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Optimal size at seaward migration in an anadromous salmonid

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19   ABSTRACT: This study gives the probabilistic reaction norm for length at different ages of

20   smolting before seaward migration of Atlantic salmon *Salmo salar*, spawning in the

21   Norwegian River Imsa. The reaction norm was compared with the optimal length at smolting

22   estimated as the product of survival and female fecundity on the return, given their length at

23   smolting. Logistic regression analysis on pre-migratory and migratory fish was used to

24   estimate the probabilistic reaction norm. Length at 50% probability of smolting varied

25   between 11.5 cm and 13.4 cm for age groups 1 to 3 years with a minimum at Age-2. The

26   estimated optimal length at smolting exhibited a maximum at 13.5 cm. Fecundity of adult

27   females was not significantly affected by their length at smolting, making survival the chief

28   variable influencing the optimal smolt size. The results lend support to the hypotheses that

29   body length at 50% probability of seaward migration was similar for all smolt-age-groups

30   independent of growth, and that mean length at each age of the young fish in fresh water

31   reflected the probability of seaward migration. The slight difference between estimated

32   optimal length at smolting and size at 50% probability of smolting may be chiefly caused by

33   size dependent mortality at sea because of the tagging and larger pre-migratory mortality of

34   young than older juveniles in the river.

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36   KEY WORDS: Migration ecology · Anadromy · Probabilistic reaction norm · Reproductive

37   rate · Logistic regression · smolt length · Atlantic salmon · *Salmo salar*

INTRODUCTION

Migration is a key life history event and occurs in all major animal taxonomic groups (Dingle & Drake 2007). In changing and diverse environments, one habitat may not offer the best conditions for survival of the young and feeding opportunities for the juveniles. By migrating, the individuals can use different habitats, food sources and breeding grounds and/or avoid adverse conditions, predators included. By doing this, they are assumed to maximize their net reproductive rate, defined as the product of expected survival and potential number of progeny they produce (Werner & Gillam 1984, Charnov et al. 2013). Thus, the migration strategy is inextricably linked to the variability of the species, and decisions about when to migrate is one of the drivers for early life history success (Sloat et al. 2014).

Large-scale field studies can provide valuable insight into forces that drive trait evolution. For instance, by use of the size distribution at each age of pre-migratory and migratory individuals, one can calculate the probability of migration. Furthermore, one can estimate the survival of each length group and number of eggs produced by the same groups, and use this to estimate their reproductive rate as a proxy for fitness. Heino et al. (2002a) introduced logistic regression as a tool to estimate the probabilistic maturation reaction norm and tested the method on data of Atlantic cod *Gadus morhua*. Corresponding estimates have been given for some other species (e.g. Morita et al. 2009, Olsen et al. 2014, Hunter et al. 2015). According to Dieckmann & Heino (2007), advantages of probabilistic reaction norms are that they overcome systematic biases, remove effects of varying mortality rates and average juvenile somatic growth rates are defined at the level of individuals and serve as indispensable ingredients in process-based dynamical models of a population's age and size structure. Probabilistic reaction norms have wider use and been fitted for size at migration (Piou & Prévost 2012, Castellani et al. 2015). Thus, probability functions can describe length at migration, where each fish length is associated with a certain probability of migration.

63 However, no one appears to have compared this reaction norm with a fitness estimate (cf.

64 Jonsson & Hindar 1982).

65   Here, we use Atlantic salmon *Salmo salar* as an example of how size at migration can

66 be estimated based on long-term monitoring data. The young, called smolts, emigrate to sea

67 when they typically are between 12 and 20 cm in body length, and grow to adult size before

68 they return to spawn (Hansen et al. 1993). They benefit from increased energy intake and

69 growth during the oceanic excursion (Jonsson & Jonsson 2003). However, mortality in the

70 ocean is high (Chaput 2012), and the risk of predation, which is assumed to be the main

71 mortality factor, is influenced by body size, especially during early migration (Salminen 1997,

