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3 **Time and size at seaward migration influence the sea survival of Atlantic salmon *Salmo***
4 ***salar***
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11 Running head: Time of seaward migration in young *S. salar*

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20 Whether time at seaward migration of young Atlantic salmon *Salmo salar* influences their
21 subsequent survival and growth was investigated in the River Imsa, south-western Norway.
22 *Salmo salar* were tagged when moving downstream through a trap near the outlet
23 between 1976 to 2010 and recaptured on their adult return. Most descended as smolts in April
24 and May, but some descended during the other months of the year. Annual variation in timing
25 of the smolt migration was significantly correlated with variation in water-temperature during
26 spring. Mean total body length of the descending *S. salar* varied with month of seaward
27 migration. The survival at sea of *S. salar* emigrating from the River Imsa between January
28 and May was 2.8 times higher than for those descending between June and December. The
29 sea survival of the various cohorts decreased with increasing river temperature in April-May,
30 prior to the smolt migration, and decreasing day number when the smolts moved to sea. Size
31 of smolts descending the river between April and May did not affect the survival at sea as
32 much as it affected the survival of migrants descending in any other month of the year. The
33 majority of the downstream migrating *S. salar* was 2 years old, but proportionally more one-
34 year-olds moved downstream in the autumn than in the rest of the year. Mean duration
35 between downstream migration of the young and the return migration of the grilse was
36 shortest (12.7 months) for those descending in July/August and longest for those descending
37 in October (21 months). Mean monthly specific growth rate was highest for those migrating
38 downstream between May and July and lowest for those emigrating in September. Based on
39 the present results, it was hypothesized that *S. salar* emigrating between April and August
40 migrated directly out into the ocean, while those which emigrated between October and
41 March stayed in the estuary until the subsequent spring.

42

43 Key words: post-smolts; recapture-rate; sea growth; seasonal seaward migration; water
44 temperature

45

INTRODUCTION

46

47 Although most young anadromous salmonids migrate downstream towards the sea during
48 spring (Jonsson & Ruud-Hansen, 1985), a part of the population may descend a river at other
49 times of the year (Youngson *et al.*, 1983; Jonsson & Jonsson, 2002; Pinder *et al.*, 2007).

50 McCormick *et al.* (1998) reviewed the smolt migration of Atlantic salmon *Salmo salar* L.

51 1758. They emphasized the importance for fisheries managers and research scientists to
52 understand not only the typical *S. salar* migrations, but the full range of possible movements
53 of the species. They assumed that the survival of young *S. salar* migrating into the estuary in
54 summer and autumn would be low because of physiological and ecological mismatches. This
55 hypothesis was at least partly based on experimental evidence that sea-water acclimated
56 groups of hatchery-reared *S. salar* survived best when released in the spring (Hansen &
57 Jonsson, 1989). Findings from anadromous brown trout *Salmo trutta* L. 1758 supported this
58 hypothesis and indicated that survival was best when the smolts entered sea water in late
59 spring, when the temperature of the coastal surface water was relatively high (Jonsson &
60 Jonsson, 2009).

61

62 *Salmo salar* is an anadromous species that spawns in rivers on both sides of the North
63 Atlantic, and is well known for its long migrations in the ocean. The survival of *S. salar*,
64 from when they leave the nursery river to their return to the home river, is usually less than 10
65 per cent (Jonsson & Jonsson, 2011), and the loss at sea is assumed to be highest soon after the
66 smolts reach the estuary, because of high predation from piscivorous fishes, sea birds and
67 marine mammals (Saloniemi *et al.*, 2004; Lacroix *et al.*, 2005; Thorstad *et al.*, 2012). As both
68 the temperature-dependent activity of *S. salar* and the presence of predators vary during the

69 year, the timing of the seaward migration is assumed to be crucial for their survival at sea
70 (McCormick *et al.*, 1998).

71

72 Prior to the seaward migrations *S. salar* undergo a major transformation pre-adapting
73 them for sea life. This transformation process is called smolting, and young *S. salar* ready for
74 migration, are called smolts. Photoperiod is recognized as the main cue influencing the timing
75 of the migration, but variation in water temperature and flow can induce annual variation in
76 the commencement of the run (Jonsson & Jonsson, 2011). Zydlowski *et al.* (2005) maintained
77 that number of degree-days is a good indicator of the initiation and termination of the
78 downstream migration period. They reported that within a population the numbers of degree-
79 days from 01 January to the end of the smolt migration period were approximately the same
80 whether the run started early or late in the season.

81

82 Here, the migration timing of first-time migratory *S. salar* was investigated in the
83 River Imsa. It was tested if month of migration influenced the recapture rate and duration of
84 the migration period, if size at outward migration influenced the recapture rate, if variation in
85 water temperature in April-May influenced the timing of the smolt migration in spring, and if
86 variation in this timing and water temperature influenced the recapture rate of adult *S. salar*.
87 In this river, where water flow usually decreases from winter through spring, it was
88 previously found that temperature, but not water flow, influences the time of the year when
89 the smolts migrate to sea in spring (Jonsson & Ruud-Hansen, 1985). Based on the review by
90 McCormick *et al.* (1998), it was hypothesized that survival and growth at sea was highest for
91 *S. salar* moving downstream to the estuary in spring. This is the first account of survival and
92 growth rate of first-time migratory *S. salar* that compares river descent within and outside the
93 regular smolting period in spring (Riley *et al.*, 2008).

94

95 MATERIAL AND METHODS

96

97 The 1-km long River Imsa, south-western Norway ($58^{\circ}50'N$, $5^{\circ}58'E$), drains into the
 98 Høgsfjord estuary (32‰ **salinity**). Water temperature and flow at the fish traps in the River
 99 Imsa were monitored daily during 1976-2012 (Jonsson *et al.*, 1998a). The mean water flow in
 100 the river **was** $5.1 \text{ m}^3\text{s}^{-1}$, with highest discharge during autumn and winter (mean value: $10 \text{ m}^3\text{s}^{-1}$
 101 $)$ and lowest discharge during summer (mean value: $2 \text{ m}^3\text{s}^{-1}$; Jonsson *et al.*, 1989). The daily
 102 mean water temperature ranged from above 20°C in the summer to *c.* 2°C in the winter.

