analyses were done using R, v. 2.15.3 (R Core Team 2012). The influence

170 of body length, density, time of day (for autumn and winter), and the presence of overyearlings

171 (summer, autumn and winter) on the depth use of individual YOY was modelled using a

172 generalized linear mixed model (GLMM) with a binomial distribution and with section and

173 replicate (nested within section) as random effects.

174   The function *lmer* from the *lme4* package was used (Bates et al. 2015). Model

175   simplification procedures followed Zuur et al. (2009) using log likelihood ratio tests to remove

176   non-significant interaction and covariate terms, while the main effects of experimental factors

177   (i.e. YOY density and overyearling presence) were kept in all final models. Final models were

178   re-fitted using restricted maximum likelihood (REML) and final model residuals were checked

179   for normal distribution, homogeneity and independence. Separate models were fitted for each

180   season because of the differences in the treatments (i.e. combination of factors tested). The

181   autumn and winter models are similar and are the most complex ones since all listed treatments

182   were performed in these seasons. The models from the other two seasons are shorter versions of

183   the autumn/winter models. The latter can be written as:

184

185    $P_{ijk} = \alpha + \beta_1 D_k + \beta_2 L_k + \beta_3 B_i + \beta_4 T_k + \beta_5 T_k D_k + \beta_6 T_k L_k + \beta_7 T_k B_i + \beta_8 D_k L_k + \beta_9 B_i D_k + \beta_{10} B_i L_k +$

186    $a_j + a_k + \varepsilon_i$

187

188   where P is the probability of an individual YOY being in the shallow depth, D is the YOY

189   density (one or three fish m^{-2}), L is overyearlings (present or absent), B is the body length and T

190   is the time of day (day or night). Indices i, j and k represent individuals, sections and replicates,

191   respectively. α and β are the fixed parameters, a_j and a_k are the random intercepts for section and

192   replicate respectively, and ε_i is the random error structure (binomial). The spring model does not

193   include the term T (time of day) and L (overyearlings), and the summer model does not include

194   the term T.

195

196   **Field study: Study sites and experimental design**

9

197   Our main focus in the field was to study salmon YOY habitat use with respect to depth

198   and distance to shore, density of YOY and density of larger conspecifics. The field data were

199   collected in the three Norwegian rivers Nausta, Stjørdalselva, and Surna by electrofishing

200   transects perpendicular to the shoreline with a portable electrofishing device (for details see:

201   Table 2). Nausta has a natural flow regime, whereas in Surna and Stjørdalselva flow regimes are

202   affected by hydropower regulation. The four fishing stations in Surna were situated from 4.5 to

203   6.5 km downstream of the power plant outlet, whereas the seven fishing stations in Stjørdalselva

204   were situated from 8.2 to 40.3 km downstream of the power plant outlet. In Surna, there are

205   periods of hydropeaking depending on inflow and market demands. However, no hydropeaking

206   took place during or in the month before our investigation in October 2007. In all three rivers

207   electrofishing took place at gradually declining discharge (Appendix Fig. A1-A3) and at water

208   temperatures between 5 and 9 °C. The rivers were fished in different years (Nausta 2008;

209   Stjørdalselva 2007; Surna 2007), but all fishing took place in October and was finished in less

210   than a week. Since we used electrofishing in our experimental study, it was a natural choice to

211   use electrofishing in our field study as well. Fishing stations were specifically chosen for this

212   study, with emphasis on the ability to electrofish far into the middle of the river, and to have

213   rather homogenous water velocities and bottom substrate over a long stretch so that the transects

214   could be placed into a homogenous habitat in each station. Electrofishing was done by a two

215   person's team using a single, handheld anode and backpack gear without any block nets to fence

216   off the stations nor to separate between shallow and deep habitats. A moveable banner net (1 m^2)

217   was used to catch any stunned fish drifting downstream. In addition, the operator of the anode

218   assisted by catching both unstunned and stunned fish with a dip-net. The banner net was emptied

219   after each sweep before being moved to position for the next planned sweep. Fish observed

10

220   escaping the fished area were noted and added to the capture if it could be identified to species

221   and age class however, such observations were very few.

222   Electrofishing was standardized by performing similar straight sweeps of about 1.2 m

223   length with the anode in transects perpendicular to the shore. Each transect was fished from the

224   shoreline to the middle of the river or until it became too deep to fish (~80 cm). The

225   perpendicular distance between sweeps was 1 m. Species (Atlantic salmon, brown trout (*Salmo*

226   *trutta*)), age class (YOY, overyearlings) and number of caught fish were noted for each sweep

227   and the water depth at the lower end of the sweep was measured to the nearest cm. Only data of

228   Atlantic salmon were used in the analyses. We carried out the sampling with as little disturbance

229   of the sampling location as possible other than the necessary movements of the two-person crew

230   to do the sampling. After completion of the first transect, both the operator and assistant went

231   back to shore on the same way they came in to avoid disturbance of nearby fish, moved upstream

232   for five meters and repeated the same procedure in the new transect (for details see: Table 3).

233   The catch was kept alive in buckets and released back to the river after finishing the sampling of

234   all transects in a station.

235

236   **Field study: Statistics**

237   The field data was used to calculate the proportion of YOY caught in the shallow and to

238   model whether this proportion was influenced by the density of YOY in the transect, the density

239   of overyearlings in the shallow, or the density of overyearlings in the transect. Therefore, an

240   assumed border between shallow and deep areas had to be classified, which also enabled us to

241   compare the results from the field study with the results from the experimental study. Since the

242   maximum water depth of the shallow area in the experimental study was 31 cm, a division value

11

243   of 30 cm was chosen for the field study. This also ensured a relatively equal sampling effort of

244   shallow and deep areas, as 46% of all fishing took place at water depths > 30 cm. The proportion

245   of fishing effort in the deep habitat was 40 % in Nausta, 47% in Stjørdalselva and 48% in Surna.

246   When preparing the original data for the analyses, each individual YOY was assigned to either

247   the deep or shallow area, depending on where it was caught. We calculated how many YOY as

248   well as overyearlings were caught per meter sweep with the electrofishing anode for each habitat

249   type (i.e. deep or shallow area), which we define here as fish density (i.e. fish m^{-1}). Then the

250   relative density in the shallow area was calculated by dividing the density of YOY in the shallow

251   by the density of YOY in the whole transect. Only transects where fish were caught were

252   analysed. Each fishing station was assigned to an individual index number which was used as a

253   random effect in the analysis.

254   As for the experimental part, the function *lmer* and model selection followed by model

255   validation was used to analyse the data. (Zuur et al. 2009; Pinheiro et al. 2013). The full model

256   can be written as:

257    $$P_{ij} = \alpha + \beta_1 D_i + \beta_2 E_i + \beta_3 F_i + \beta_6 R_i + a_j + \varepsilon_i$$

258   where P_{ij} is the relative density of YOY in the shallow habitat in transect i within section j, D_i is

259   the density of YOY in the transect, E_i is the density of overyearlings in the shallow, F_i is the

260   density of overyearlings in the transect, and R_i are the three rivers. α and β are the fixed

261   parameters, and a_j is the random intercepts for the station.

262

263

264   **Results**

265   **Experimental study**

Spring

266

267   For the spring data, the interaction between YOY density and fish size (log likelihood

268 ratio test: $X^2 = 2.45$; df = 1; $P = 0.118$) could be removed from the full model during model

269 simplification, but fish size remained ($X^2 = 37.0$; df = 1; $P < 0.0001$). Based on the final model,

270 YOY density had no effect on the probability of YOY occupying the shallow area ($z = 0.33$; $P =$

271 0.74). However, this probability decreased significantly with increasing fork length (slope-value

272 ± SE: -0.09 ± 0.01; $z = -6.11$; $P < 0.0001$; Fig. 2).

