

1 Fecundity and water flow influence recruitment of Atlantic salmon

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6 Short title: Dynamics of Atlantic salmon

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14 Abstract - Populations are retained at reduced levels by resource competition and
15 environmental stochasticity. In the Norwegian River Imsa, the relationship between fecundity
16 of Atlantic salmon (*Salmo salar*) spawners and number of smolts per unit river area,
17 investigated for cohorts spawned from 1976 to 2011, was best modelled by a density-
18 dependent model. Number of smolts produced each year was described by a multiplicative
19 model and increased with the fecundity of the females as proxy for number of eggs deposited,
20 and minimum water flow in August towards the end of the first growth season. Thus, smolt
21 abundance appeared regulated by density-dependence in fresh water. Water temperature
22 during the first year had no significant effect on recruitment. At sea, there was an almost
23 linear relationship between number of emigrating smolts and returning adults. Survival
24 appeared density-independent, possibly because population density of Atlantic salmon is low
25 relative to the carrying capacity in the ocean.

26

27 Key words: density dependence; River Imsa; *Salmo salar*; sea survival; stock-recruitment

28

29 **Introduction**

30 In any population, number of fertilized eggs defines maximum recruitment, but from
31 fertilization onwards, recruitment is reduced by mortality affected by density-dependent and
32 density independent factors (Elliott 1994). After emergence, density-dependent factors, such
33 as intraspecific resource competition, may be critical for population abundance, and for
34 stream-spawning fish, low water flow may increase the mortality (Nicola et al. 2009; Lobón-
35 Cervía 2014). Because of the ongoing climate warming, river flow has changed. In south-
36 western Norway, for instance, water flow has increased, although periods with drought have
37 also become more severe (Hisdal et al. 2006). This may have affected stream-rearing fish
38 such as Atlantic salmon (*Salmo salar*).

39 Atlantic salmon has a complex life-cycle. The young fish (parr) spend from one to
40 more than five years in fresh water, depending on growth rate and size. At 12 to 25 cm in total
41 length, they move to sea as smolts for feeding (Økland et al. 1993). Atlantic salmon usually
42 spend one to three years in the ocean before returning to the home river for spawning
43 (Jonsson & Jonsson 2011). Less is known about the relationship between number of smolts
44 and number of returning adults in Atlantic salmon, but a previous investigation performed on
45 the River Imsa salmon from 1976 to 1990 did not reveal any density-dependent population
46 regulation in the ocean (Jonsson et al. 1998). A similar relationship was reported for the
47 closely related anadromous brown trout (Jonsson et al. 2009).

48 In the River Imsa, Atlantic salmon have been monitored since 1976 (Jonsson et al.
49 1998). The fish leave the river as smolts to feed in the North Atlantic Ocean, and as adults
50 return to the river for spawning (Hansen et al. 1993). Here, we tested river flow and
51 temperature in any month during the first year after spawning in addition to the fecundity of
52 the females, influenced cohort abundance measured as annual number of emigrating smolts
53 per unit river area. Water flow and temperature are important climatic variables in rivers.

54 Furthermore, we compared number of emigrating smolts and number of adults back to the
55 river from each cohort.

56

57 **Materials and methods**

58 The River Imsa, south-western Norway (58°50'N, 6°E) drains into the Høgsfjord estuary (~32
59 ‰ salt). The river, which is approximately 1 km long, has a restricted spawning area. The
60 river area was ca. 10 000 m² until 1993 when an upstream impassable waterfall was built,
61 precluding salmon from using the upper 165 m of the river and lakes above. The installation
62 of the wear reduced the usable part of the River Imsa by 900 m² to ca. 9100 m². The water
63 temperature in the river was recorded daily at 08.00 hours from 1976 to 2014. The river
64 temperature typically ranges from 2 to 3 °C in winter to a mean summer maximum of 18 °C
65 in July. Annual mean water discharge ranged from 2-3 m³s⁻¹ in summer to a mean autumn
66 maximum at about 8 m³s⁻¹ (Fig. 1). Minimum summer flow was below 5 m³s⁻¹ all years.