103

104 The river supports a small population of anadromous *S. salar*. The mean annual
 105 number of smolts is *c.* 1000 individuals; range of variation during the sampling period was
 106 from 325 to 3208 individuals. Smolt age varies between 1 (14%), 2 (78%) or ≥ 3 (8%) years,
 107 and most of the *S. salar* (on average 82% of the returning adults) attain maturity after one
 108 winter at sea (Jonsson *et al.*, 1998a). Smolt age was determined from scales sampled from
 109 every 10th downstream migrating first-time migrant (Jonsson *et al.*, 1998b). The returning
 110 one-sea-winter *S. salar* often denoted grilse, were shorter than 70 cm in total length (L_T) and
 111 less than 3 kg in total wet body-mass. The rest (18%) of the adults mature after two or three
 112 winters at sea (multi-sea-winter), with a decreasing trend during the study period (Jonsson *et*
 113 *al.*, 2003b). *Salmo salar* spawn in the river and the young, called parr, use the river as nursery
 114 before smolting and migration into the ocean. In the River Imsa, *S. salar* cannot move far
 115 upstream because of an impassable waterfall *c.* 1 km above the river mouth. For more details

116 on the population structure and dynamics of *S. salar* in the River Imsa, see Jonsson *et al.*
117 (1991a, 1998a).

118

119 *Salmo salar* were sampled in traps situated 150 m above the river estuary. A Wolf trap
120 (Wolf, 1951; apertures 10 mm, inclination 1:10) catches all descending *S. salar* larger than c.
121 100 mm, and a box trap catches all ascending *S. salar* in the river. The traps (*c.f.* Fig. 6.5 in
122 Jonsson & Jonsson, 2011) were emptied twice a day, at 08:00 and 15:00 h, during the study
123 period (1976-2010) except for 1994, when the trap was closed because an experiment was
124 performed in the river. Almost all smolts entered the downstream trap during night.

125

126 L_T of the *S. salar* was measured (mm), and the downstream moving first-time migrants
127 were tagged with individually numbered Carlin tags (Carlin, 1955) after being anaesthetized
128 with chlorobutanol (<http://pubchem.ncbi.nlm.nih.gov/summary/summary.cgi?cid=5977>) . In
129 total 33 638 smolts were tagged when descending the river [Fig. 1(a)].

130

131 Recapture rate was used as an index of survival (Jonsson *et al.*, 1998a), and was estimated as
132 number of adults recaptured divided by the number of seaward-migrating young. *Salmo salar*
133 is chiefly caught on their return migration from the ocean as adults along the coast, in fjords
134 and in the fish trap of the River Imsa. The River Imsa *S. salar* return in summer and enter the
135 River Imsa from late July to October depending on the water flow in the river (Hansen *et al.*,
136 1993; Jonsson *et al.*, 2007). There have been changes in marine *S. salar* fisheries during the
137 study period. The main changes are the closure of long-line fishery north of the Faroe Islands
138 (1991) and the cessation of the driftnet fishery (1989) in the Norwegian Sea (Jensen *et al.*,
139 1999; Jacobsen *et al.*, 2012). However, none of these alterations is likely to have significantly
140 influenced the present results. Even though marine fisheries have been closed, no increase in

141 the river catches has been seen. A main reason why the River Imsa *S. salar* have been little
142 affected is that the population largely consists of one-sea-winter *S. salar*, too small in size to
143 be targeted in these fisheries. There are only occasional catches of smolts along the western
144 Norwegian coast on their way to the feeding area in the North Atlantic Ocean (Jonsson *et al.*,
145 1993).

146

147 Because of differences in survival between *S. salar* migrating downstream from
148 January through May and June through December, these periods were analysed separately.
149 The figures were not adjusted for any possible mortality effect of the tagging. However,
150 experimental evidence suggests that the tagging may double the expected mortality at sea
151 (Hansen, 1988). In his study, Hansen (1988) found that total recapture rates of adult *S. salar*
152 were 7.7% for unmarked and 3.1% for Carlin tagged smolts. These estimates were not
153 corrected for possible straying, *i.e.* *S. salar* from other populations entering the River Imsa.
154 Recaptures of adult *S. salar* in the coastal sea were reported by fishermen. They gave tag
155 number, L_T , time and place of recapture.

156

157 Specific growth rate of the grilse (≤ 700 mm) was estimated as:

158 $[\ln L_T \text{ recapture (mm)} - \ln L_T \text{ descending (mm)}] \text{ (months at sea)}^{-1}$.

159

160 The smolt migration period was previously determined to be April-May, when the
161 water temperature increases almost linearly. Jonsson & Ruud-Hansen (1985) found that the
162 linear regression of daily water temperature on day number (T) from 09 April to 16 May was
163 the best predictor of the time of *S. salar* seaward migration in May, 1977-83. This period was
164 used when describing the relationship between water temperature and day number each year
165 for the present 34 year-long study period (1976-2010) [increment (X_1) and constant (X_2),

166 [Appendix I]. The increment and constant from these 34 temperature equations were used
167 when testing the effect of water temperature on day number of seaward migration (Y) by use
168 of multiple regression analysis (SPSS) (model: $Y = \beta_1X_1 + \beta_2X_2 + \varepsilon$). Water flow (m^3s^{-1})
169 during this period, as a third independent variable, did not add significantly ($P > 0.05$) to the
170 equation describing time of seaward migration, and was therefore omitted. The
171 commencement of the smolt migration in April-May was defined as time when 5% of the
172 annual number of smolts had descended ($Y_{5\%}$), middle of the smolt migration was when 50%
173 of the smolts had descended ($Y_{50\%}$), and the end of the smolt migration was when 95% of the
174 annual number of smolts had passed the trap near the outlet of the River Imsa ($Y_{95\%}$). The
175 smolts were classified in the field based on that they entered the downstream trap, displayed a
176 silvery colouration and had a stream-lined body form compared to stream living conspecifics
177 (parr) (c.f. Jonsson *et al.*, 1990). This classification relates well with the physiological status
178 of the wild smolts in this river (e.g. Singer *et al.*, 2003). *Salmo* *salar*, denoted smolts, that
179 returned back upstream without any sign of sea growth were few (4) and omitted from the
180 present analysis. The rest of the *S. salmon* were used in the analysis, but only those descending
181 in April – May were called smolts because the physiological status of *S. salmon* descending
182 outside the regular smolt-migration period was not known. It was also not known if *S. salmon*
183 that moved downstream passed the trap outside the smolt migration period were smolted or
184 not. They were therefore denoted first-time migrants to distinguish them from postspawners
185 (called kelts) which also return to sea. The survival of the post-spawners, however, is low and
186 not treated in this, but other papers (Jonsson *et al.*, 1991b, 1997). Some of the smolts were
187 previously mature male parr and described in other studies (Bohlin *et al.*, 1986; Hansen *et al.*,
188 1989; review in Jonsson & Jonsson, 2011).

189

190 Variation in recapture-rate relative to time and size at migration to the estuary and
191 number of *S. salar* that returned to the home river relative to other rivers were tested by χ^2 -
192 tests with number of *S. salar* as input data. Also, differences in length frequencies were tested
193 by χ^2 -tests with numbers as input data. Variations in L_T length of time below the trap, and
194 growth rates at sea relative to month of seaward migration were tested by use of analysis of
195 variance (ANOVA). All calculations were performed by use of SPSS
196 (<http://spss.no.softsonic.com/>).