72 Jonsson & Jonsson 2014). The fish leave the river in small schools and various trade-offs may

73 determine size at migration. Predation may be high if the fish is small (Magurran 1990). On

74 the other hand, the fish risk mortality in rivers and lose growth opportunities by staying long

75 in fresh water. For instance, growth at sea increases with decreasing size at outmigration

76 (Jonsson & Jonsson 2007). Thus, it is important that the size at migration is well adapted so

77 that the product of survival and growth is maximized when integrated over the entire life span

78 (e.g. Jonsson et al. 1984, Charnov et al. 2013).

79   Salmonid smolts typically migrate to sea in spring (Jonsson & Jonsson 2014), and the

80 decision about smolting is made in the previous autumn or winter (Thorpe 1987, Vainikka et

81 al. 2012). The length and age at the decision can thus be estimated from the annuli marked in

82 the scales of the fish that are formed during winter (Jonsson 1976). In the present study, we

83 used the back-calculated lengths at early ages of returning adults to the Norwegian River Imsa

84 to estimate the probabilistic reaction norm of how size varied with age at seaward migration

85 of the young Atlantic salmon. Body length at 50% probability of seaward migration was used

86 as an index of the threshold size for seaward migration. We denote optimale length at

87 smolting the smolt associated with the highest product of total survival and fecundity at

88　adulthood. We hypothesized that: (1) The probability of seaward migration is size-dependent

89　and age-independent. (2) For females, the reproductive rate is highest at 50% probability of

90　seaward migration.

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92　　　　　　　　　　　　　　　　　**METHODS**

93　　　　The 1 km long River Imsa, south-western Norway (58° 50′ N; 5° 58′ E), drains into the

94　Høgsfjord estuary (salinity: 32), near Stavanger. The Atlantic salmon population produces

95　approximately 1000 smolts annually, ranging from 325 to 3208 individuals during the study

96　period. Smolt age varied between 1 to 4 years (Jonsson et al. 1998b). For details on the

97　population structure and dynamics see Jonsson et al. (1991, 1998a).

98　　　　Atlantic salmon were sampled in traps situated 150 m above the river estuary. A Wolf

99　trap (Wolf 1951; apertures 10 mm, inclination 1:10) catches all descending fish larger than ca

100　10 cm, and a box trap catches all ascending Atlantic salmon in the river. The traps

101　(illustrations in Jonsson & Jonsson 2011) were emptied twice a day, at 0800 and 1500 hours,

102　during the study period (1976–2014) except for 1994, when the river was closed because an

103　experiment was performed in the river (Fleming et al. 2000). Total length (0.1 cm) and mass

104　(g) of the fish were measured, and all smolts 12 cm and longer were individually tagged with

105　numbered Carlin tags (Carlin 1955) after being anaesthetized with chlorobutanol before they

106　left the river. Adults were monitored on the return. They were sexed based on external

107　characters, and scales were taken on a subsample (N=671) of the fish for aging and back-

108　calculation of growth (Jonsson 1976, Jonsson & Stenseth 1976).

109　　　　In total, 33 638 smolts were tagged when descending the river 1976-2011 and 1268

110　adults were caught on the return 1977-2014 (Jonsson & Jonsson 2014). Age and length of the

111　fish the winter when they smolted, were estimated by analysis of the scales (Jonsson 1976).

112   Fecundity (F_L) at return to the River Imsa was estimated from the length (L cm) of the

113   females at maturity:

114   $$F_L = 0.052 \,(\pm 0.005) \cdot L^{2.67 \,(\pm 0.024)}; \; r^2 = 0.95, \; df = 2605, \; P < 0.001 \quad \text{(cf. Jonsson et al.}$$

115   1996).