67 In the river, a Wolf trap (Wolf 1951; apertures 10 mm, inclination 1:10) situated 150
68 m above the river outlet, catches all descending smolts. All ascending fish are captured in a
69 fixed box trap located alongside the Wolf trap on the top of a three steps fish ladder (Jonsson
70 & Jonsson 2011). The traps were emptied twice a day all year round during the study period,
71 and natural tip lengths (mm, Ricker 1979), masses (g) and sexes of the spawners were
72 recorded. Before leaving the river, all smolts were individually tagged with numbered Carlin
73 tags (Carlin 1955). Stress caused by capturing, anaesthetizing, handling and tagging of the
74 smolts reduced survival after release by approximately 50 % (cf. Jonsson et al. 1998). From
75 1983 onwards, every tenth smolt descending into the trap was sampled for age determination
76 by use of scales and otoliths (Jonsson 1976). The smolt age distribution was used to calculate
77 the number of smolts originating from different brood years, and for years before 1983, we

78 assumed that the distribution was the average of that observed from the age determination
79 between 1983 and 2012. We estimated number of smolts (S) produced from egg cohort of
80 year i as: Number of smolts in year $i + 2$ times the proportion of 1-year-olds that year, plus
81 number of smolts in year $i + 3$ times the proportion of 2-year old smolts that year, plus
82 number of smolts in year $i + 4$ times the proportion of 3-year-olds that year. There was no
83 smolt younger than 1 year or older than 3 years sampled.

84 All adult Atlantic salmon ascending the river were recorded from 1976 to 2014. The
85 fish were divided in two groups. One group was taken into the hatchery for stripping whereas
86 the other group was released upstream of the trap for natural reproduction. This latter group
87 was used for estimating the within river stock-recruitment. During 1982-2015, some sea-
88 ranched salmon of the River Imsa stock, that were hatchery-reared until smolting and then
89 released at the river mouth, were also allowed to spawn in the river. During 1991-1993 no
90 adults were released upstream the trap for spawning in the river.

91 Relationship between fecundity (F) and total body mass (M) of the River Imsa
92 Atlantic salmon are (Jonsson et al. 1996):

93 $F=1.22 M +741.90$, d.f.=16, $r^2=0.79$, $P<0.001$ for wild females and

94 $F=1.79 M +238.18$, d.f.=41, $r^2=0.85$, $P<0.001$ for sea-ranched females.

95 From these regressions, we calculated the number of egg of females allowed to spawn in the
96 river each year. This was used as proxy for number of eggs deposited. Experimental tests
97 indicates that this is a reasonable assumption (Fleming et al. 1997).

98 There is no salmon fishing in the river. Variation in annual number of out-migrating
99 smolts did not differ significantly from normality (Kolmogorov-Smirnov ($K-S$) test with
100 Lilliefors correction = 0,135, d.f. = 37, $P >0.05$). Ln-transformed values of number of out-
101 migrating smolts ($K-S = 0.085$, d.f.=38, $P >0.05$) and returning adults $K-S = 0.111$, d.f.=38,

102 $P > 0.05$) did not differ significantly from normal distributions. However, as the variance in
103 number of smolt and adults increased with sample size, ln-transformed values were used in
104 the regressions.