273

Summer

274

275   For the summer data, both the interaction between overyearlings presence and fish

276 density ($X^2 = 0.13$; df = 1; $P = 0.72$) and the interaction between fish density and fish size ($X^2 =$

277 3.04; df = 1; $P = 0.08$) could be removed from the full model during model simplification, but

278 the interaction between overyearlings presence and fish size remained ($X^2 = 39.59$; df = 1; $P <$

279 0.0001). Based on the final model, YOY density had no significant effect on the probability for

280 YOY to be in the shallow area ($z = 0.62$, $P = 0.54$). Without overyearlings present, an increase in

281 fork length significantly decreased this probability (-0.11 ± 0.02; $z = -5.11$; $P < 0.0001$; Fig. 3),

282 whereas with overyearlings present an increase in fork length significantly increased the

283 probability for a YOY to be in the shallow area (0.13 ± 0.02; $t = 0.53$; $P < 0.0001$; Fig. 3).

284

Autumn

285

286   For the autumn data, both the interactions between overyearlings presence and density

287 ($X^2 = 0.0002$; df = 1; $P = 0.99$), time of day and fish size ($X^2 = 1.03$; df = 1; $P = 0.31$), density

288 and fish size ($X^2 = 1.46$; df = 1; $P = 0.23$), and overyearlings presence and fish size ($X^2 = 2.45$; df

13

289   = 1; P = 0.12) could be removed during model simplification. Both the interaction between time

290   of day and overyearlings presence (X^2 = 4.94; df = 1; P = 0.026), time of day and density (X^2 =

291   5.35; df = 1; P = 0.021) and the main effect of fish size (X^2 = 39.14; df = 1; P < 0.0001)

292   remained. Based on the final model, an increase in fish size generally decreased the probability

293   of finding a YOY in the shallow area (-0.03 ± 0.004; z = -6.19; P < 0.0001; Fig. 4). During

294   daytime (with and without overyearlings present) an increase in density (from one to three YOY

295   m^{-2}) significantly decreased the probability of a YOY to be in the shallow area (-0.66 ± 0.26; z =

296   -2.57; P = 0.010; Fig. 4). The presence of overyearlings during daytime at both densities

297   significantly increased the probability of finding a YOY in the shallow area (1.47 ± 0.28; z =

298   5.34; P < 0.0001; Fig. 4). During nighttime (with and without overyearlings present) an increase

299   in density significantly increased the probability of a YOY to be in the shallow area (0.76 ± 0.32;

300   z = 2.35; P = 0.019; Fig. 4). The presence of overyearlings during nighttime at both densities

301   significantly decreased the probability of finding a YOY in the shallow area (-0.74 ± 0.34; z = -

302   2.21; P = 0.027; Fig. 4).

303

304   **Winter**

305   For the winter data, both the interactions between overyearlings presence and fish size

306   (X^2 = 0.0062; df = 1; P = 0.94), time of day and density (X^2 = 0.29; df = 1; P = 0.59),

307   overyearlings presence and density (X^2 = 1.51; df = 1; P = 0.22), density and fish size (X^2 = 2.67;

308   df = 1; P = 0.10), and time of day and fish size (X^2 = 2.83; df = 1; P = 0.09) could be removed

309   during model simplification. Both the interaction between time of day and overyearlings

310   presence (X^2 = 4.40; df = 1; P = 0.036), and the main effect of fish size (X^2 = 44.22; df = 1; P <

311   0.0001) remained. Based on the final model, YOY density had no significant effect on the

312   probability of finding a YOY in the shallow area (z = -1.17, P = 0.24). In general, an increase in

313   fish size significantly decreased this probability (-0.03 ± 0.004; z = -6.75; P < 0.0001; Fig. 5).

314   There was a tendency for a decreased probability of finding a YOY in the shallow area during

315   daytime when overyearlings were present (-0.47 ± 0.27; z = -1.77; P = 0.078; Fig. 5). The

316   presence of overyearlings during nighttime significantly increased the probability of finding a

317   YOY in the shallow area (0.75 ± 0.36; z = 2.10; P = 0.036; Fig. 5).

318

Field study

320   The field study was performed to test whether the findings from the experiments could be

321   confirmed in natural rivers: The relative density of YOY in the shallow was not significantly

322   affected by the density of YOY in the whole transect (X^2 = 3.45; df = 1; P = 0.06). Furthermore,

323   it was independent both of the density of overyearlings in the whole transect (X^2 = 0.12; df = 1; P

324   = 0.73) and the density of overyearlings in the shallow (X^2 = 0.78; df = 1; P = 0.38). Finally, the

325   relative density of YOY in the shallow was independent of river (X^2 = 4.35; df = 2; P = 0.11).

326

Discussion

328   Stranding of riverine organisms is one of the main adverse ecological effects of

329   hydropower development of rivers, particularly when hydropower production entails frequent

330   and rapid changes in water discharge (i.e. hydropeaking) (e.g. Irvine et al. 2015; Hauer et al.

331   2017; Kelly et al. 2017). Mitigation of adverse effects depends on detailed knowledge about the

332   way the use of "risky" areas is influenced by population density. The experimental results based

333   on reared fish in relatively narrow confinements were confirmed by observations of native fish in

334   rivers to ensure the generality of our results. Density-dependent habitat use in juvenile Atlantic

15

335   salmon has been studied previously (e.g. Bult et al. 1999; Gibson et al. 2008), but primarily with

336   a mesohabitat scale focus (e.g. pools, riffles, runs). By focusing on the microhabitat scale, we

337   were able to address the issue of density-dependent depth use in more detail. The effects of

338   hydropeaking on organisms are assessed by a combination of stranding risk and the effects

339   (especially mortality) of stranding on organisms like fish. This latter part has been investigated

340   by e.g. Harby and Noack (2013) and Puffer et al. (2017).

341   Although the differences between the low (one YOY m^{-2}) and high density (three YOY

342   m^{-2}) treatment in our experiments were relatively large, none or only very subtle effects of fish

343   density on YOY depth use were observed. Density effects were apparent during autumn, but of

344   small magnitude and thus of low biological importance. Maximum fish densities observed in the

345   field study were not as high as the high density in the experiments, but nonetheless covered a

346   relatively broad and representative range. Neither density of YOY nor density of overyearlings

347   influenced depth use of YOY in the field. Overall, our results suggest that the use of the shallow

348   and hence "risky" areas is **density-independent** (scenario 2 in introduction), i.e. the same

349   proportion of the population will use the shallow area regardless of population density.

350   Nonetheless, juvenile salmon from deep areas may distribute into the shallow areas even when

351   fish density becomes reduced due to stranding mortalities. Thus, low density does not lead to

352   reduced stranding risk and shallow areas may therefore function as a sink in a within-generation

353   source-sink dynamic under a repeated hydropeaking scenario.

354   Population-level effects of anthropogenically induced mortality will also depend on

355   which individuals are at the highest risk. If mortality is selective and for a given life stage

356   primarily targets individuals with poor future prospects, then the population effects can be

357   expected to be less severe than under the converse situation or if mortality is non-selective. Our

16

358 study demonstrates that for a given life stage (i.e. regardless of the season), the smallest juvenile

359 salmon had always the highest probability of being in the shallow area, which suggests that they

360 will face the highest stranding risk. Thus, under strong size-selective mortality (i.e. selection

361 against small individuals) during later life-stages, this will reduce the population-level effects.

362 However, existing data suggests that this may not be the case for Atlantic salmon, as patterns of

363 size-selective mortality may vary both across years and seasons (Hendry et al. 2003). Modelling

364 of the effects of stranding of salmon parr and smolt, emphasises the effect of larger fish

365 (presmolts and smolts) where no compensatory mechanisms operate if large fish die in

366 freshwater (Sauterleute et al. 2016). The experimental conditions ensured identical areas for deep

367 and shallow depths, and if the experimental fish are composed of sedentary, floaters or

368 wanderers (Roy et al. 2013), they have similar areas to disperse into or distribute within the

369 experimental areas. We emphasize that we did not monitor individual behaviour in the

370 experiments and the present investigation focus on density dependent use of shallow areas under

371 a set number of conditions like season, diurnal pattern etc. As the experiment was performed

372 with a balanced replication structure, any increase in experimental parameters would lead to a

373 large increase the number of experiments.

374   A second additional factor influencing population-level effects is the timing (i.e. life-

375 stage) of anthropogenically induced mortality. Different life stages may be targeted to different

376 extents, and this will be of importance if populations are regulated by sequential density

377 dependence (Ratikainen et al. 2008). For example, high induced mortality during early stages

378 will have little effect if the population experiences strong density-dependence later in life (i.e.

