

1 **Migratory behaviour and survival rates of wild northern**
2 **Atlantic salmon (*Salmo salar*) post-smolts: effects of**
3 **environmental factors**

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22 Running headline: Migration and survival of northern post-smolt

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ABSTRACT

To study smolt behaviour and survival of a northern Atlantic salmon (*Salmo salar*) population during river descent, sea entry and fjord migration, 120 wild *S. salar* were tagged with acoustic tags and registered at four automatic listening station arrays in the mouth of the North Norwegian River Alta and throughout the Alta Fjord. An estimated 75% of the post-smolts survived from the river mouth, through the estuary and the first 17 km of the fjord. Survival rates in the fjord varied with body length, and ranged from 97.0–99.5% per km. On average, the post-smolts spent 1.5 days (36 h, range 11–365 h) travelling from the river mouth to the last fjord array, 31 km from the river mouth. The migratory speed was slower (1.8 bl sec^{-1}) in the first 4 km after sea entry compared to the next 27 km (3.0 bl sec^{-1}). Post-smolts entered the fjord more often during the high or ebbing tide (70%). There was no clear diurnal migration pattern within the river and fjord, but most of the post-smolts entered the fjord at night (66%, 2000–0800 hours), despite the 24 h daylight at this latitude. The tidal cycle, wind-induced currents and the smolts' own movements seemed to influence migratory speeds and routes in different parts of the fjord. A large variation in migration patterns, both in river and fjord, might indicate that individuals in stochastic estuarine and marine environments are exposed to highly variable selection regimes resulting in different responses to environmental factors on both temporal and spatial scales. Post-smolts in northern Alta Fjord had similar early marine survival rates to those observed previously in southern fjords; however fjord residency in the north was shorter.

Key words: sea entry; diurnal migration; horizontal distribution; migratory speed; acoustic telemetry; Program MARK.

INTRODUCTION

51

52 Over the last decades, the abundances of many Atlantic salmon (*Salmo salar* L.)
53 populations in Europe and North America have declined drastically (Hansen *et al.*, 2008;
54 ICES, 2008). In contrast, most of the populations in northern Norway and Russia have
55 not experienced the same reductions (Niemelä *et al.*, 2004). While reasons for the
56 continued decline are not entirely clear (Parrish *et al.*, 1998), the period of sea entry and
57 first phase of marine life is often considered to be the time at which the majority of
58 marine mortality occurs (Jacobsen & Hansen, 2000; Hvidsten *et al.*, 2009).

59

60 In a recent study, Rikardsen *et al.* (2004) showed that post-smolts had higher feeding
61 rates in the northern fjords more so than those from southern fjords along the Norwegian
62 coast. Northern populations also had the largest and oldest smolts, potentially reducing
63 the risk of predation while entering the sea. Later, Knudsen *et al.* (2005) used marine
64 endoparasites as bio-indicators of feeding and sea residence of post-smolt and reported a
65 prolonged feeding migration up to several weeks in northern fjords compared with those
66 in the south. Overall, however, little information exists about the early marine survival
67 and migration pattern in southern populations (Lacroix *et al.*, 2004b; Thorstad *et al.*,
68 2007; Lacroix, 2008) and virtually no published information exists on the early marine
69 survival during sea entry and duration of migration of northern populations.

70

71 Among factors that can affect the migration behaviour and survival is the fjord
72 morphology. Many southern Norwegian fjords are characterised by long and narrow sill
73 fjords with several rivers draining into them, resulting in a brackish surface water layer.
74 North Norwegian fjords are often shorter and wider with only one main river in the fjord
75 bottom. They are usually more productive, more strongly influenced by the coastal and
76 tidal current, and with less clearly defined sills (Rikardsen *et al.*, 2004). As potential

77 predators are most abundant within fjords (Hvidsten & Lund, 1988; Svenning *et al.*,
78 2005), a long fjord may increase the predation risk. A longer fjord residency, as
79 postulated for post-smolt in the northern fjords (see above), also increases predation risk.
80