105 The relationship between estimated number of eggs (E) and number of smolts
106 produced (S) 100 m² river area from the two periods, 1976 to 1990 and 1994 to 2011 was
107 similar (ANOVA: $F_{1,28} = 2.62$, $P > 0.05$), thus the data were pooled. A negatively accelerating
108 stock-recruitment model gave a better fit than the dome shaped Ricker (1954) and the
109 asymptotic Beverton-Holt model (Beverton & Holt 1957) to the data:

$$110 \quad S = E^b$$

111 or in the linear form:

$$112 \quad \ln S = b \ln E. \quad \text{(Equation 1)}$$

113 where b is constant estimated by least squares regression. The estimated intercept did not
114 differ significantly from 0 and was not included in the model. Furthermore, we tested if
115 minimum or mean water flow (W m³s⁻¹) any month during the first year after spawning added
116 significantly to the model:

$$117 \quad S = E^b \cdot W^c$$

118 Or in the linear form:

$$119 \quad \ln S = b \ln E + c \ln W. \quad \text{(Equation 2)}$$

120 where b and c are constants estimated by multiple regression analysis. We also tested if mean
121 water temperature any month during the first year after spawning added significantly to the
122 model, but no significant relationship was found. The best model was chosen based on the
123 AIC_C -criterion (corrected for small sample sizes, Burnham & Anderson 2002). The coefficient
124 of variation ($CV = SD/N$, where SD is standard deviation of number of fish in each cohort and

125 N is mean cohort size) was used to compare variation of number of eggs versus smolts and
126 number of smolts versus adults (Snedecor & Cochran 1973).

127

128 **Results**

129 Number of smolts migrating downstream to the trap in the River Imsa varied considerably
130 between year classes (Fig. 2). For the duration of the study, the overall mean number of
131 smolts 100 m⁻² river area was 11.93 (range 2.64-22.81). Mean number of eggs spawned was
132 2929 100 m⁻² (range of variation 97-13205). The coefficient of variation was 56% lower for
133 number downstream migrating smolts ($CV = 0.432$) than for number of eggs 100 m⁻² river
134 area ($CV = 0.987$) indicating that the variation among cohorts was reduced by the losses
135 during the parr period in the river.

136 The stock-recruitment model (Equation 1) was a highly significant fit ($P < 0.001$)
137 indicating that number of smolts depended on egg density at the start of each year class (Fig.
138 2). Furthermore, minimum flow in August ($W \text{ m}^3\text{s}^{-1}$) towards the end of the first growth
139 season, as a second independent variable, improved the fit (Fig. 3):

$$140 \quad \ln S = 0.282 (\pm 0.044) \ln E + 0.285 (\pm 0.071) \ln W \quad (\text{Equation 3})$$

141 $R^2 = 0.71$, $F_{2,29} = 35.58$, $P < 0.001$, $AIC_C = -74.98$, $t_{\ln E} = 6.42$, $P < 0.001$, $t_{\ln W} = 4.03$, $P <$
142 0.001 .

143 Comparing the two model showed that ΔAIC_C was 11.48 lower in Equation 3 than in
144 the model without minimum flow in August included (Fig. 2). Thus, minimum water flow
145 towards the end of the first summer influenced number of smolts produced from the various
146 egg cohorts. The intercept did not differ significantly from zero ($P > 0.5$) and omitted. Mean
147 water flow in August was also significantly correlated with number of smolts produced, but

148 the fit was poorer than for minimum flow ($\Delta AIC_C = 5.97$). Maximum flow in August or
149 minimum, mean or maximum flow in any other month during the first year after spawning did
150 not add significantly to the model. We did not find any significant effect of mean monthly
151 water temperature in any other month during the first year after the eggs were spawned.

152 There was a linear relationship between number of emigrating smolts and number of
153 returning adults returning to the river (Fig. 4). The coefficient of variation among cohorts
154 increased from 0.624 in number of emigrating smolts to 0.916 in returning adults. Thus, there
155 appeared not to be any tendency of density-dependent regulation of survival at sea.

156

157 **Discussion**

158 The relationship between numbers of emigrating smolts and eggs deposited per unit area
159 exhibited similar relationships during the first and second half of the study period, i.e. before
160 and after the installation of the waterfall preventing salmon access to the upper part of the
161 river and lakes above. Thus, the manipulation of the river had little effects on the recruitment
162 other than that caused by the reduction of the river area. The study did not lend support to the
163 hypothesis that juvenile salmon used lakes in the system as feeding habitat prior to the
164 installation of the wear. This accords with our test fishing before the wear was installed, when
165 no lake dwelling Atlantic salmon parr was found (Jonsson et al. 1988). This result is of
166 relevance to habitat improvement projects.