197

198

RESULTS

199

200 Most first-time migrants moved downstream during the smolt migration period (April
 201 and May), but some came downstream in other months [Fig. 1(a)]. There was a
 202 smaller peak in downstream migration in November.

203

204 Total recapture rate was 2.8 times higher for adult *S. salar* that descended the river as
 205 first-time migrants between January and May than those that descended between June and
 206 December [$\chi^2 = 134$, $P < 0.001$; Fig. 1(b)]. There was variation in monthly mean (\pm S.D.)
 207 adult recapture rate between those that descended the trap between January through May (7.1
 208 \pm 1.4%; $\chi^2 = 33.3$, $P < 0.001$); a minimum percentage in January (3.8%) and a maximum in
 209 May (7.4%). For first-time migrants descending from June through December, adult recapture
 210 rates were similar among months (mean \pm S.D.: 2.55 \pm 0.72%; $\chi^2 = 8.09$, $P > 0.05$). The return
 211 rate of adult *S. salar* to freshwater was 3.1 times higher for those descending between January
 212 and May (3.7%) than those descending between June and December [1.2%; $\chi^2 = 89.3$, $P <$
 213 0.001; Fig. 1(b)]. The percentage recaptured at sea, relative to fresh water, of *S. salar* moving
 214 downstream from January through May, did not differ significantly from those descending
 215 between June and December (48.0% vs. 52.9%; $\chi^2 = 1.32$, $P > 0.05$).

216

217 The time of the smolt migration in April-May decreased gradually for the smolt
 218 cohorts descending the river between 1976 and 2010. Year explained 46 % of the variation in
 219 5 % river descent with dates ranging from 18 April to 11 May (Fig. 2). The regression
 220 illustrates that time of river descent commenced 2 weeks earlier in 2010 than in 1977, and that

221 the change per decade was 4.2 days. Furthermore, year ($X_{50\%}$) explained 51% of the annual
222 variation in 50% smolt descent ($Y_{50\%}$). Between 1977 and 2010 it ranged from 02 May to 25
223 May ($Y_{50\%} = 977.8 - 0.424X_{50\%}$; $r^2 = 0.51$, $F_{1,30} = 30.9$, $P < 0.001$). Thus, time of 50% river
224 descent was also c. 14 days earlier in 2010 than in 1977. Similarly, year ($X_{95\%}$) explained 39%
225 of the annual variation in 95% river descent ($Y_{95\%}$). Between 1977 and 2010 it ranged from 08
226 May to 30 May ($Y_{95\%} = 921.3 - 0.39X_{95\%}$; $r^2 = 0.39$, $F_{1,30} = 18.8$, $P < 0.001$), and the mean
227 delay in 34 years was 13 days.

228

229 The water temperature development during spring, described by the increment (X_i) and
230 constant (X_c) of the linear relationship between water temperature and day number from 09
231 April to 16 May 1976-2010 (Appendix I), was a good predictor for the timing of the smolt
232 migration. The water temperature development explained 70% of the variation in
233 commencement time [5% smolt descent ($Y_{5\%}$)]: $Y_{5\%} = -556.1X_i - 4.86X_c + 156.1$; $r^2 = 0.70$,
234 $F_{2,29} = 33.8$, $P < 0.001$. A similar relationship explained 74% of the variation in 50% smolt
235 descent in April and May: $Y_{50\%} = -523.0X_i - 4.48X_c + 166.7$; $r^2 = 0.74$, $F_{2,29} = 40.3$, $P < 0.001$.
236 Water temperature development also seemed to influence the end of the smolt run: $Y_{95\%} = -$
237 $403.3X_i - 3.25X_c + 170.3$; $r^2 = 0.57$, $F_{2,29} = 19.5$, $P < 0.001$.

238

239 The number of degree-days during spring was not found to be an appropriate proxy for
240 the time of the smolt run. Number of degree-days between 01 January and the end of the
241 smolt migration period (when 95% of the smolts had descended) varied among years from a
242 minimum of 476.8 degree-days in 1979 to a maximum of 802.2 degree-days in 1998 with a
243 mean number (\pm S.D.) of 635.0 ± 85.5 degree-days.

244

245 The return of adult of one-sea-winter *S. salar*, from 1978 to 2010, correlated
246 significantly with day number of 5% cumulative smolt descent in the River Imsa in April-
247 May the year before, when the smolts moved to sea (Fig. 3). Thus, the survival to adulthood
248 increased with increasing day number when the smolt migration started. When using 50% and
249 95% cumulative river descent, the similar relationships were also significant ($r_{50\%}^2 = 0.29$,
250 $F_{1,28} = 11.28, P < 0.01$; $r_{95\%}^2 = 0.13, F_{1,28} = 4.19, P = 0.05$). Furthermore, the multiple
251 regression of adult return-rate of one-sea-winter *S. salar* (Y ; arcsin $\sqrt{\%}$) from 1978 to 2012
252 over the increment (X_i) and constant (X_c) of the temperature equations (Appendix I) was also
253 significant as was all the predictor variables and the constant term (all $P < 0.01$):

254
$$Y = -212.43X_i - 1.74X_c + 29.52; r^2 = 0.35; F_{2,27} = 7.20, P < 0.01$$

255 Thus, the sea-survival, measured as the return rate back to freshwater of adult *S. salar*
256 increased with decreasing water temperature just prior to the smolt emigration period in
257 spring.

258 L_T of descending first-time migrant *S. salar* in the River Imsa varied between 115 mm
259 and 382 mm with a maximum (46.4%) between 150 and 170 mm in L_T [Fig. 4(a)]. The L_T
260 distribution of the recaptured *S. salar* was significantly different from that of the *S. salar*
261 migrating to sea [Fig. 4(b); χ^2 -test for each 20 mm group from 110-129 mm to 270-289 mm,
262 $\chi^2_8 = 57.4, P < 0.001$]. Between June and March, there was positive selection for *S. salar* being
263 larger than 250 mm compared with those being smaller ($\chi^2_1 = 6.88, P < 0.01$). For smolts
264 longer than 150 mm in April-May, L_T at seaward migration showed little influence on the
265 recapture rate ($P > 0.05$), except that there was no recapture of *S. salar* that were between 230
266 and 249 mm in L_T at emigration. Furthermore, there was no recapture of *S. salar* being shorter
267 than 130 mm in L_T at seaward migration.

269 Mean L_T of first-time migratory *S. salar* varied among months of river descent
270 [ANOVA: $F_{11,33620}=772.1, P<0.001$; Fig. 5(a)]. Mean L_T increased from May (163 mm) to a
271 maximum in September (224 mm). Then, it decreased to a minimum in November (154 mm)
272 and December (158 mm). Thereafter, mean L_T increased until March (198 mm) before the
273 spring minimum in April (166 mm). Mean age of the descending first-time migrants varied
274 little among months, but was slightly lower between September and December (1.85 years)
275 than between January and August (1.97 years) indicative that more one-year-olds descended
276 the river towards the end of the year than during spring and summer.