116   We have not investigated the annual mortality of the pre-smolts in the river. Thus, this

117   was set according to Symons (1979) as found for Canadian Atlantic salmon, at 60% mortality

118   during the first winter, 50% mortality from age-1 to age-2 and 40% annual mortality for older

119   smolts. Mortality from eggs to smolts in the River Imsa was estimated at 0.45 % (Jonsson &

120   Jonsson 2016), which is similar to the total pre-smolt mortality found in Canadian Atlantic

121   salmon, ranging from 0.16% to 0.52% (Cunjak & Terrien 1998). By applying the product-rule

122   of probability theory (Devore & Berk 2012), the cumulative mortality for each smolt age in

123   the river was calculated.

124   For estimation of sea survival given their smolt length, we grouped the smolts in 2.5

125   mm groups, starting at lengths 11.0-11.25 cm, 11.25-11.50 cm, etc. Recapture rate (l) of the

126   tagged fish was used as an index of survival at sea and estimated as number of adults

127   recaptured divided by the number of seaward-migrating young of the same cohort (Jonsson &

128   Jonsson 2014). The product-rule was used to estimate the probability of surviving in both

129   river and at sea for each 2.5 mm group of smolts (l_L), and we used unparameterized

130   bootstrapping to estimate lengths and number of fish that died in the river before smolting at

131   Age-1, Age-2 and Age-3 (Heino et al. 2002b).

132   The reaction norm for size at smolting was estimated by 3 logistic regressions, using

133   the bootstrap data along with the observed smolt data. We analyzed the relationship between

134   the length at smolting (L) and the probability of migrating to sea at each age by the logistic

135   model:

136
$$P(X = 1|L) = \frac{\exp(\beta_0 + \beta_1 L)}{1 + \exp(\beta_0 + \beta_1 L)}$$

137   The curves were fitted using maximum likelihood estimation (Devore & Berk 2012),

138   and we give 1, 25, 50, 75 and 99 % probability of smolting at ages 1, 2, and 3 years.

139   Differences between the lengths at 50% probability of smolting of the various age groups

140   were evaluated by creating a 95% bootstrap percentile confidence interval for each smolt age

141   group.

142   To estimate the optimal length at migration we used the log-transformed linear

143   regression of fecundity relative to length at smolting. Then, we fitted a fifth-degree

144   polynomial to estimate mean survival rate given their smolt length. A 95% prediction interval

145   was estimated for new observations of the random variable, assuming that the observations

146   were independent, normally distributed with constant variance. The reproductive rate (R)

147   relative to length at smolting was estimated as: $R = l_L F_L$, where l_L denotes total survival and

148   F_L the fecundity of adult females, given their length at smolting (Mangel 1996). We did not

149   separate survival by sea-age at return, because all individuals were tagged and all those that

150   returned to the River Imsa were recaptured in the trap at the river mouth whether they stayed

151   one or two years at sea. Thus, survival at sea could be estimated for each 2.5 mm smolt length

152   group independent of their sea-age at return.

153

154   **RESULTS**

155   Atlantic salmon of the River Imsa migrated to sea from Age-1 to Age-4, with the

156   majority being Age-2 fish (Table 1). Mean smolt age ($\pm$ SD) was 2.06 $\pm$ 0.32 years, and mean

157   length at seaward migration was 16.3 $\pm$ 1.5 cm. There was no significant difference in length

158   at seaward migration between sexes (t=0.87, df = 1238, $P > 0.05$), and there was no

159   significant relationship between back-calculated length at the end of the first growth season

160   and length at smolting ($r^2 = 0.007$, $P > 0.05$)

161   Young salmon exhibited accelerated growth the last year before smolting relative to

162   those that smolted older (Table 1). For instance, back-calculated mean length of Age -1

163   smolts were 5 cm longer at the end of the first growth season than the length of the non-

164   migrants at that age, that smolted at Age-2 ($t = 6.6$, df = 622, $P < 0.001$). Similarly, Age-2

165   smolts were significantly longer at the end of the second growth season than the non-migrants

166   that smolted at Age-3 ($t = 12.5$, df = 653, $P < 0.001$), and Age-3 smolts were longer than Age-

167   4 smolts at their end of the third year ($t = 2.55$, df = 45, $P < 0.01$). Moreover, smolt length

168   increased with age, and mean length of those smolting at Age-4 was longer already one year

169   prior to smolting, than the smolt length of those that smolted at Age-1. Back-calculated length

170   in winter prior to smolting was on average 2 cm shorter than the observed length of the smolts

171   when they left the river. This difference is due to growth from the winter zone is formed to the

172   fish leave fresh water, and possibly underestimation caused by the scale reading method.