379 compensatory mortality). Our study shows a decrease in the use of the shallow areas throughout

380 the first year of their lives. This is consistent with previous studies (Greenberg et al. 1996; Mäki-

381 Petäys et al. 2004; Hedger et al. 2005; Ayllón et al. 2009; Ayllón et al. 2013), suggesting that the

382 earliest stages following emergence from nests will be most susceptible to stranding during

383 hydropeaking. The population-level effect will then depend on whether increased early mortality

384 will be **compensated for** later in life due to sequential density dependence. This issue has been

385 debated for salmonids, where so-called self-thinning lines have been interpreted as showing

386 continuous density dependence throughout the juvenile stage by some authors (Elliott 1993), but

387 not others (Armstrong 1997). Later empirical studies have demonstrated that the temporal pattern

388 of density dependence, i.e. whether density dependence occurs only early in life or more

389 continuously throughout life, will depend on the relative abundance of habitat types that are

390 suitable for the different life stages (Elliott and Hurley 1998). For example, in rivers where a

391 high proportion of the habitat is suitable for early life stages, low competition and high survival

392 during these stages will cause intense competition for the rarer habitat suitable for later stages,

393 and hence density dependence will occur more continuously throughout the freshwater stage

394 (Teichert et al. 2013). Thus, the population-level effect of hydropeaking will be site-specific. In

395 general, rivers with abundant habitat for older juveniles (particularly structural shelter (Finstad et

396 al. 2009)), which are expected to experience little density dependence for older juvenile stages,

397 are predicted to be most negatively influenced by hydropeaking and associated high mortality

398 during early stages. On the other hand, Bellmore et al. (2015) infers that increased spatial

399 complexity may reduce interactions like predation. We have deliberately held substrate

400 composition in both shallow and deep areas identical in both experiments and field studies, since

401 substrate coarseness is important for hiding, but hiding into substrate increase risk of stranding

402 (Puffer et al. 2015).

18

403   The experimental set up had identical areas for shallow and deep areas and trapdoors

404   ensured a precise separation between the two areas. Depth use determination was ensured

405   without knowledge on parameters like feeding and predation protection (e.g. Bellmore et al.

406   2015) or the existence of hierarchical (dominant/subdominant) and non-hierarchial (floater)

407   strategies (Roy et al. 2013) among juvenile salmonids.

408   The present study also demonstrates that the effect of hydropeaking may depend on the

409   population structure, because the presence of overyearlings had significant effects on YOY

410   habitat use. Surprisingly, the presence of overyearlings in summer mainly influenced the depth

411   use of the larger YOY, who responded by increased use of the shallow habitat. Visual

412   observations helped to explain this phenomenon, since we were able to observe the arenas from a

413   nearby platform and could distinguish between two reactions of YOY when overyearlings were

414   approaching them: small YOY, who actively swam in the water column, stopped swimming and

415   hid in the substrate, whereas larger YOY actively swam away. The less overt response among

416   the smaller individuals may contribute to the previously reported difference in growth responses

417   to inter-cohort competition, where growth of larger YOY was more strongly influenced by

418   overyearling densities than that of smaller YOY (Einum and Kvingedal 2011). The reaction to

419   overyearlings was more consistent in autumn, since the presence of an overyearling always

420   resulted in an increased use of the shallow areas. Here we observed the classical situation of

421   intercohort competition, where smaller individuals are outcompeted by larger individuals and are

422   forced to use sub-optimal habitats (Mäki-Petäys et al. 2004; Ayllón et al. 2013). The same was

423   true for winter, but the effect size was small and thus biologically less important. Because of the

424   population structure found in natural rivers, YOY are forced to use shallower waters than they

425   would without intercohort competition and thus are more susceptible to stranding. This is

19

426   beneficial from a production perspective, as the mortality of larger smolt or presmolt will be less

427   compensated for if they die compared to smaller/younger fish (Sauterleute et al. 2016).

428   Both during autumn and winter YOY were more often in the shallow area during night-

429   time than during daytime, and this effect was as large as the effect of presence of overyearlings.

430   This behaviour is well documented in the literature (e.g. Schmutz et al. 2015) and may lead to

431   the naïve prediction that discharge reductions will be more damaging during night than during

432   day. Yet, field observations have shown that discharge reductions in winter led to fewer

433   stranding casualties during night than during day (Saltveit et al. 2001). This is most likely due to

434   the diurnal change in activity at low water temperatures (Puffer et al. 2015), as they become

435   sedentary and hide in the substrate during daytime, when water temperatures drop below 5–8 °C

436   (e.g. Heggenes and Dokk 2001; Scruton et al. 2005). Thus, even if a larger proportion of the

437   population inhabits shallow areas at night, they are less susceptible to stranding as they are better

438   able to detect and respond to the decreasing water level when active.

439   In the present study, we found no or small effects of fish density on the use of shallow

440   shorelines of YOY Atlantic salmon. However, the lack of a density-dependent pattern show that

441   there is a potential for each stranding event to cause a more or less constant mortality rate due to

442   redistribution of fish into shallow areas. Shallow areas may thus function as a sink in a within-

443   generation source-sink system under repeated hydropeaking. Furthermore, our data suggest that

444   the earliest stages following emergence from nests will be most susceptible to stranding during

445   hydropeaking. Depending on the habitat characteristics, such increased early mortality may be

446   compensated by reduced mortality during later stages. Thus, site-specific population-level effects

447   of hydropeaking can be expected. Caution has therefore to be exercised in the hydropeaking

448   activity where water is led into rivers where seasonal and diurnal patterns and ramping rates are

449　key parameters to be considered in the operating manuals for hydroelectric power plants (e.g.

450　Forseth and Harby 2014; Hauer et al. 2017). These manuals are usually issued by governmental

451　agencies and are under severe public awareness as exemplified with the use of the endangered

452　species act, red lists or EU Water framework directive as examples of management tools.

453

Acknowledgements

461

462

References

Armstrong, J.D. 1997. Self-thinning in juvenile sea trout and other salmonid fishes revisited. J.

Anim. Ecol. 66(4): 519-526. doi:10.2307/5946.

Armstrong, J.D., Kemp, P.S., Kennedy, G.J.A., Ladle, M., and Milner, N.J. 2003. Habitat

requirements of Atlantic salmon and brown trout in rivers and streams. Fish. Res. 62(2): 143-

170.

Ayllón, D., Almodovar, A., Nicola, G.G., and Elvira, B. 2009. Interactive effects of cover and

hydraulics on brown trout habitat selection patterns. River Res. Appl. 25(8): 1051-1065.

doi:10.1002/rra.1215.

472 Ayllón, D., Nicola, G.G., Parra, I., Elvira, B., and Almodovar, A. 2013. Intercohort density

473 dependence drives brown trout habitat selection. Acta Oecol.-Int. J. Ecol. 46: 1-9.

474 doi:10.1016/j.actao.2012.10.007.

475 Bates, D., Maechler, M., Bolker, B., and Walker S. 2015. Fitting Linear Mixed-Effects Models

476 Using lme4. J. Stat. Softw. 67(1): 1-48.

477 Berg, O.K., Bremset, G., Puffer, M., and Hanssen, K. 2014. Selective segregation in intraspecific

478 competition between juvenile Atlantic salmon (Salmo salar) and brown trout (Salmo trutta).

479 Ecol. Freshw. Fish. 23(4): 544-555. doi:10.1111/eff.12107.

480 Bellmore, J.R., Baxter, C. V., and Connolly, P. J. 2015. Spatial complexity reduces interaction

481 strengths in the meta-food web of a river floodplain mosaic. Ecology **96** (1): 274-283.

482 Bradford, M.J. 1997. An experimental study of stranding of juvenile salmonids on gravel bars

483 and in side channels during rapid flow decreases. Regul. Rivers: Res. Manage. 13(5): 395-401.

484 doi:10.1002/(sici)1099-1646(199709/10)13:5<395::aid-rrr464>3.0.co;2-l.