81 The northernmost post-smolts are exposed to 24 h sunlight during their migration
82 (Veselov *et al.*, 1998; Davidsen *et al.*, 2005), in contrast to the southern populations, for
83 whom the sun sets at night. In the south, smolt migration usually takes place at night.
84 However, towards the end of the migration period and during periods with high water
85 temperatures, migration may take place both night and day (Hvidsten *et al.* 1995,
86 Ibbotson *et al.* 2006). Nocturnal migration might be a strategy to prevent or minimize
87 predation by visual predators (Solomon, 1982; Jepsen *et al.*, 2006), and this migration
88 pattern seems to continue when smolts are entering the sea, as most smolts seem to enter
89 salt water during hours of darkness (Moore *et al.*, 1995; Koed *et al.*, 2006). In contrast,
90 the within-river smolt migration in northern rivers with 24 h light showed smolts
91 descending during both night and day (Veselov *et al.*, 1998; Davidsen *et al.*, 2005). For
92 northern populations, no information has been published on the timing of smolt migration
93 into the fjord.

94

95 Overall, there is a lack of information on early ocean migrations, especially for northern
96 *S. salar* populations. Given the potential importance of the initial life-history stage of
97 post-smolts at sea to overall marine survival, the focus of this study was to examine the
98 survival and migratory speeds of northern smolts and post-smolts during i) final within-
99 river migration, ii) sea entry, and iii) fjord migration. The observed fish behaviour was
100 correlated with the tidal cycle, day and night periods, fjord currents and wind speeds and
101 directions.

102

MATERIAL AND METHODS

103

104

105 STUDY AREA

106 The River Alta, northern Norway (70°N 23°E), has a mean annual water discharge of
107 $75 \text{ m}^3 \text{ s}^{-1}$ and a catchment area of $7\,400 \text{ km}^2$ (Fig. 1). A 46 km long river stretch is
108 available to *S. salar*. The river drains into the Alta Fjord, which has three channels to the
109 northern Atlantic. This is a large, open fjord, which is 15 km at its widest and 488 m at its
110 deepest. Tidal range is about 1.5–2.5 m. The temperature in the river usually varies from
111 10–15° C during the main smolt run, which occurs during late June–middle July
112 (Hvidsten *et al.*, 1998).

113

114 SMOLT CAPTURE AND TAGGING

115 A smolt trap (fyke net with guiding fences) operated 11 km upstream of the river mouth
116 during the entire smolt run in 2004–2006 (22 June–17 July 2004, 17 June–27 July 2005
117 and 14 June–02 August 2006). In 2007, the trap was operating from 24 June–17 July,
118 only covering the last half of the smolt run. The diurnal pattern of the smolt decent was
119 therefore based on the 2004–2006 catches. The trap was emptied 2–4 times every 24
120 hours, with day catches sampled from 0700–1000 hours until 1800–2200 hours, and night
121 catches sampled from 1800–2200 hours to 0700–1000 hours. Number of fish caught per
122 hour was used as an indication of the movement of the smolt. Smolts were distinguished
123 from parr based on external phenotypic characteristics (Wedemeyer *et al.*, 1980). Only
124 1% of smolts were smaller than 120 mm fork length (L_F).

125

126 In 2007, 120 wild smolts caught in the smolt trap were tagged with individually coded
127 acoustic transmitters (Thelma AS, Norway, model LP-7.3, diameter of 7.3 mm, length of
128 18 mm, mass in water/air of 1.2/1.9 g). The smolts were tagged during two periods, 26–

129 28 June (period 1, $n = 60$, mean L_F 146 mm, range 133–168 mm, S.D. = 6; mean mass 28
130 g, range 22–39 g, S.D. = 4) and 2–4 July (period 2, $n = 60$, mean L_F 147 mm, range 134–
131 177 mm, S.D. = 9, mean mass 30 g, range 22–51 g, S.D. = 6). There was no difference in
132 body length (t -test, $n = 120$, $P = 0.63$) or mass (t -test, $n = 120$, $P = 0.10$) between the two
133 groups. The smolts were kept in a tank with circulated water for up to two hours before
134 tagging. Surgical implantation of transmitters was performed as described in Davidsen *et*
135 *al.* (2008). Approximately ten minutes after recovery, the smolts were released into the
136 river at the capture site. In each period, the smolts were tagged and released into four
137 groups ($n = 15$ in each group), of which two groups were released at 0900–1000 hours
138 and two at 2100–2200 hours.