277

278 Mean duration of the period *S. salar* grilse (< 700 mm L_T) spent between descending
279 the river and returning as adults, differed among months of seaward migration. It spanned
280 between 10 and 23 months [ANOVA: $F_{11,1561}=61.7, P<0.001$; Fig. 5(b)]. Those descending
281 the River Imsa as first-time migrants in July and August spent on average 12.7 months in the
282 estuary and at sea whereas those descending in October stayed the longest (mean 21 months).
283 There was a switch in time between August and October with September as the intermediate
284 months when the grilse stayed either one or two winters in the estuary and/or at sea before
285 they returned to the river for spawning.

286

287 Monthly specific growth-rate of grilse during the sea-sojourn differed among months
288 of seaward migration (ANOVA: $F_{11,1614}=24.9, P<0.001$). It was highest for young descending
289 between May – July (monthly mean 0.082-0.087), and lowest for those descending in
290 September (0.0583). The L_T of the grilse appeared to be independent of month of seaward
291 migration (ANOVA: $F_{11,1561}=1.15, P>0.05$), and the overall mean L_T (\pm S.D.) of the grilse
292 was 598 ± 6.0 mm ($n=1574$).

293

294 DISCUSSION

295

296 Young *S. salar* moved to the estuary of the River Imsa in all months of the year,
297 although the majority of them reached the outlet area in April and especially in May. From
298 eastern Canada, Cunjak *et al.* (1989) reported that some young *S. salar* migrated downstream
299 into the estuary during autumn. Power & Shooner (1966) maintained that young *S. salar*,
300 occurring in the estuary in the autumn, were remnants of the previous year's spring smolt run.
301 However, as shown here, young *S. salar* can move downstream outside the smolting season.
302 Even more so in the River Frome, England where as much as 25% of the young *S. salar*
303 emigrated from the river into the estuary during the autumn (Pinder *et al.*, 2007). Thus, most
304 young *S. salar* emigrated in spring, but can move to the outlet area during any month of the
305 year. Apparently, the proportion of the population that descends the river outside the regular
306 smolt-migration period varies among water courses, and it was low in the River Imsa.

307

308 Why do young *S. salar* descend into the outlet area outside the regular smolting
309 season? Armstrong & Griffiths (2001) suggested that *S. salar* entering the estuary in winter
310 may be subordinate, or constrained by insufficient overwintering-habitats (*i.e.* shelter refuges)
311 at the natal sites. The size of the present *S. salar* entering the estuary during January-March
312 was relatively large indicating that they were not subordinate. The alternative explanation
313 appears more probable that *S. salar* moved downstream owing to lack of suitable shelter
314 further upstream. Also, by moving downstream into the estuary in the autumn, the parr may
315 avoid aggressive attacks from the sexually mature *S. salar* fighting for spawning opportunities
316 in the river. In the River Imsa, *S. salar* spawn in November and December (*cf.* Fleming *et al.*,
317 2000), and the dominant adults attack both parr and other adults that approach the spawning

318 grounds. The downstream movement of relatively large parr in winter may also reflect a
319 higher activity of these *S. salmon* than among smaller conspecifics at low temperature (*cf.*
320 Elliott, 1994; Morita *et al.*, 2010). This hypothesis is further explained in the penultimate
321 paragraph of the discussion.

322

323 Smolts migrated earlier to sea in recent years than 30 years ago, and in the River Imsa,
324 the time of the smolt migration in April-May has advanced by 2 weeks since the 1970s. A
325 similar trend has been observed in other populations of anadromous salmonids (Crozier *et al.*,
326 2008; Kennedy & Crozier, 2010; Jensen *et al.*, 2012). However, 4.2 days 10 years⁻¹ is more
327 than the average estimated at 2.9 days 10 years⁻¹ for *S. salmon* in western Europe and eastern
328 North America (Otero *et al.*, 2014), and also slightly higher than the current estimates of
329 global shifts of phenological responses to the temperature increase in spring across the
330 northern hemisphere for multiple taxonomic groups (Parmesan, 2007). The apparent stronger
331 climatic effect in the River Imsa than the general European trend may be because the climatic
332 change is stronger as far north as Norway, than further south in the northern hemisphere as
333 assumed by IPCC (2007). Thus, one may expect an even greater advancement of the smolt
334 migration period further north, and particularly so in small rivers where the water temperature
335 to a larger extent reflects the air temperature than in big rivers.

336

337 The time of the smolt migration probably echoes the timing of the temperature
338 dependent parr-smolt transformation as proposed by Zydlowski *et al.* (2005). This is in
339 agreement with findings reported from work on other salmonids, such as Chinook salmon
340 *Oncorhynchus tshawytscha* (Walbaum 1792) (Achord *et al.*, 2007), Arctic charr *Salvelinus*
341 *alpinus* (L. 1758) (Jonsson *et al.*, 1989), and *S. trutta* (Jonsson & Jonsson, 2002, 2009).

342 However, the present study does not support Zydlowski *et al*'s. (2005) contention that the
343 number of degree-days, from 01 January to the end of the smolt migration period in spring,
344 are approximately the same each year, independent of whether the migration commenced
345 early or late in the season. The reason for the discrepancy is unknown. However, a possible
346 explanation may be that the smolting process starts later than 01 January, and high
347 temperature in winter may add noise to the data set. If so, water temperature in April and early
348 May, as used here, may be a more relevant predictor for the timing of the smolt migration
349 than the water temperature through the winter and spring from 01 January onwards.

350

351 The sea survival and adult return of the *S. salar* moving to the outlet in summer and
352 autumn was lower than that of winter and spring descending *S. salar*. It has been hypothesized
353 that the timing of a smolt's arrival in the estuary is crucial for their successful acclimation and
354 subsequent sea-water survival (Boeuf *et al.*, 1985; Hansen & Jonsson, 1985; Berglund *et al.*,
355 1992; McCormick *et al.*, 1998). The smolts should reach the estuary under favourable
356 environmental conditions maximizing their ability to escape predators (Hansen & Jonsson,
357 1989; Antonsson & Gudjonsson, 2002; Jutila *et al.*, 2003, 2005). The salinity of the water in
358 the outlet area and/or at sea may be stressful if the *S. salar* enter salt water in late autumn or
359 winter when the sea is cold. On the other hand, the winter descending *S. salar* appeared to
360 survive well, making this hypothesis unlikely. Alternatively, predation may be more severe
361 during summer and autumn than winter and spring. Both seagulls *Larus* spp., common
362 mergansers *Mergus merganser* L. 1758, and harbour seals *Phoca vitulina* L. 1758 are present
363 in the estuary, and there are also predatory fishes, such as Atlantic cod *Gadus morhua* L.
364 1758, in the estuary feeding on smolts (Hvidsten & Lund, 1988). Any variation in predator
365 rate during the year was not investigated, but it is assumed that predation may be reduced

366 when many smolts enter seawater simultaneously as a functional response (Wood & Hand,
367 1985).