485 Bult, T.P., Riley, S.C., Haedrich, R.L., Gibson, R.J., and Heggenes, J. 1999. Density-dependent

486 habitat selection by juvenile Atlantic salmon (Salmo salar) in experimental riverine habitats.

487 Can. J. Fish. Aquat. Sci. 56(7): 1298-1306. doi:10.1139/f99-074.

488 Donovan, T.M., and Thompson, F.R. 2001. Modeling the ecological trap hypothesis: A habitat

489 and demographic analysis for migrant songbirds. Ecol. Appl. 11(3): 871-882. doi:10.1890/1051-

490 0761(2001)011[0871:MTETHA]2.0.CO;2.

491 Einum, S., and Kvingedal, E. 2011. Relative importance of size-based competitive ability and

492 degree of niche overlap in inter-cohort competition of Atlantic salmon (Salmo salar) juveniles.

493 Can. J. Fish. Aquat. Sci. 68(6): 969-976. doi:10.1139/f2011-042.

494   Elliott, J.M. 1993. The self-thinning rule applied to juvenile sea-trout, Salmo trutta. J. Anim.

495   Ecol. 62(2): 371-379. doi:10.2307/5368.

496   Elliott, J.M., and Hurley, M.A. 1998. Population regulation in adult, but not juvenile, resident

497   trout (Salmo trutta) in a lake district stream. J. Anim. Ecol. 67(2): 280-286. doi:10.1046/j.1365-

498   2656.1998.00185.x.

499   Finstad, A.G., Einum, S., Ugedal, O., and Forseth, T. 2009. Spatial distribution of limited

500   resources and local density regulation in juvenile Atlantic salmon. J. Anim. Ecol. 78(1): 226-235.

501   doi:10.1111/j.1365-2656.2008.01476.x.

502   Forseth, T., and Harby, A. 2014. Handbook for environmental design of regulated salmon rivers.

503   Norwegian Institute for Nature Research, Trondheim.

504   Gibson, A.J.F., Bowby, H.D., and Amiro, P.G. 2008. Are wild populations ideally distributed?

505   Variations in density-dependent habitat use by age class in juvenile Atlantic salmon (Salmo

506   salar). Can. J. Fish. Aquat. Sci. 65(8): 1667-1680. doi:10.1139/f09-087.

507   Grant, J.W.A., and Imre, I. 2005. Patterns of density-dependent growth in juvenile stream-

508   dwelling salmonids. J. Fish Biol. 67: 100-110. doi:10.1111/j.1095-8649.2005.00916.x.

509   Greenberg, L., Svendsen, P., and Harby, A. 1996. Availability of microhabitats and their use by

510   brown trout (Salmo trutta) and grayling (Thymallus thymallus) in the River Vojman, Sweden.

511   Regul. Rivers: Res. Manage. 12(2-3): 287-303. doi:10.1002/(sici)1099-

512   1646(199603)12:2/3<287::aid-rrr396>3.3.co;2-v.

513   Hale, R., and Swearer, S.E. 2016. Ecological traps: current evidence and future directions. Proc.

514   R. Soc. Lond. [Biol] 283(1824). doi:10.1098/rspb.2015.2647.

515   Halleraker, J.H., Saltveit, S.J., Harby, A., Arnekleiv, J.V., Fjeldstad, H.P., and Kohler, B. 2003.

516   Factors influencing stranding of wild juvenile brown trout (Salmo trutta) during rapid and

517   frequent flow decreases in an artificial stream. River Res. Appl. 19(5-6): 589-603.

518   doi:10.1002/rr.752.

519   Harby, A., and Noack, M. 2013. Rapid Flow Fluctuations and Impacts on Fish and the Aquatic

520   Ecosystem. In Ecohydraulics: an integrated approach. John Wiley & Sons, Ltd. pp. 323-335.

521   Hauer, C., Siviglia, A., and Zolezzi, G. 2017. Hydropeaking in regulated rivers – From process

522   understanding to design of mitigation measures. Sci. Total Environ. 579: 22-26.

523   doi:10.1016/j.scitotenv.2016.11.028.

524   Hedger, R.D., Dodson, J.J., Bergeron, N.E., and Caron, F. 2005. Habitat selection by juvenile

525   Atlantic salmon: the interaction between physical habitat and abundance. J. Fish Biol. 67(4):

526   1054-1071. doi:10.1111/j.1095-8649.2005.00808.x.

527   Heggenes, J., Bagliniere, J.L., and Cunjak, R.A. 1999. Spatial niche variability for young

528   Atlantic salmon (Salmo salar) and brown trout (Salmo trutta) in heterogeneous streams. Ecol.

529   Freshwat. Fish 8(1): 1-21. doi:10.1111/j.1600-0633.1999.tb00048.x.

530   Heggenes, J., and Dokk, J.G. 2001. Contrasting temperatures, waterflows, and light: Seasonal

531   habitat selection by young Atlantic salmon and brown trout in a boreonemoral river. Regul.

532   Rivers: Res. Manage. 17(6): 623-635. doi:10.1002/rrr.620.

533   Hendry, A.P., Letcher, B.H., and Gries, G. 2003. Estimating natural selection acting on stream-

534   dwelling Atlantic salmon: Implications for the restoration of extirpated populations. Conserv.

535   Biol. 17(3): 795-805. doi:10.1046/j.1523-1739.2003.02075.x.

536   Irvine, R.L., Thorley, J.L., Westcott, R., Schmidt, D., and DeRosa, D. 2015. Why do fish strand?

537   An analysis of ten years of flow reduction monitoring data from the Columbia and Kootenay

538   rivers, Canada. River Res. Appl. 31(10): 1242-1250. doi:10.1002/rra.2823.

539 Kelly, B., Smokorowski, K.E., and Power, M. 2017. Impact of river regulation and hydropeaking

540 on the growth, condition and field metabolism of Brook Trout (Salvelinus fontinalis). Ecol.

541 Freshw. Fish. 26(4): 666-675. doi:10.1111/eff.12310.

542 Kennedy, G.J.A., and Strange, C.D. 1980. Population-changes after 2 years of salmon (Salmo

543 salar L.) stocking in upland trout (Salmo trutta L.) streams. J. Fish Biol. 17(5): 577-586.

544 doi:10.1111/j.1095-8649.1980.tb02789.x.

545 Kokko, H., and Sutherland, W.J. 2001. Ecological traps in changing environments: Ecological

546 and evolutionary consequences of a behaviourally mediated Allee effect. Evol. Ecol. Res. 3(5):

547 603-610.

548 Melcher, A.H., Bakken, T.H., Friedrich, T, Greimel, F., Humer, N., Scmutz, B., and Webb, J.A.

549 2016. Drawing together multiple lines of evidence from assessment studies of hydropeaking

550 pressures in impacted rivers. Freshw. Sci. 36: 220-230.

551 Mäki-Petäys, A., Erkinaro, J., Niemela, E., Huusko, A., and Muotka, T. 2004. Spatial

552 distribution of juvenile Atlantic salmon (Salmo salar) in a subarctic river: size-specific changes

553 in a strongly seasonal environment. Can. J. Fish. Aquat. Sci. 61(12): 2329-2338.

554 doi:10.1139/f04-218.

555 Nagrodski, A., Raby, G.D., Hasler, C.T., Taylor, M.K., and Cooke, S.J. 2012. Fish stranding in

556 freshwater systems: Sources, consequences, and mitigation. J. Environ. Manage. 103: 133-141.

557 doi:10.1016/j.jenvman.2012.03.007.

558 Nielsen, J. L. 1992. Microhabitat-specific foraging behavior, diet, and growth of juvenile coho

559 salmon. Trans. Am. Fish. Soc. **121** (5): 617-634.

560 Pang, M., Zhang, L., Ulgiati, S., and Wang, C. 2015. Ecological impacts of small hydropower in

561 China: Insights from an emergy analysis of a case plant. Energy Policy 76: 112-122.

562 doi:10.1016/j.enpol.2014.10.009.