167 The hypothesis of density-dependent population regulation in the river was supported
168 by the negatively accelerating recruitment curve and the smaller variation among cohorts of
169 smolts than of corresponding egg cohorts. Each extra egg meant less to the number of smolts
170 produced, but the density did not approach an asymptotic value within the egg densities
171 tested. Similar stock-recruitment curves have been fitted for other fish species, such as North

172 Sea herring (*Clupea harengus*) (Rothschild 1986), and several populations of flatfishes
173 (Pleuronectiformes) (Iles 1994). This functional relationship assumes a gradual increase in
174 intraspecific competition among adults on the spawning grounds and/or young fish in the
175 nursery area with increasing adult and recruit density. An alternative would be decreased
176 fecundity or quality of the young with increasing adult density as a maternal effect. However,
177 the present Atlantic salmon is anadromous. Thus, post-smolts and sub-adults at sea do not
178 share feeding habitat with the young in the river, and there was no indication of density-
179 dependent loss in the ocean. Thus, we feel that there is little reason to assume a density-
180 dependent effect on fecundity or offspring quality.

181 The hypothesis of a gradually increasing competition intensity with increasing female
182 and egg densities in the river appears probable. More females may mean increased level of
183 superimposition of nests with more destruction of earlier spawned eggs. This is common in
184 Atlantic salmon (Taggart et al. 2001). Consequently, increased female density may mean
185 more eggs in stream drifts and diets of resident fishes (Moore et al. 2008), and gradually
186 keener competition for food among the offspring during early life, when losses are
187 particularly large (Elliott 1994; Amundsen et al. 2001). This density-dependent, non-linear
188 effect of competition may be the reason why the present model suited well (cf. Jones 1973).

189 Climate variation appears to influence the recruitment of Atlantic salmon through
190 effects on river flow. Years with low water flow in August the year after spawning correlated
191 significantly with weak year classes. We did not find any significant effect of flow in any
192 other month. Earlier during summer, the fish were smaller and may be less dependent on deep
193 water (Heggenes et al. 1999). From September onwards, space may be less restricted because
194 of the increased river flow and gradually reduced appetite and need for space (Metcalf &
195 Thorpe 1992). Thus, low flow in August may restrict recruitment, and less so earlier during
196 summer when the young of the year are smaller, and later in the autumn when flow is higher.

197 Gibson & Myers (1988) found a positive influence of high water discharge on recruit
198 survival of first year Atlantic salmon in Canadian rivers, and Hvidsten et al. (2014), reported
199 that smolt production increased with increasing minimum water discharge for first-year
200 Atlantic salmon in the River Orkla, mid-Norway. Similarly, Nicola et al. (2009) reported that
201 drought caused mortality in Spanish brown trout, and Elliott & Elliott (2006) found low
202 survival in the English Black Brows Beck in years of drought. Thus, there are reasons to
203 believe that low flow is negative for survival in stream-spawning salmonids.

204 In the ocean, density-independent factors seemed important for survival of the fish in
205 accordance with findings from 1976 to 1990 (Jonsson et al. 1998). Number of adults
206 increased linearly with annual number of smolts. Probably, population density is far below the
207 carrying capacity for Atlantic salmon in the North Atlantic. However, growth during the first
208 year at sea has decreased by ca. 40 % since the 1970s (Jonsson et al. 2016), possibly as an
209 effect of reduced zooplankton density, increased interspecific competition from other pelagic
210 fishes and climate change (Beaugrand & Reid 2012; Mills et al. 2013; Friedland et al. 2014).
211 A similar effect was reported for pink salmon (*Oncorhynchus gorbuscha*), where increased
212 survival was associated with increased zooplankton biomass in the North Pacific (Springer &
213 van Vliet 2014).