173   The probability of seaward migration increased with size within each smolt-age-group

174   (Fig. 1a-c). The fit was best for the two youngest age-groups. At Age-3, most of the

175   remaining fish migrated. The reaction norm for 50 % probability of migration to sea ($L_{50\%}$)

176   was relatively flat, but with a minimum at Age-2, as $L_{50\%}$ was significantly higher at Age-1

177   than Age-2, but did not change significantly from Age-2 to Age-3 (Fig. 1d). Lengths at 50 %

178   probability of seaward migration were 13.0 cm, 11.5 cm and 13.4 cm at Age-1, Age-2 and

179   Age-3, respectively. If not corrected for the effect of pre-smolts mortality in the river, the

180   estimates would have been approximately 1 cm shorter than these lengths. The width of the

181   migration envelope ($L_{25\%}$ - $L_{75\%}$) increased much from Age-2 to Age-3. Within smolt age

182   groups, fish that were shorter than $L_{50\%}$ most probably stayed in the river one more year,

183   whereas longer fish most probably left, but there is no exact minimum length at migration.

184   The probability of migrating at Age-1 was ca. 1 %, and the corresponding estimated mean

185   length of all the fish the first winter at Age-1 was 6.8 cm (Fig. 1d). At Age-2, the probabiₗity

186   of migrating was 93% and estimated mean length was 15.9 cm, and at Age-3 it was 89% of

187   the remaining fish migrated, and their mean length was 18.5 cm. Thus, there was close

188   relationship between mean smolt length and the probability of seaward migration (error less

189   than 5%).

190   Estimated female fecundity of the returning fish did not change significantly with

191   increasing length at seaward migration (Fig. 2a). The variation in fecundity was large

192   exhibiting that fecundity was not an important variable influencing variation in fitness among

193   smolt-length groups. Total survival, on the other hand, varied depending on length at smolting

194   with a maximum at 13.6 cm (Fig 2 b). Thus, the estimated reproductive rates as measure of

195   the optimal smolt length of the fish in the various smolt-length groups mimicked the survival

196   curve with a maximum at 13.5 cm (Fig. 2c). If not corrected for the effects of pre-smolt

197   mortality in fresh water, the maximum was estimated at 15.1 cm.

198

199   **DISCUSSION**

200   Based on the present data, the reaction norm of length (~11.5-13.4 cm) at 50%

201   migration probability was slightly shorter than the length maximizing the reproductive rate (~

202   13.5 cm), estimated as the product of survival at sea and fecundity at return to the river

203   (hypothesis 2). However, the curve illustrating expected reproductive rate was rather flat

204   between 13 and 14 cm. We do not know why the optimal smolt length was slightly longer

205   than the estimated reaction norm, but assume that this may be related to the mortality

206   estimates of the pre-smolts and tagging mortality at sea. With a relatively higher survival of

207   old than younger pre-smolts than used here (Symons 1979), the reaction norm of length at

208 50% probability of migration would have been longer and closer to the length maximizing the

209 reproductive rate. On the other hand, the smolt length maximizing the reproductive rate of

210 untagged fish may have been shorter than our estimates based on tagged fish indicate, because

211 tagging mortality increases with decreasing smolt size. Our survival estimates were not

212 adjusted for any possible mortality effect of tagging. However, experimental evidence

213 suggests that the tagging on average may double the expected mortality at sea, and is highest

214 for small smolts (Hansen 1988). Isaksson & Bergman (1978) estimated marine mortality of

215 Carlin-tagged smolts. They found that the mortality at sea of 9.5-14.5 cm long Carlin tagged

216 smolts was 3 times higher than for micro-tagged smolts of corresponding length. For longer

217 smolts, the marine mortality was 1.5 times higher for Carlin-tagged than micro-tagged smolts.