563 Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., EISPACK, and R-core. 2013. nlme: Linear and

564 Nonlinear Mixed Effects Models. http://cran.rproject.org/web/packages/nlme/index.html

565 Poff, N.L., Allan, J.D., Bain, M.B., Karr, J.R., Prestegaard, K.L., Richter, B.D., Sparks, R.E., and

566 Stromberg, J.C. 1997. The natural flow regime: a paradigm for river conservation and

567 restoration. Biosci. 47(11): 769-784. doi:10.2307/1313099.

568 Puckett, K.J., and Dill, L.M.1985.The energetics of feeding territoriality in juvenile coho salmon

569   (*Oncorhynchus kisutch*). Behaviour **92** (1): 97-111.

570 Puffer, M., Berg, O.K., Huusko, A., Vehanen, T., Forseth, T., and Einum, S. 2015. Seasonal

571 effects of hydropeaking on growth, energetics and movement of juvenile Atlantic salmon (Salmo

572 salar). River Res. Appl. 31(9): 1101-1108. doi:10.1002/rra.2801.

573 Puffer, M., Berg, O.K., Einum, S., Saltveit, S.J., and Forseth, T. 2017. Energetic Consequences

574 of Stranding of Juvenile Atlantic Salmon (Salmo salar L.). J. Wat. Res. Prot. 9(2): 20.

575 doi:10.4236/jwarp.2017.92012.

576 R Core Team. 2012. R: A Language and Environment for Statistical Computing. R Foundation

577 for Statistical Computing, Vienna, Austria. http://www.r-project.org/

578 Ratikainen, I.I., Gill, J.A., Gunnarsson, T.G., Sutherland, W.J., and Kokko, H. 2008. When

579 density dependence is not instantaneous: theoretical developments and management

580 implications. Ecol. Lett. 11(2): 184-198. doi:10.1111/j.1461-0248.2007.01122.x.

581 Roy, M. L., Roy, A. G., Grant, J.W.A., and Bergeron, N.E. 2012. Individual variability in the

582 movement behaviour of juvenile Atlantic salmon**. Can. J. Fish. Aquat. Sci. **70** (2):339-347.

583 Saltveit, S.J., Halleraker, J.H., Arnekleiv, J.V., and Harby, A. 2001. Field experiments on

584 stranding in juvenile Atlantic salmon (Salmo salar) and brown trout (Salmo trutta) during rapid

585 flow decreases caused by hydropeaking. Regul. Riv.: Res. Manage. 17(4-5): 609-622.

586 doi:10.1002/rrr.652.

587 Sauterleute, J.F., Hedger, R.D., Hauer, C., Pulg, U., Skoglund, H., Sundt-Hansen, L.E., Bakken,

588 T.H., and Ugedal, O. 2016. Modelling the effects of stranding on the Atlantic salmon population

589 in the Dale River, Norway. Sci. Tot. Env. 573: 574-584.

590 doi:http://dx.doi.org/10.1016/j.scitotenv.2016.08.080.

591 Schlaepfer, M.A., Runge, M.C., and Sherman, P.W. 2002. Ecological and evolutionary traps.

592 Trends Ecol. Evol. 17(10): 474-480. doi:10.1016/s0169-5347(02)02580-6.

593 Heggenes, J., and Borgstrøm, R. 1991. Effect on habitat types on survival, spatial distribution

594 and production of an allopatric cohort of Atlantic salmon, *Salmo salar* L., under conditions of

595 low competition. J. Fish Biol. 38, 267-280.

596 Schmutz, S., Bakken, T.H., Friedrich, T., Greimel, F., Harby, A., Jungwirth, M., Melcher, A.,

597 Unfer, G., and Zeiringer, B. 2015. Response of fish communities to hydrological and

598 morphological alterations in hydropeaking rivers of Austria. River Res. Appl. 31(8): 919-930.

599 doi:10.1002/rra.2795.

600 Scruton, D.A., Pennell, C.J., Robertson, M.J., Ollerhead, L.M.N., Clarke, K.D., Alfredsen, K.,

601 Harby, A., and McKinley, R.S. 2005. Seasonal response of juvenile Atlantic salmon to

602 experimental hydropeaking power generation in Newfoundland, Canada. N. Am. J. Fish.

603 Manage. 25(3): 964-974. doi:10.1577/m04-133.1.

604   Teichert, M.A.K., Einum, S., Finstad, A.G., Ugedal, O., and Forseth, T. 2013. Ontogenetic

605   timing of density dependence: location-specific patterns reflect distribution of a limiting

606   resource. Popul. Ecol. 55(4): 575-583. doi:10.1007/s10144-013-0387-0.

607   Van Cappellen, P., and Maavara, T. 2016. Rivers in the Anthropocene: Global scale

608   modifications of riverine nutrient fluxes by damming. Eco. Hydrobiol. 16(2): 106-111.

609   doi:10.1016/j.ecohyd.2016.04.001.

610   Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., and Smith, G.M. 2009. Mixed Effects

611   Models and Extensions in Ecology with R. Springer, New York.

Tables

Table 1: Overview over the experiments, listing the different treatments and which factor combinations that were tested in the four

seasons. YOY are the young-of-the-year Atlantic salmon, overyearlings are the >1 year old fish, size of fish was measured as fork

length in mm (mean ± SD), and relative size difference between overyearlings and YOY is the size of overyearlings divided by the size

of YOY.

Season	Time of Day	Density YOY (fish m^{-2})	Overyearlings	Number of replicates	Size YOY (mm)	Number of YOY	Size overyearlings (mm)	Relative size difference
Spring	Day	1	absent	36	33 ± 4	353	–	–
	Day	3	absent	37	34 ± 4	1014	–	–
Summer	Day	1	absent	21	49 ± 10	222	–	–
	Day	3	absent	21	48 ± 10	620	–	–
	Day	1	present	61	47 ± 7	596	167 ± 16	3.6
	Day	3	present	57	46 ± 7	1551	172 ± 15	3.7

Autumn	Day	1	absent	21	80 ± 12	200	–	–
	Day	3	absent	21	80 ± 12	614	–	–
	Day	1	present	24	81 ± 12	244	208 ± 12	2.6
	Day	3	present	24	81 ± 13	660	206 ± 14	2.5
	Night	1	absent	24	83 ± 11	236	–	–
	Night	3	absent	24	82 ± 11	721	–	–
	Night	1	present	24	85 ± 12	243	205 ± 12	2.4
	Night	3	present	24	82 ± 12	664	205 ± 10	2.5
Winter	Day	1	absent	24	102 ± 23	242	–	–
	Day	3	absent	24	106 ± 22	706	–	–
	Day	1	present	24	106 ± 21	244	172 ± 11	1.6
	Day	3	present	22	112 ± 20	647	175 ± 11	1.6
	Night	1	absent	26	110 ± 21	256	–	–
	Night	3	absent	25	114 ± 18	719	–	–
	Night	1	present	23	112 ± 18	229	176 ± 11	1.6

30

Night	3	present	24|	119 ± 14	717	176 ± 10	1.5

619   Table 2: Details of the three rivers of the field study. Size of fish was measured as fork length in mm (mean ± SD).

River	Number of stations	Number of transects	Range max. distance from shore (m)	Range max. depth (cm)	Size YOY (mm)	Size overyearlings (mm)	Relative size difference
Nausta	2	16	10–15	33–63	51 ± 4	88 ± 14	1.7
Stjørdalselva	7	71	5–47	45–90	42 ± 4	65 ± 6	1.5
Surna	4	43	5–16	25–70	41 ± 3	79 ± 17	1.9

621 Table 3: Details of the two year classes of Atlantic salmon caught in the three rivers of the field study. YOY are the young-of-the year

622 and overyearlings are > 1 year old individuals. Fish densities are given as mean ± SD values.

River	Number of caught YOY	YOY density in shallow (fish m^{-1})	YOY density in transect (fish m^{-1})	Number of caught overyearlings	Overyearlings density in shallow (fish m^{-1})	Overyearlings density in transect (fish m^{-1})
Nausta	197	0.87 ± 0.47	0.95 ± 0.59	133	0.73 ± 0.64	0.75 ± 0.60
Stjørdalselva	261	0.63 ± 1.08	0.31 ± 0.24	112	0.14 ± 0.23	0.13 ± 0.15
Surna	293	1.14 ± 0.78	0.76 ± 0.39	129	0.18 ± 0.23	0.32 ± 0.23

623

Figure Legends

624

625

626 Fig. 1: Top view and perspective view of an arena used in the experiments. 1: Water inlet,

627 2: deep area, 3: shallow area, 4: mesh screen separating two sections, 5: trapdoor

628 separating the deep and shallow sections, 6: Water outlet.