214 In all, the close fit of the recruitment data to the power function provides strong
215 evidence for density-dependent regulation of the juveniles in the River Imsa, where flow
216 conditions towards the end of the first growth season also seemed to influence recruitment.
217 Post-smolt survival appeared mainly density independent, but the causes for annual variation
218 in abundance, except for number of emigrating smolts, are unknown.

219

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227

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- 327

329 **Legend to figures**

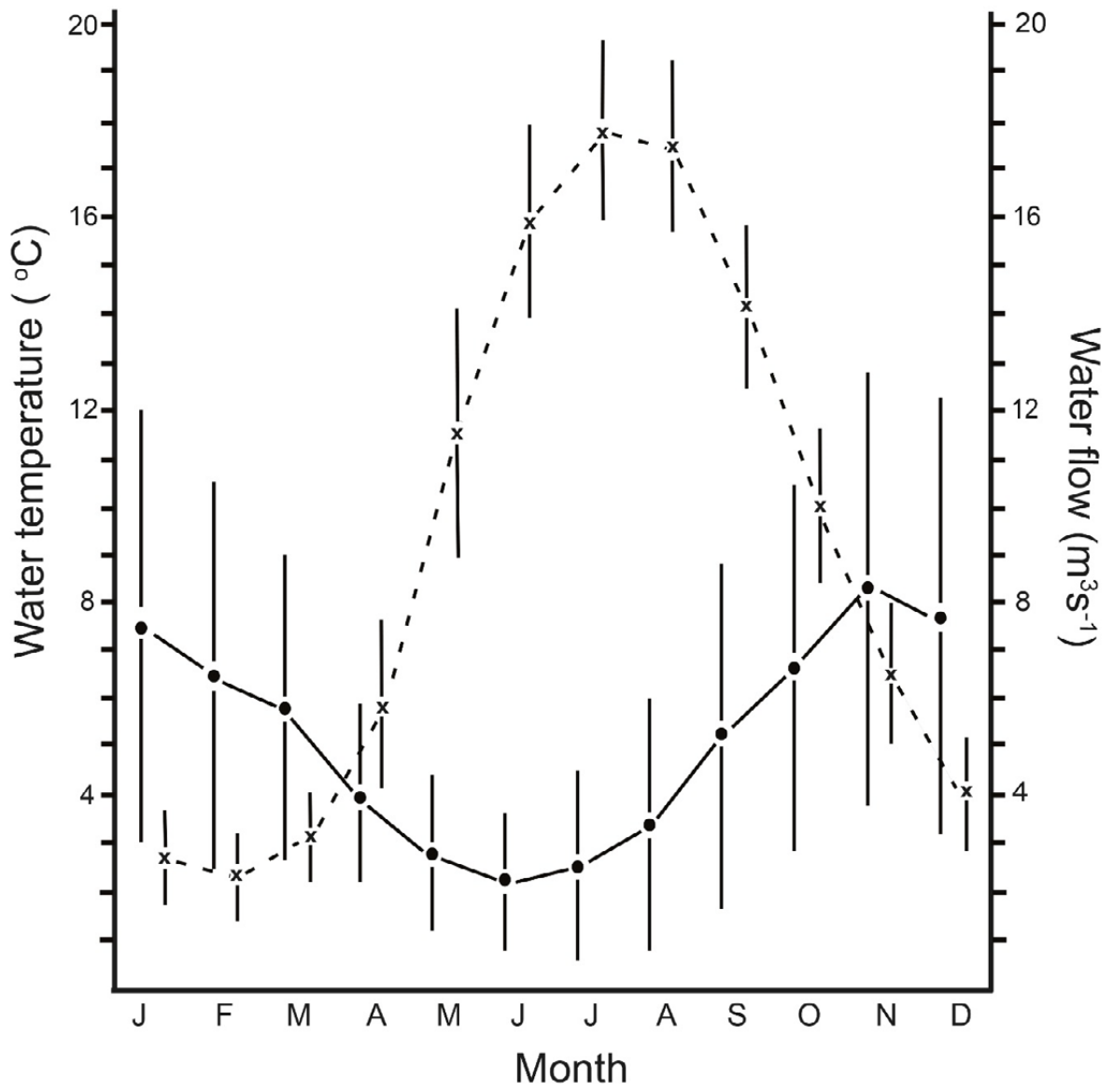
330 **Fig. 1.** Mean monthly water temperature (----°C) and water flow (— m³s⁻¹) ± SD of daily
331 measurements at 08.00 hours in the morning at the outlet of the River Imsa, Norway from
332 1976 to 2014.