368

369 Previous studies on the seaward smolt migration of *S. salar* during spring have indicated
370 that the smolts proceed directly into the sea without hesitating in the fjord (Jonsson *et al.*,
371 1993; Holm *et al.*, 2000). The survival was best for cohorts moving to sea when the spring
372 was relatively cold and the migration period was relatively late in the season (Fig. 3). Too
373 early migration into seawater may be disadvantageous because of low seawater temperature.

374 Also, the reserve energy of the smolts may be low (Jonsson & Jonsson, 2003), and young *S.*
375 *salar* may not start growing before the water temperature reaches 6-7° C (Jonsson *et al.*,
376 2001; Finstad & Jonsson, 2012). In the northern Baltic, Jutila *et al.* (2005) found that the
377 survival of released hatchery reared smolts was related to the sea surface temperature during
378 the smolt migration, and this relationship followed a dome-shaped pattern with highest
379 survival between 9 and 12° C. Such a high sea temperature along the west coast of southern
380 Norway is usually not reached before after the middle of May. It appears reasonable to
381 assume that the timing of the seaward smolt migration is adapted to the thermal regime in the
382 river during spring helping *S. salar* to reach the estuary at an expected, proper time. Being in
383 the river, they cannot know the temperature at sea. However, in the present study period, with
384 a relatively higher temperature increase in river and over land than in the ocean (IPCC, 2007),
385 this adaptation may result in decreased sea survival, because the young can smolt and migrate
386 too early in the season, at a time when the ocean is cold. The changed climate appears also to
387 have influenced other life-history variables, such as increased growth rate in fresh water with
388 younger age at smolting as a phenotypically plastic response (Jonsson *et al.*, 2005; Finstad &
389 Jonsson, 2012). At the same time, the marine growth-rate has decreased and there is a higher
390 frequency of one-sea-winter *S. salar* accompanied with increased marine mortality and

391 decreased production (Jonsson *et al.* 2003b; Jonsson & Jonsson, 2004). Experimental research
392 indicates that the latter change is a combined effect of increased water temperature and
393 reduced feeding at sea (Jonsson *et al.*, 2012, 2013).

394

395

396 Apparently, the survival “window” for smolts from the River Imsa is open in the
397 middle of May. Windows of opportunity, when the survival is relatively high, have been
398 described in relation to migration of other diadromous species such as coho salmon
399 *Oncorhynchus kisutch* (Walbaum 1792) (Spence & Hall, 2010), European eel *Anguilla*
400 *anguilla* L. 1758 (Durif & Elie, 2008) and European shads, *Alosa* spp. (Lochet *et al.*, 2009).
401 Furthermore, examples of synchronization patterns of multiple processes such as
402 reproduction, growth or migration to match the optimal environmental conditions are
403 widespread in both marine and terrestrial ecosystems (Durant *et al.*, 2007).

404

405 Young *S. salmon*, which enter the estuary from October and later during autumn and
406 winter, may stay in the outlet area until they smolt and migrate into the ocean in spring
407 concurrently with the smolts in the river, as hypothesized by Cunjak *et al.* (1989) and Cunjak
408 (1992). These *S. salmon* may smolt while staying in the outlet area and join the seaward
409 migrating smolt schools, as observed for released hatchery-reared smolts [a ‘pied piper effect’
410 *sensu* Weber & Fausch (2003)]. This may explain why the survival is relatively high for *S.*
411 *salar* moving downstream in winter. However, *S. salmon* moving downstream from June
412 through August probably came too late to join the large smolt schools. Hence, they may be
413 more exposed to predators when moving to sea. *Salmo salmon* that descended between October
414 and March may dwell in the estuary until the subsequent spring as judged by inspecting their
415 scales in relation to the time and growth rate at sea (Jonsson *et al.*, 199b). Their high mortality

416 may be a reflection of their smaller size and a longer stay in the outlet area. Those descending
417 the river in September appeared to be split between individuals residing near the river outlet
418 to the subsequent spring and individuals moving directly to sea. This assumption is based on
419 the increased variation in time the grilse descending in this month stayed at sea until return for
420 spawning, either one or two years, while their body sizes were similar [Fig 5(b)]. Thus, the
421 present view is based on the length time each individual spent at sea relative to their observed
422 increase in size. Also, if *S. salar* had emigrated to sea during autumn and winter, they should
423 have strayed more to other rivers, but this was not observed (Jonsson *et al.*, 2003a). Increased
424 straying was observed for hatchery *S. salar* released to sea 4 km from the mouth of the River
425 Imsa all months of the year (*cf.* Hansen & Jonsson, 1991). *Salmo salar* appears not able to
426 imprint on the location of their home area during autumn and winter. *Salmo salar* that
427 emigrated from April through August increased from approximately 50 g to between 1 and 2
428 kg, which is the typical growth for *S. salar* staying 15 months at sea. Thus, there is reason to
429 believe that *S. salar* emigrate from the river to the ocean from April to September, but that
430 some individuals dwell in the river estuary from October to April. To verify this, one has to
431 investigate the microchemistry of the otoliths (Kennedy *et al.*, 2002), but this has not yet been
432 done.

433

434 The increase in mean size of the downstream migrating *S. salar* from May through
435 September is probably a reflection of their summer growth in the river, as almost all of them
436 were 2 years old (Jonsson *et al.*, 1990). The sudden drop in size from October to November
437 concurs with a higher percentage of one-year-old first-time migrants. Thereafter, there is an
438 increase in size of the descending *S. salar* until March followed by a decrease in April. The
439 increase in size through the coldest winter period may be because large individuals are more
440 active at low temperature than smaller ones, as the optimal temperature decreases with

441 increasing body size (Morita *et al.*, 2010) and that the metabolic scope at low temperature is
442 higher for large than smaller conspecifics (Elliott, 1994). This was recently illustrated in a
443 study on zander *Sander lucioperca* (L. 1758) (Frisk *et al.*, 2012).

444

445 In conclusion, the results showed that young *S. salar* moved downstream into the
446 estuary during all months of the year. The survival of those moving downstream in the
447 summer and autumn is reduced relative to those moving downstream in winter and spring.
448 *Salmo salar* moving to the estuary between October and March may remain in the outlet area
449 until April-May before moving to sea. The timing of the smolt migration in spring appears
450 strongly influenced by the water temperature, and the migration has started 4 days earlier per
451 decade since the 1970s. The cohort survival was highest in years when the smolts migrated to
452 sea relatively late in May and the spring was relatively cold. Mean monthly growth rate after
453 passing the downstream trap was lowest for those descending the river in autumn and winter.
454 There appears to be selection against moving to the estuary in summer and autumn.