629

630 Fig. 2: Probability for a YOY Atlantic salmon being in the shallow area in relation to its

631 fork length (in mm) in spring (black solid line). Grey lines indicate posterior calculated

632 95% confidence intervals.

633

634 Fig. 3: Probability for a YOY Atlantic salmon being in the shallow area in relation to its

635 fork length (in mm) in summer, either without (black solid line) or with (black dashed

636 line) overyearlings present. Grey solid and dashed lines indicate the posterior calculated

637 95% confidence intervals.

638

639 Fig. 4: Probability for a YOY Atlantic salmon being in the shallow area in relation to its

640 fork length (in mm) in autumn in either the low (black solid line) or high (black dashed

641 line) density experiments, A) during daytime without overyearlings present, B) during

642 daytime with overyearlings present, C) during night-time without overyearlings present

643 and D) during night-time with overyearlings present. Grey solid and dashed lines indicate

644 the posterior calculated 95% confidence intervals.

645

646   Fig. 5: Probability for a YOY Atlantic salmon being in the shallow area in relation to its

647   fork length (in mm) in winter either without (black solid line) or with (black dashed line)

648   overyearlings present, A) during daytime and B) during night-time. Grey solid and

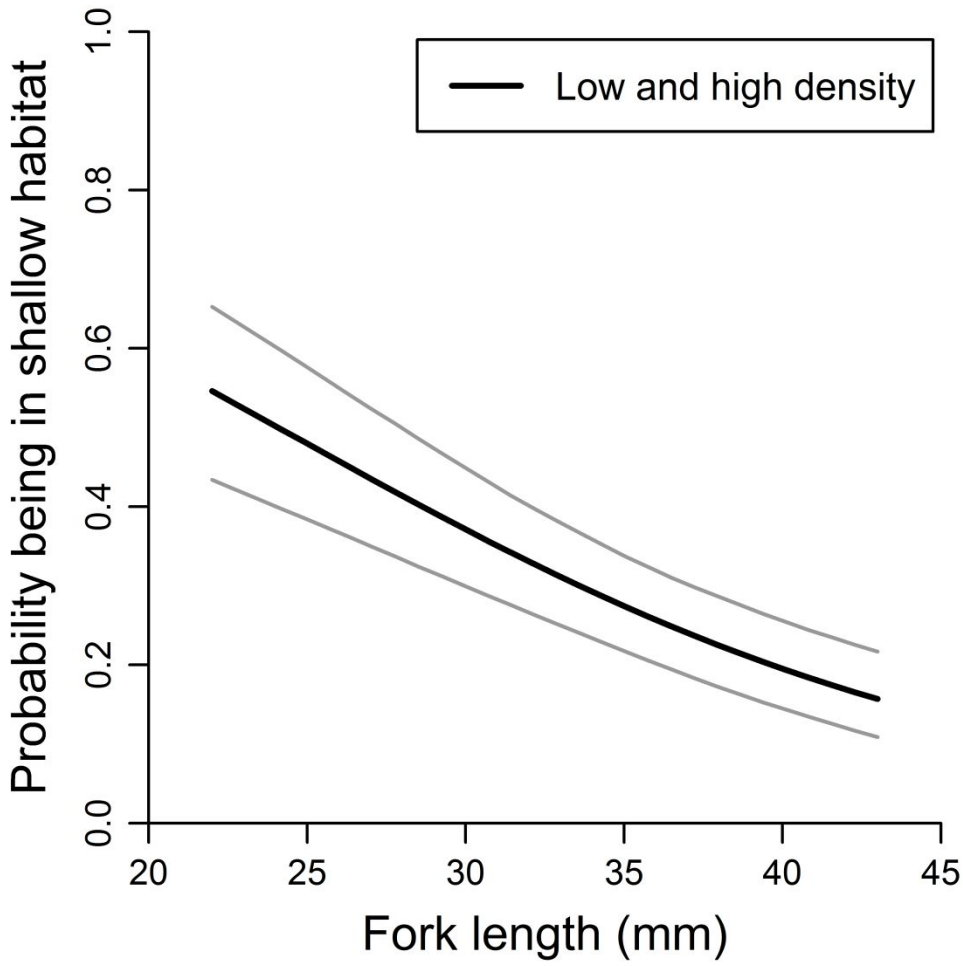649   dashed lines indicate the posterior calculated 95% confidence intervals.