333 **Fig. 2.** Relationship (±SE) between number of Atlantic salmon eggs spawned (*E*) each year
334 from 1976 to 2011 and number of smolts (*S*) 100 m² area of the River Imsa. Figures at the
335 data points refer to year when the eggs were spawned: $\ln S = 0.319 (\pm 0.053) \ln E$, $r^2 = 0.55$,
336 $F_{1,30} = 36.6$, $P < 0.001$, $AIC_C = -63.50$, $t_{\ln E} = 6.04$, $P < 0.001$.

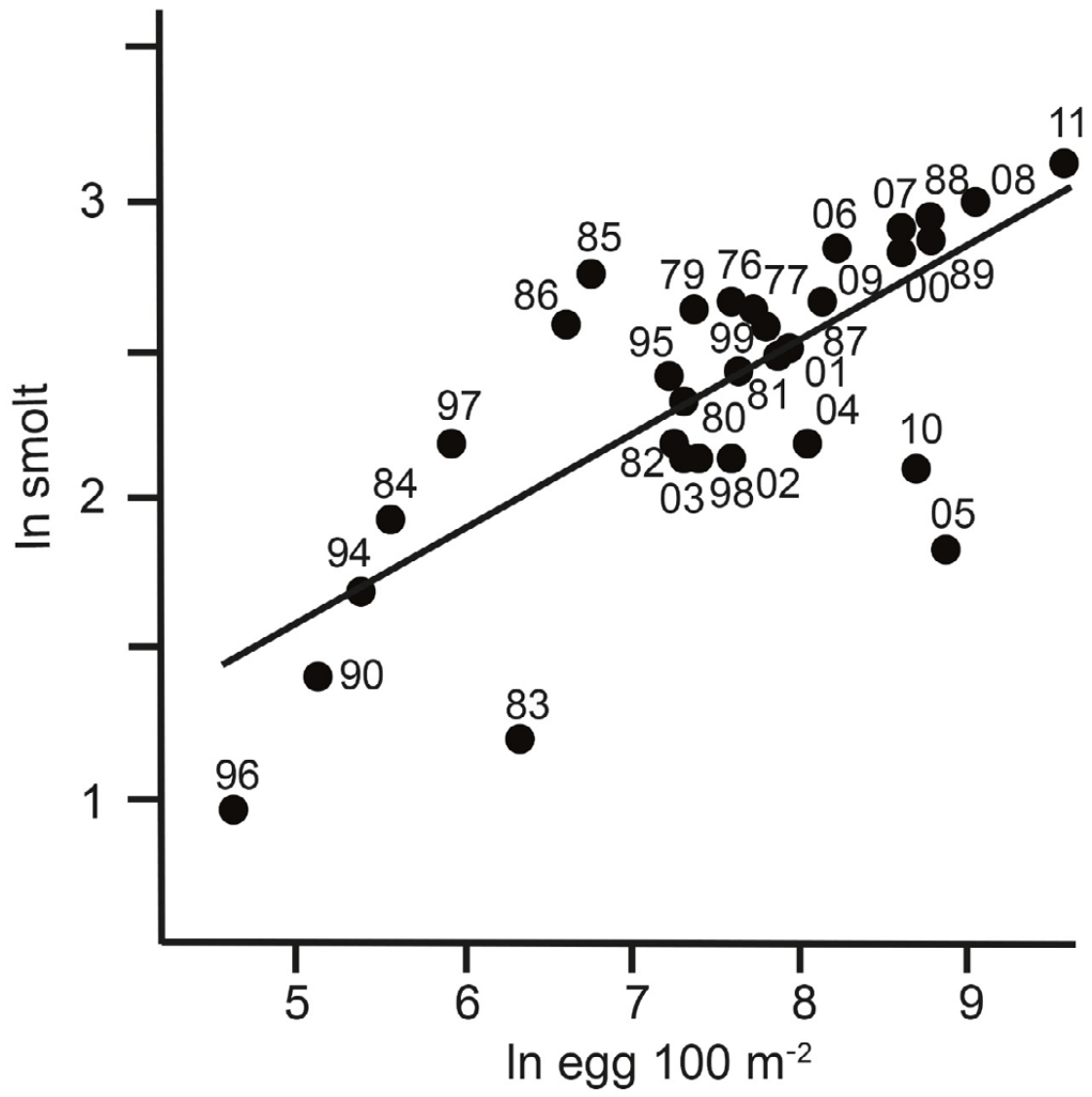
337 **Fig. 3.** Modelled number of Atlantic salmon smolts produced 100 m² river area based on egg
338 density and minimum water flow in August towards the end of the first growth season
339 (Equation 3 in the text).