139

140 **RECORDING OF FISH BY AUTOMATIC LISTENING STATIONS AND** 141 **MANUAL TRACKING**

142 Two automatic listening stations (ALS) (Vemco INC, Canada, model VR2) were
143 deployed two meters below the water surface in the river mouth (Fig. 1). Three ALS
144 arrays were deployed across the fjord at 4 km (11 ALSs), 17 km (14 ALSs) and 31 km
145 (21 ALSs) from the river mouth (Fig. 1). The ALSs within each array were deployed five
146 meters below the water surface and separated horizontally by 400 m. The ALSs recorded
147 the acoustic id code of the tagged post-smolts and the time from when they were within a
148 range of 50–300 m from the ALS (detection range depended on environmental
149 conditions). The last registration of individual smolt in the river mouth was used as the
150 time of sea entry. At the three arrays in the fjord, the first registration was used as the
151 time of arrival at the array. Manual river tracking was performed every second week
152 during 28 June–14 October by using an acoustic receiver with an omnidirectional
153 hydrophone (Vemco INC, Canada, model VR100) to detect any smolts remaining in the
154 river.

155

156 **ENVIRONMENTAL VARIABLES**

157 Environmental variables (temperature, salinity, tidal cycle, light intensity, water current
158 and wind speed and direction) were recorded in the fjord. Temperature and salinity were
159 measured in order to describe the fjord system, while tidal cycle, light intensity, water
160 current and wind speed and direction were correlated with post-smolt behaviour. Salinity
161 and temperature profiles were recorded at every second ALS across all arrays down to 12
162 meters depth on 6 July at low tide (Fig. 2), using an SD204 CTD-sonde (SAIV AS,
163 Norway). The dataset was analysed, gridded and plotted using Matlab7.0.4.365 (R14).
164 The tidal cycle was recorded using a depth sensing data storage tag (Star-Oddi, Iceland,
165 model DST-milli-L) placed at the fjord bottom 1 km from the river mouth, storing data
166 every 10 minutes. An SD6000 water current meter (Sensordata AS, Norway) was placed
167 three meters below the surface at the southern and northern side of the innermost array
168 (Fig. 1), recording the direction and velocity of the water current every 30 min (Fig. 3). A
169 light meter and a wind meter (anemometer) with a data logger (Onset Computer
170 Corporation, USA, model HOBO UA-002-64) were placed on a small island in the inner
171 part of the fjord (Fig. 1), recording light intensity, wind speed and wind direction every
172 15 minutes.

173

174 **DATA ANALYSES**

175 Not all post-smolts migrating through the fjord were registered at each ALS array. There
176 are three reasons why fish might not be detected by a specific array. The post-smolts may
177 have died at an earlier stage, they may have passed without being registered (not
178 'captured') or the acoustic tag failed. To solve the problem of confusion between the two
179 first mentioned factors, the results were analysed as a capture-mark-recapture (CMR)
180 experiment, where a registration on an ALS array was regarded as a recapture. CMR

181 modelling provides maximum likelihood estimates of survival between the ALSs arrays
182 and for the probability of registration by each array. An exception is for the last sampling
183 interval (between the second and third array), where survival and registration are
184 confounded. For this reason, survival can not be estimated between these two last arrays
185 and probability of capture cannot be estimated for the last array.

186

187 Using the Program MARK (White & Burnham, 1999), 14 models of varying complexity
188 were fitted for hypothesis testing (See Lebreton *et al.*, 1992 for more details). The global
189 model [Surv(G*D), Recapt(G*D)] included interaction effects between survival rate
190 (Surv), tagging groups (G), distance-dependency (D) and recapture rates (Recapt). Body
191 length and mass were included as individual covariates. The other 13 models were all
192 nested models from the global model. The hypothesis that the survival rate of post-smolts
193 was size dependent and changed with distance moved from the release site was tested
194 with a Cormack-Jolly-Seber (CJS) mark-recapture model for live recaptures. Probabilities
195 of 'capture' (registration) at each ALS array and survival rates between the arrays were,
196 in addition, estimated. To allow comparison of survival between the ALS arrays, survival
197 estimates were scaled to the distance between arrays to provide an estimate of survival
198 per km. Body length and mass at tagging were included as individual covariates. Three
199 approaches for modeling the individual covariates were used: body size with no trend, a
200 linear trend on body size, or a second order quadratic trend on body size.