455

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702 **Legend to figures**

703 FIG. 1. (a) Monthly number of descending first-time migrant *Salmo salar* in the River Imsa
704 between 1976-2010, $n = 33638$. (b) Percentage recaptured as adult *S. salar* at sea (open
705 columns, $n = 2024$) and in freshwater (black columns, $n = 1102$) relative to month of seaward
706 migration.

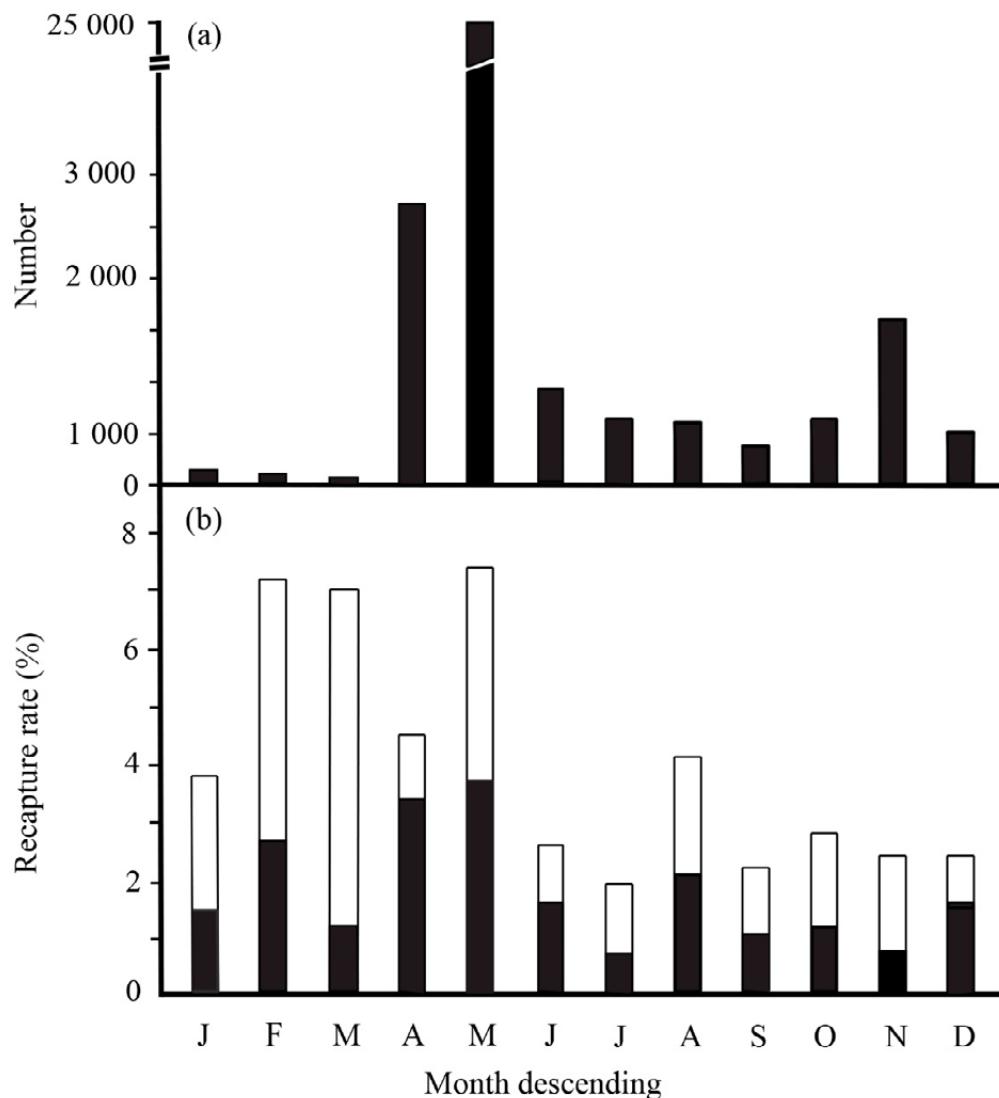
707 FIG. 2. Day number of 5% river descent ($Y_{5\%}$) of young *S. salar* with dates ranging from 18
708 April to 11 May on year of descent between 1977 and 2010 (X). Linear regression equation:
709 $Y_{5\%} = 967.14 - 0.43 X, r^2 = 0.46, F_{1,30} = 30.9, P < 0.001$.

710 FIG. 3. Total recapture rates (R) of adult one-sea-winter *S. salar* between 1978 and 2010 over
711 day number of 5% smolt descent (X) of the cohort the year before; $R = 0.32 X - 24.69, r^2 =$
712 0.25, $F_{1,28} = 9.21, P < 0.01$.

713 FIG. 4. (a) L_T distribution given as number of *S. salar* between 110-129 mm, 130-149 mm etc.
714 of first-time migratory *Salmo salar* caught in the trap at the outlet of River Imsa in April and
715 May (open columns) and rest of the year (black columns) between 1976 and 2010. (b)
716 Recaptures of adults *S. salar* from the various L_T groups of first time migrants.