218 Thus, Carlin tags increase the mortality even for relatively large smolts, but less so than for

219 smaller smolts. It is uncertain how large the extra mortality cost for smaller body size may be,

220 but if we adjust the estimate with extra mortality as found by Isaksson & Bergman (1978) in

221 their 1974 experiment, the length of smolts giving maximum reproductive rate changed to

222 12.8 cm, which is within the variation at 50 % probability of seaward migration. Thus, both

223 our assumption about pre-smolt mortality in the river following Symons (1979) and higher

224 tagging mortality of small smolts (Isaksson & Bergman 1978) may have contributed to our

225 finding of the optimal smolt length at seaward migration being slightly longer than the

226 reaction norm for 50 % probability of smolting.

227 Survival at sea decreased for fish being longer than 13.5 cm at smolting. This may

228 come as a surprise (cf. Saloniemi et al. 2004), but may be because unusually large smolts are

229 more susceptible to predation. Smolts migrate to sea in small schools, and predators may

230 easily spot fish being different in size from the majority (Rogers et al. 2015). Thus, in this

231 case big body may not give better protection against predators as assumed for larval fish

232 (Miller et al. 1988, Meekan et al. 2006).

233   Length at 50% probability of seaward migration was little influenced by the age of the

234 fish. Still, the estimated smolt size increased with age at smolting (Table1). This may look

235 like a paradox, and one can easily believe that smolt-age is growth dependent as assumed by

236 Økland et al. (1993). However, the observed result is theoretically expected (cf. Heino et al.

237 2002a, their Fig. 4), and parallels the finding by Morita et al. (2005) who showed that that the

238 average size at maturity increase with age although the threshold size for maturity decreased

239 with age in chum salmon (*Oncorhynchus keta*). Based on the present data, length and not

240 growth-rate appeared to be the major determinant for age at smolting as expected if survival at

241 sea is highly dependent on size and not age of the fish. This result lends support to our first

242 hypothesis. Increasing smolt size with age is chiefly a consequence of that older fish were

243 larger the year prior to smolting. Hence, relatively more fish surpassed the length at 50%

244 probability of migration in the subsequent year, and consequently, the smolts become larger

245 with age.

246   There is a close relationship between estimated mean length of the fish in an age group

247 and the observed proportion of fish that migrate at this length. The present estimates of 50%

248 probabilistic reaction norm for length at smolting is ca. 2 cm longer than that suggested by

249 Elson (1957) to be the minimum length at smolting for Atlantic salmon. More recent

250 estimates of length at 50% migration probability of smolting varies between 8.9 cm in the

251 River Scorff, France (Piou & Prévost 2012), and 11.3 cm in the River Stryn, Norway (Hedger

252 et al. 2013). There may be population-specific differences in smolt length among populations

253 because of varying survival and growth (Jonsson et al. 1991), reflected by the genetics of the

254 fish (Piché et al. 2008). Within populations, on the other hand, variation in size at migration

255 may be chiefly due to phenotypic plasticity associated with variation in growth rate (Morita et

256 al. 2009).

257   Individual fecundity did not change significantly with smolt size. This may be a

258   reflection of that the same fish may not do well in both fresh and salt water. For instance,

259   Einum et al. (2002) reported a strong negative correlation between pre- and post-smolt

260   growth, a difference that also holds for the River Imsa salmon (Jonsson & Jonsson 2007). The

261   variation in individual fecundity also increases because sea-age at return varies, which may

262   decouple the relationship between smolt and adult sizes. We do not expect influences of

263   variation in egg size on the optimal smolt size, because fecundity and egg size are highly

264   correlated (Jonsson et al. 1996).