651   **FIGURES**

652
653   Fig. 1

37
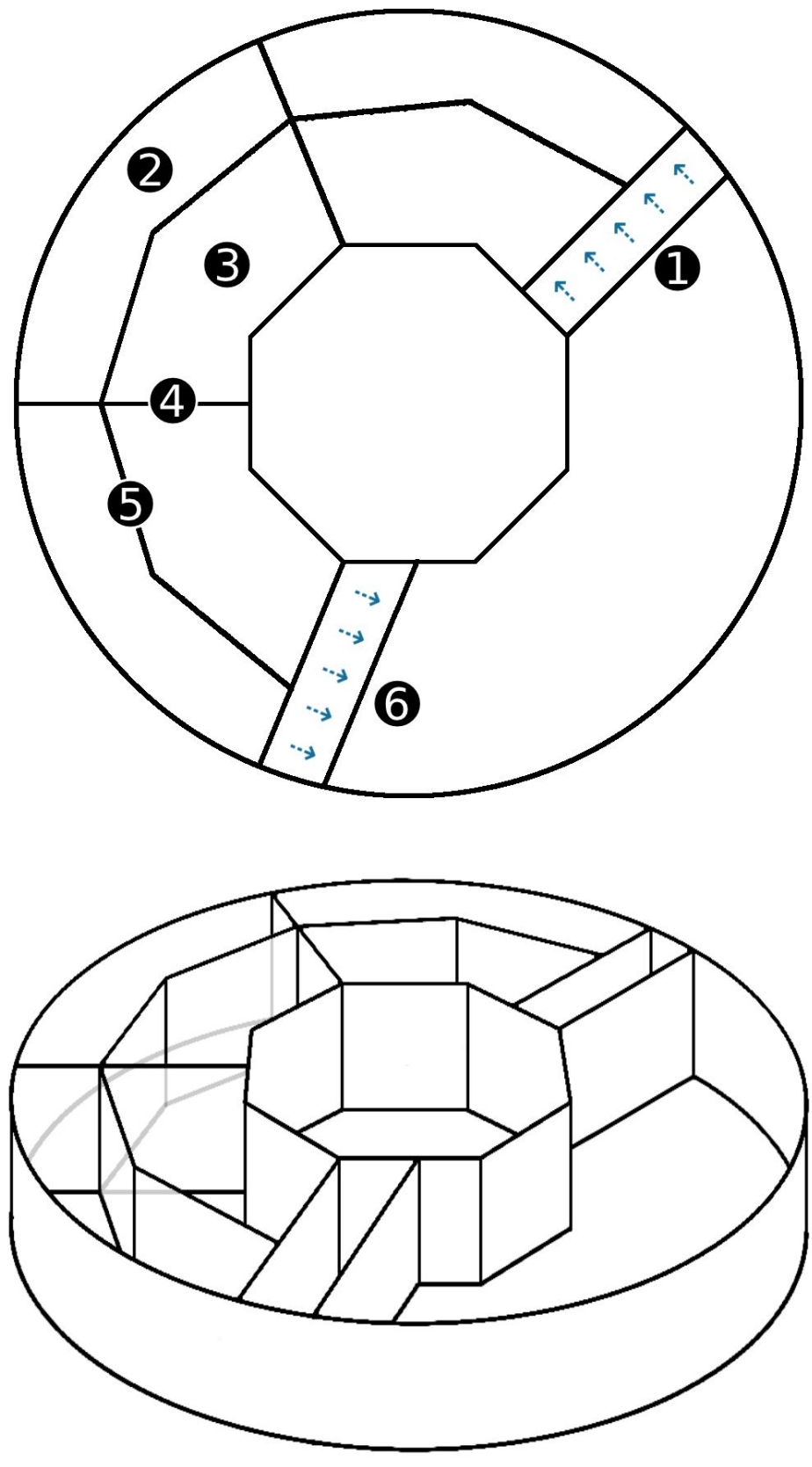
654

655   Fig. 2
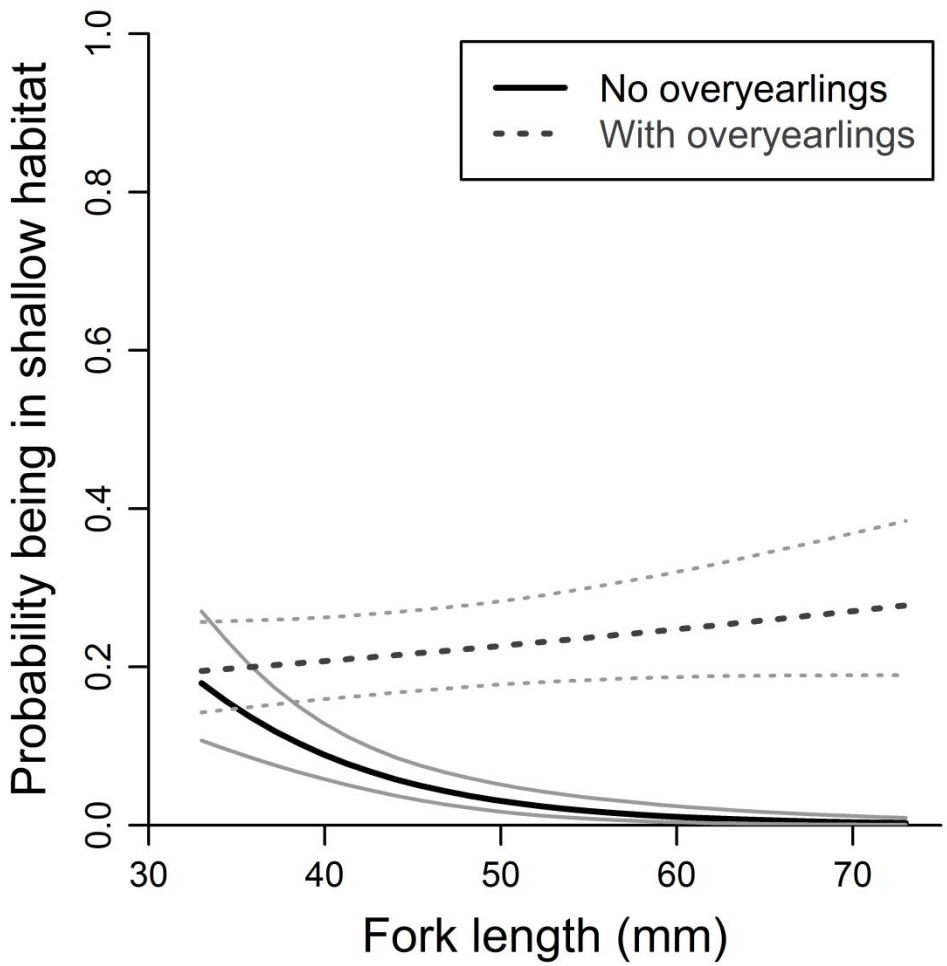
656

657   Fig. 3
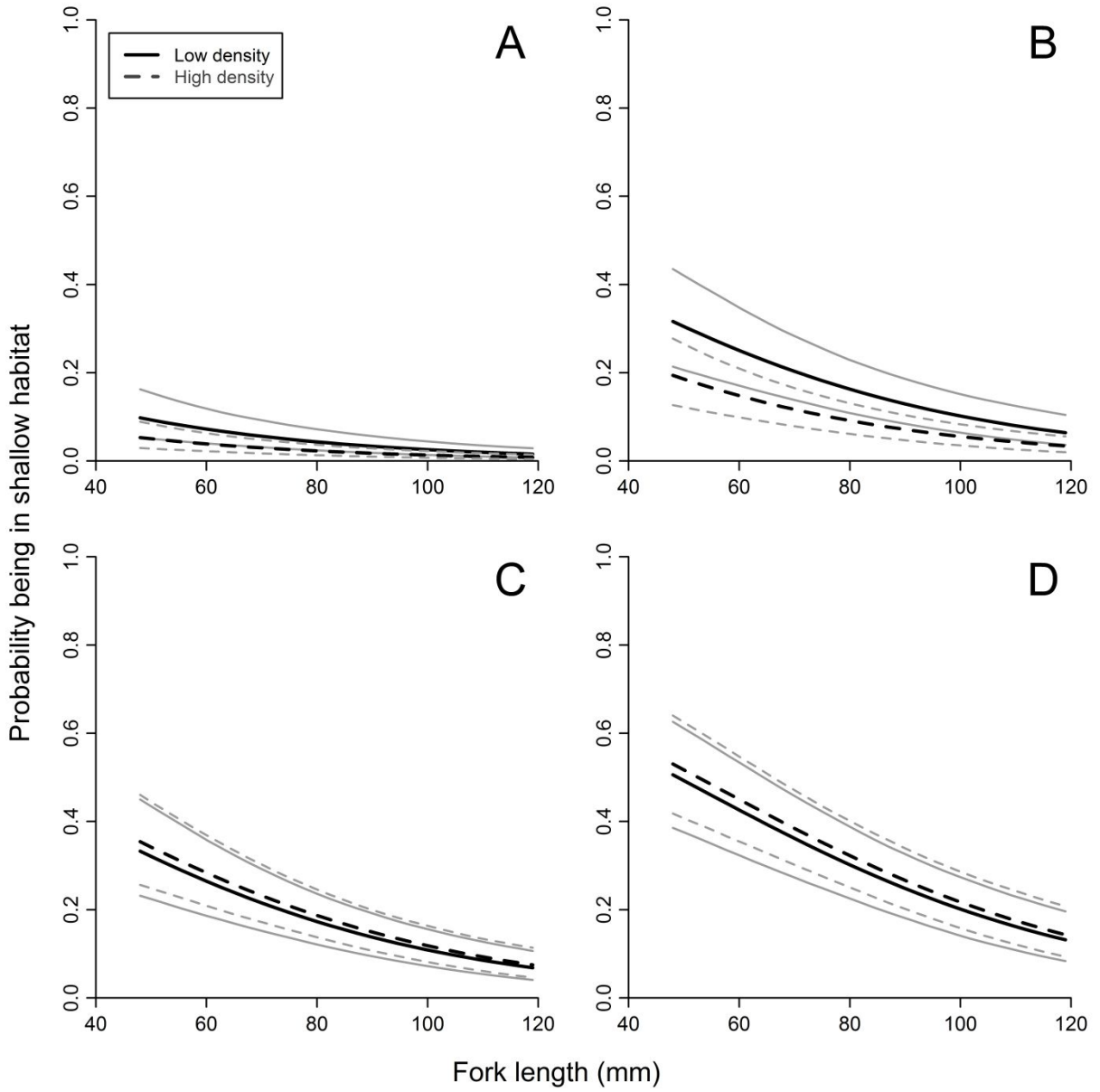
658

659   Fig. 4
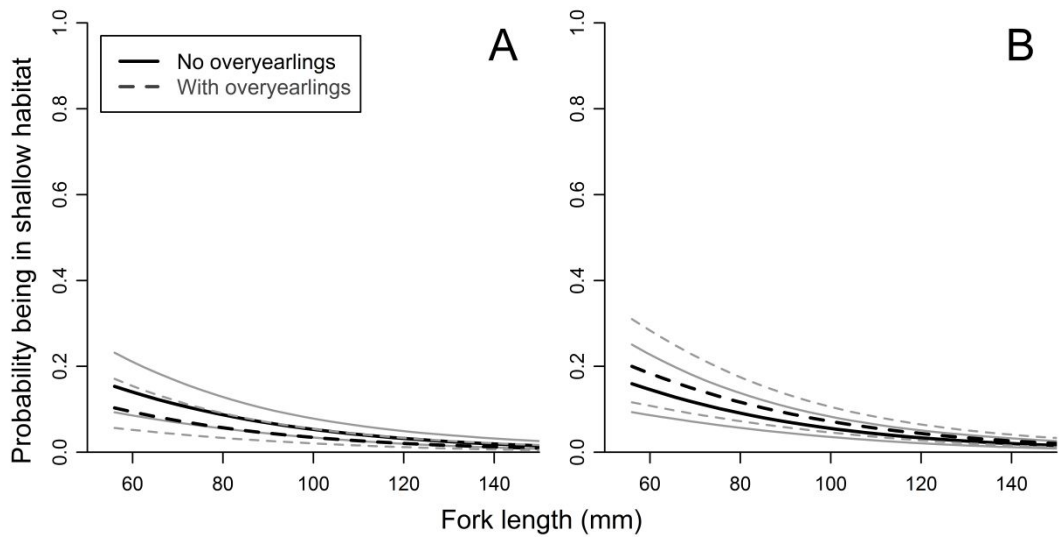
660

661   Fig. 5

Appendix:
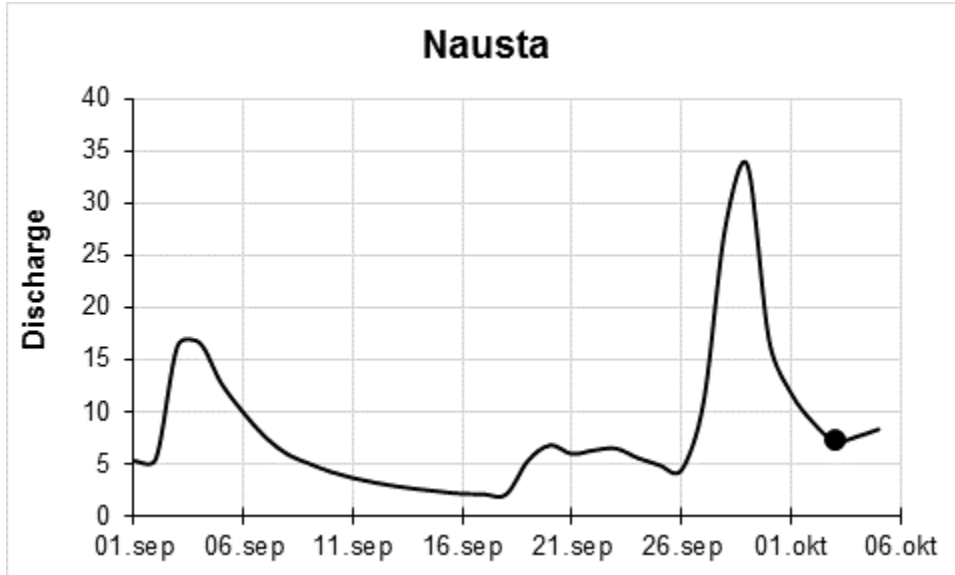
Fig. A1: Hydrograph for river Nausta depicting the period one month before electrofishing (mean daily discharge in m^3s^{-1}). The actual date of electrofishing is marked with a black dot.
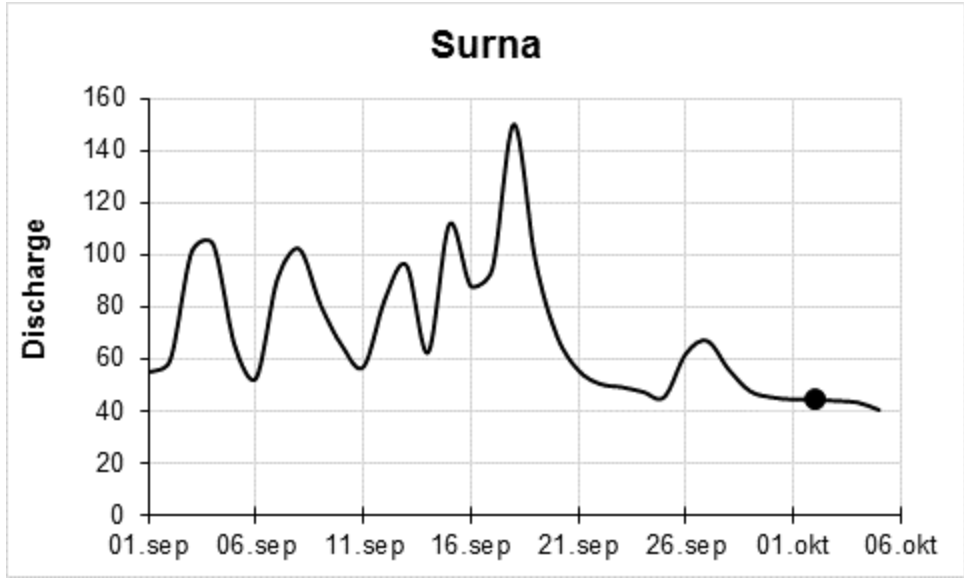
Fig. A2: Hydrograph for river Surna depicting the period one month before electrofishing (mean daily discharge in $m^3 s^{-1}$). The actual date of electrofishing is marked with a black dot.
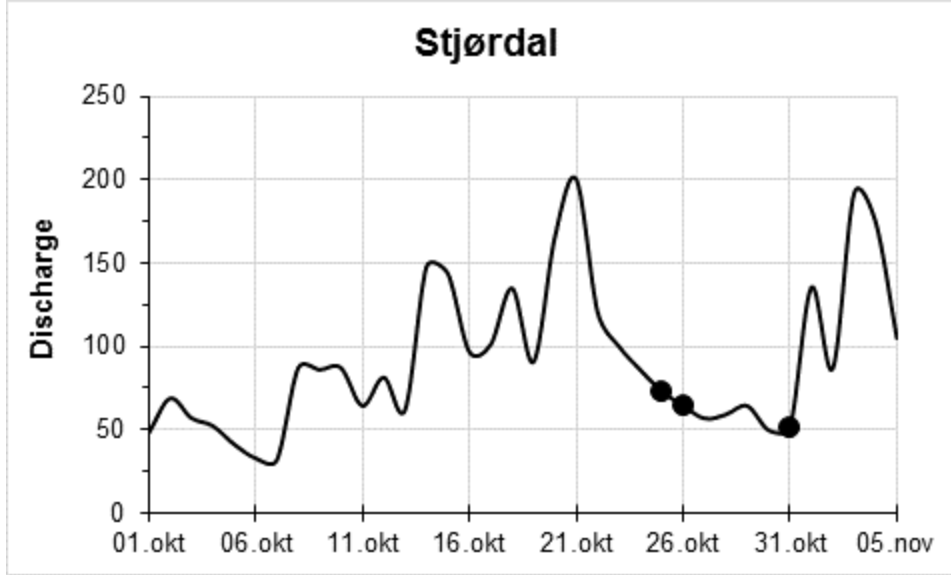
Fig. A3: Hydrograph for river Stjørdalselva depicting the period one month before electrofishing (mean daily discharge in m³s⁻¹). The actual dates of electrofishing are marked with black dots.

Fig. A4: One of the arenas used in the experiments. The water inlet is on the right side, the water outlet on the left. White tarps are providing shade and overhead protection. The photo depicts the 20 hour acclimatisation period when fish could swim freely around in the sections to choose their preferred habitat, i.e. the deep area close to the outer wall or the shallow area close to the inner wall. The mesh screens ("trap doors") are therefore in the upper position, suspended over the water surface. The ropes that are used to activate the trap doors are leading to the centre of the whole construction, which is the place the operator will be standing when releasing them and thus ending the 20 hour acclimatisation period.

Fig. A5: One of the arenas during the 20 hours acclimatisation period seen from upstream. White tarps cover about 50% of each section. The "trap doors" are locked in place above the water surface and are ready to get dropped by removing the metal bolts that are attached to ropes.

Fig. A6: Arena during fishing: The tarps are removed and the trap doors are lowered to separate the shallow from the deep area.

Fig. A7: Inside of the arena: Detail of the downward slope from the shallow to the deep area. The metal rail in the middle will hold the trap door in place once lowered. Fine plastic mesh is fastened to a wooden construction separating the sections from each other.