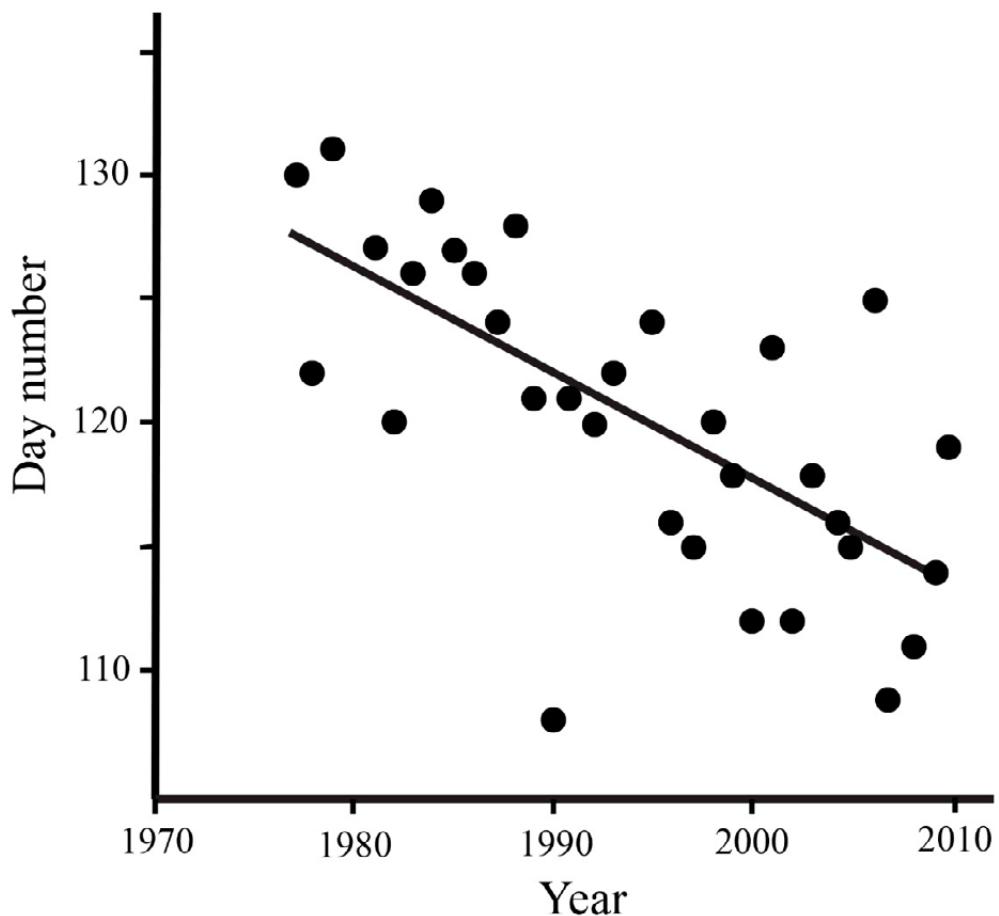
717 FIG. 5. (a) Monthly mean L_T of first time migratory *Salmo salar* descending the River Imsa
718 between 1976 and 2010. (b) Mean number of months at sea (\pm S.D.) of adult *S. salar* grilse
719 ($L_T \leq 700$ mm) in relation to months they descended as first time migrants.

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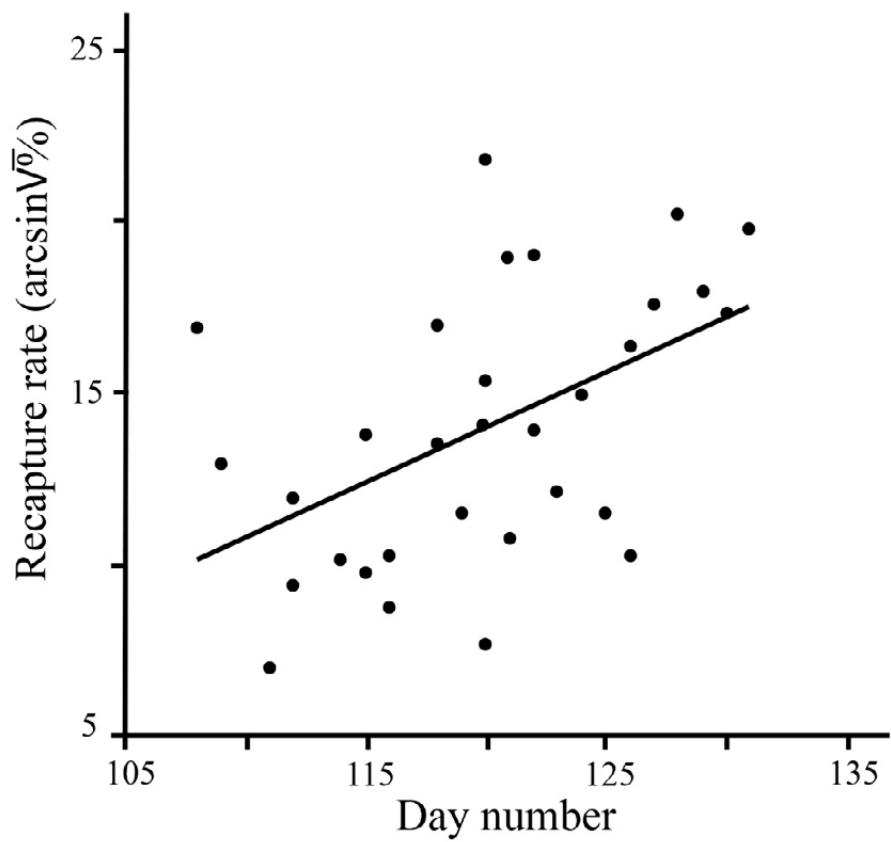
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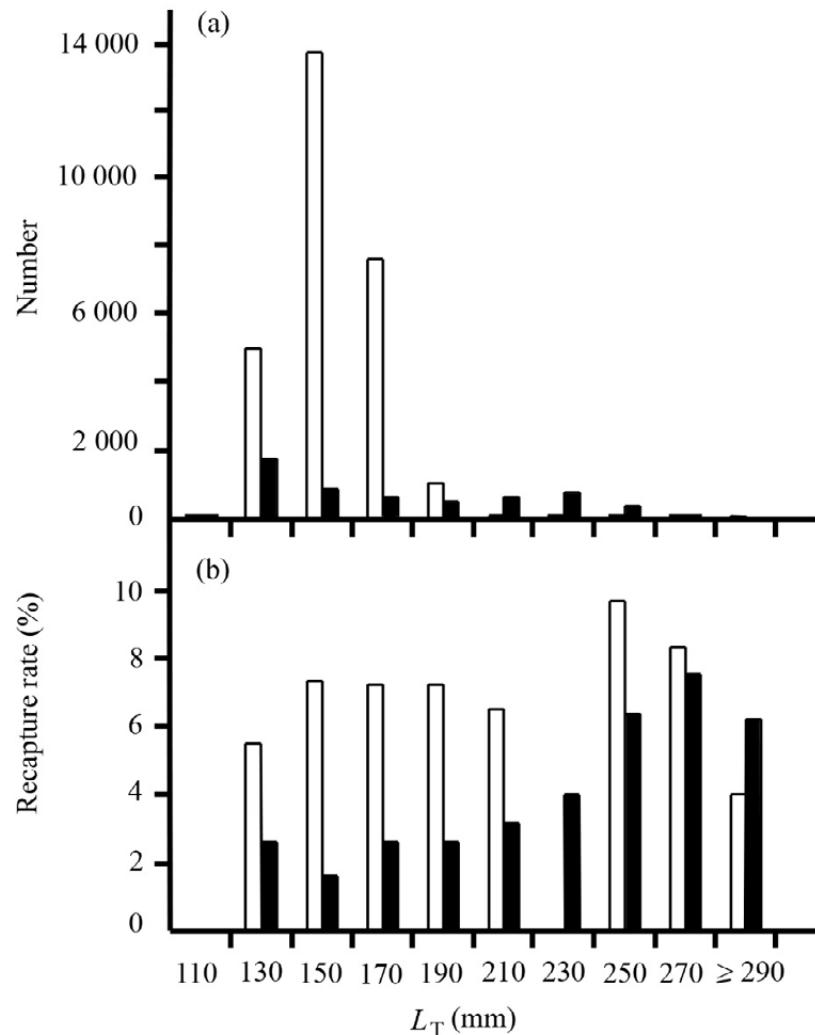