265   Survival was the chief factor responsible for variation in expected reproductive rate of

266   the fish moving to sea at different lengths. At sea, early natural mortality is high and may be

267   chiefly related to predation (Craig et al. 2006, Mäntyniemi et al. 2012). There may be also a

268   physiologically-based mortality associated with migration from fresh to salt water (Hoar

269   1988, Webster & Dill 2006, Jonsson et al. 2016). Furthermore, Beamish & Mahnken (2001)

270   hypothesized that coho salmon *Oncorhynchus kisuch* year-class strength is influenced by

271   winter mortality during the first year in the ocean. They suggested that juvenile salmon that

272   fail to reach a critical size by the end of their first marine summer do not survive the

273   following winter. This may also hold for Atlantic salmon. So far, however, there is no

274   knowledge about a minimum threshold size for winter survival in this species (Friedland et al.

275   2009).

276   In all, our empirical assessment shows that the probabilistic reaction norm approach

277   performed well for size at seaward migration. Mean length of pre-smolt fish relative to the

278   reaction norm reflected well the probability of migration. Furthermore, the probability of 50

279   % migration appeared largely independent of the age of the fish. The most important factor

280   influencing the estimated reproductive rate of the fish was size dependent survival at sea,

281   which was highest for medium-sized smolts. In addition, the reaction norm of 50% probability

282 of seaward migration appeared to be shorter than the length that maximized survival. The

283 exact optimal size at migration is, however, difficult to estimate because of size-dependent

284 tagging mortality and no information on how the pre-migratory mortality varied with age and

285 size of the fish in the River Imsa.

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295

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431   Table 1. Back-calculated lengths (± SD, cm) of Atlantic salmon *Salmo salar* at the end of first

432   (L-1), second (L-2), third (L-3) and fourth (L-4) growth season.

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Smolt age	Sample size	L-1	L-2	L-3	L-4
1	11	11.8 ± 2.5			
2	613	6.8 ± 1.6	16.3 ± 2.4		
3	42	5.5 ± 1.4	11.7 ± 2.5	18.8 ± 3.7	
4	5	4.7 ± 1.5	9.8 ± 2.0	15.4 ± 2.7	20.7 ± 3.2

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Legend to figures

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441 Fig. 1. Probability of smolting of Atlantic salmon *Salmo salar* given their length at (a) Age-1,

442 test of regression coefficient = 0, $P < 0.001$, (b) Age-2, test of the regression coefficient = 0, P

443 < 0.001, (c) Age-3 years, test of the regression coefficient = 0, $P < 0.02$. The curves were

444 fitted by logistic regression, circles along the left axes give length of pre-migratory fish, and

445 circles along the right axes give length of migrating smolts. The figures were tilted 90° as

446 reference to size at 50 % probability of migration. (d) Salmon probabilistic migration reaction

447 norm, showing the reaction norm midpoint (L_{P50}, solid line) and envelope (L_{P25}–L_{P75}, gray

448 polygon), and L_{P1} and L_{P99} (dotted lines).The crosses denote proportion of fish that smolted at

449 the respective ages (corresponding to the probability lines), and the circles estimated mean

450 length of the salmon in the river at these ages.

451

452 Fig. 2 (a) Fecundity of returning adult female Atlantic salmon *Salmo salar* relative to their

453 lengths at smolting estimated from their scales ($r^2 = 0.00$). Broken lines give the 95%

454 prediction interval for future fecundity values. (b) Survival (l_L) was estimated for fish

455 smolting at back-calculated lengths (11.0-11.25, 11.25-11.5 cm, etc) fitted by least squares

456 regression. Broken lines give 95% prediction interval. (c) Estimated reproductive rate (R) of