340 **Fig. 4.** Relationship (±SE) between number of Atlantic salmon smolts (*S*) migrating to sea
341 from 1975 to 2012 and number of returning adults (*A*) returning from each smolt cohort
342 adjusted for mortality due to tagging. Figures at the data points refer to year when the smolts
343 left the River Imsa: $\ln A = 0.89 (\pm 0.146) \ln S - 1.85 (\pm 1.01)$, $r^2 = 0.52$, d.f. = 1,36, $P < 0.001$.

344

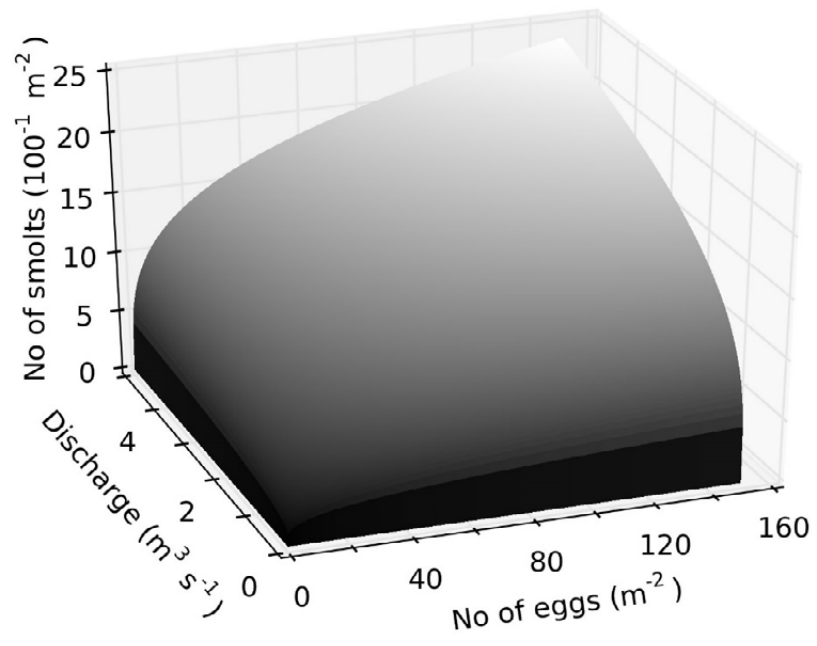


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