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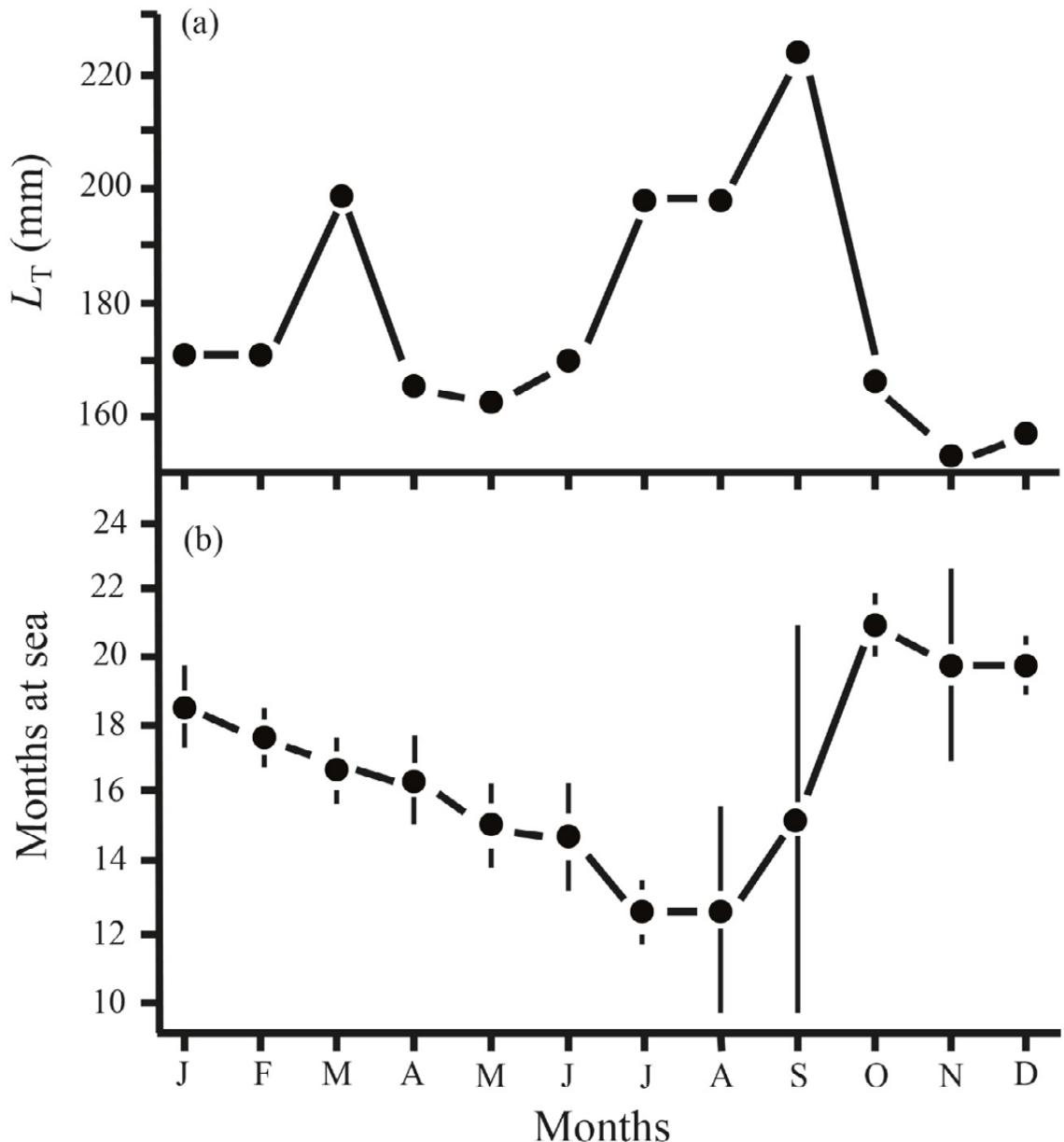


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729 Appendix I. Water temperature (T °C) at the outlet of the Norwegian River Imsa from 09

730 April to 16 May 1976 – 2010. X is day number. The F-statistics and coefficient of

731 determination (r^2) show that all equations are highly significant ($P < 0.001$).

732

Year	Temperature equation	$F_{1,36}$	r^2
1976	$T = 0.178X - 13.99$	358.4	0.91
1977	$T = 0.158X - 12.17$	417.2	0.92
1978	$T = 0.190X - 15.29$	253.0	0.88
1979	$T = 0.090X - 4.97$	255.0	0.88
1980	$T = 0.283X - 24.84$	593.7	0.94
1981	$T = 0.150X - 10.49$	109.2	0.75

1982	$T = 0.102X - 5.22$	56.0	0.61
1983	$T = 0.166X - 12.24$	1018.5	0.97
1984	$T = 0.222X - 18.76$	275.7	0.88
1985	$T = 0.193X - 15.65$	199.1	0.85
1986	$T = 0.234X - 20.36$	288.8	0.89
1987	$T = 0.196X - 15.41$	256.5	0.88
1988	$T = 0.192X - 15.73$	207.3	0.85
1989	$T = 0.099X - 4.04$	164.6	0.82
1990	$T = 0.313X - 26.81$	362.3	0.91
1991	$T = 0.175X - 12.24$	209.9	0.85
1992	$T = 0.083X - 2.68$	94.5	0.72
1993	$T = 0.312X - 27.83$	492.2	0.93
1994	$T = 0.198X - 16.14$	305.4	0.90
1995	$T = 0.175X - 13.44$	246.9	0.87
1996	$T = 0.159X - 11.10$	162.4	0.82
1997	$T = 0.160X - 11.57$	240.4	0.87
1998	$T = 0.254X - 21.84$	355.7	0.91
1999	$T = 0.146X - 9.419$	126.4	0.78
2000	$T = 0.362X - 32.95$	457.3	0.93
2001	$T = 0.303X - 27.65$	375.6	0.91
2002	$T = 0.142X - 7.25$	149.5	0.81
2003	$T = 0.112X - 4.57$	56.6	0.61
2004	$T = 0.234X - 18.40$	750.2	0.95
2005	$T = 0.207X - 15.40$	407.8	0.92
2006	$T = 0.284X - 25.72$	405.2	0.92
2007	$T = 0.194X - 13.39$	121.5	0.77
2008	$T = 0.348X - 30.99$	627.7	0.95
2009	$T = 0.129X - 4.61$	55.3	0.61
2010	$T = 0.146X - 9.34$	253.7	0.88

733

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