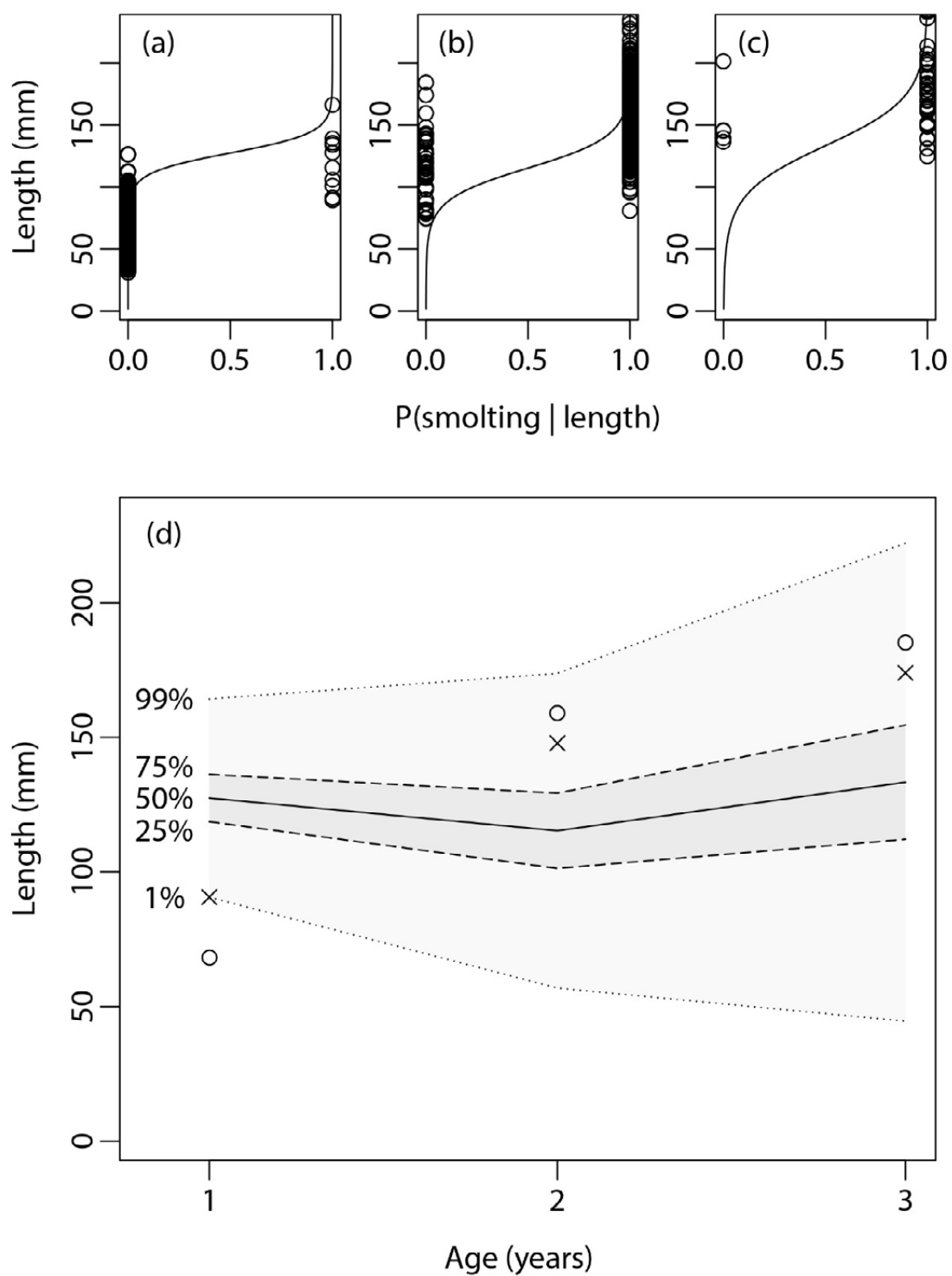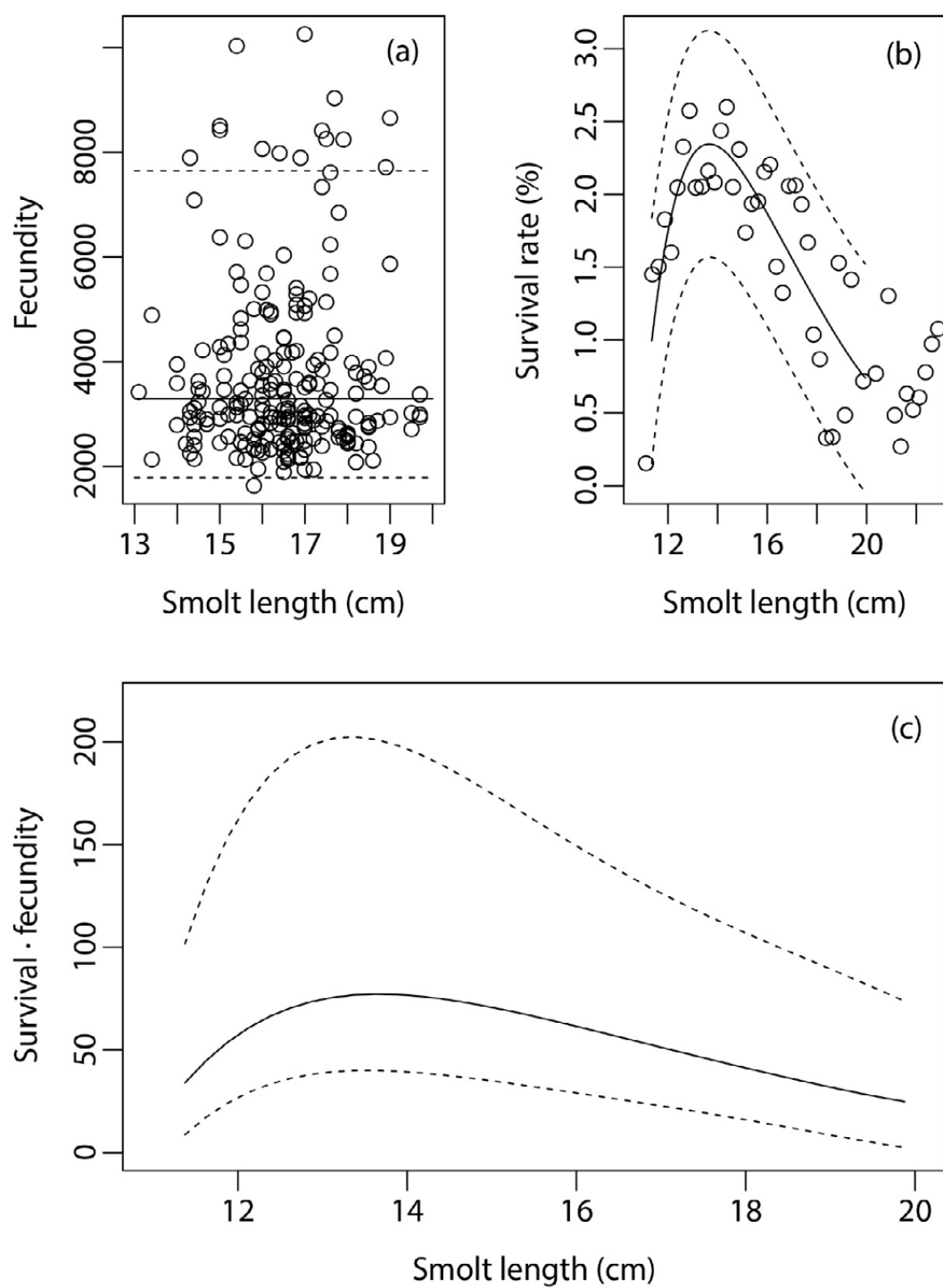457 adult females given their length at smolting (solid line) with 95% prediction interval (broken

458 lines).

459

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Figure 1.

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467
468   Figure 2.