201

202 The CJS model assumes that all individuals in a release group behave identically (that is,
203 they have common survival and recapture probabilities), and that all survival and
204 recapture probabilities are independent (Cormack, 1964; Jolly, 1965; Seber, 1965).

205 Before conducting the analysis, a goodness-of-fit (GOF) test for each tagging group was
206 performed using the program UCARE V2.2.5 (global test) (Choquet *et al.*, 2005) to

207 determine whether the assumptions of the CJS model were violated. The GOF test
208 indicated (first tagging group: $P(\text{Chi-square}) = 0.91$, $df = 6$; second tagging group: $P(\text{Chi-}$
209 $\text{square}) = 0.91$, $df = 6$) that the global model described the data adequately, indicating that
210 the assumptions of the CJS model were not violated. The approximating models were
211 compared using Akaike's Information Criterion (AIC) (Anderson *et al.*, 2001). AIC ranks
212 the candidate models to determine which model provides the best description of the data
213 with the fewest parameters.

214

215 Time spent in the different parts of the fjord system and migratory speeds could be
216 calculated only for those post-smolts recorded both entering and leaving a particular fjord
217 location. The sample sizes for these analyses were, therefore, smaller than the total
218 number of post-smolts recorded. Migratory speed was estimated as individual body
219 lengths per second and km per hour by using the shortest distance between the river
220 mouth and the arrays, thus giving minimum estimates (Thorstad *et al.*, 2004; Økland *et*
221 *al.*, 2006).

222

223 To test if post-smolts followed outgoing currents when passing the first ALS array, time
224 of post-smolt passage at the two ALSs positioned nearest to each of the two current
225 meters were compared to the current speed and direction. To test if smolt and post-smolts
226 migrated during day or at night, night time was defined as 2000–0800 hours,
227 corresponding to light intensities less than 20 000 lx.

228

229 Potential differences in survival between post-smolts entering the fjord during day or
230 night and during the different phases in the tidal cycle (divided into three hour phases:
231 high, ebbing, low or flooding tide) were tested by using registration ('recapture') rates
232 from the river mouth and the second ALS array. Since the survival analysis in Program

233 MARK showed that the recapture rate was constant (see results), it could be assumed that
234 timing of sea entry did not affect the registration rate by the ALS arrays. Following this,
235 the registration rate in this case was the same as the survival rate, and a Chi-square test
236 was used to test for differences in the proportion from each of the groups (i.e. day/night
237 and tidal phases) that survived from the river mouth to the second array 17 km from the
238 river mouth.

239

240 Differences in the horizontal distribution along the different ALS arrays were tested with
241 Spearman's rank correlation and differences in the horizontal distribution between
242 periods with and without wind were tested with a Chi-square test. To take into account
243 the time lag of wind forces on the water currents, mean average wind speed and direction
244 from the last four hours (corresponds to mean average time used for the last three km
245 before the array) before the passage of the post-smolt in the ALS array were used. Due to
246 the low number of post-smolts registered at each ALS array, the wind speeds were
247 divided into two categories: "no wind" was defined as wind speeds less than 3.0 m sec^{-1}
248 and "wind" as wind speeds from $3.1\text{--}12.5 \text{ m sec}^{-1}$ (highest measured value).

249

250

RESULTS

251 In total, 98 (82%) of the 120 smolts were registered at least on one occasion following
252 release. Of these, 86 (72%) were detected in the fjord while 12 (10%) were only
253 registered during manual tracking in the river. The remaining 22 smolts (18%) were
254 never registered after release. Sixty four post-smolts (53%) were registered in the river
255 mouth, 46 (38%) by the first array, 46 (38%) by the second array and 34 (28%) by the
256 third array.

257

258 The first detection in the river mouth was two days after release and the last detection 48
259 days after release. The groups of smolts released during the day or night did not differ in
260 within-river survival (Chi-square test, first tagging group, $n = 31$, $P = 0.37$; second
261 tagging group, $n = 33$, $P = 0.60$) or in the diurnal timing of sea entry (Chi-square test,
262 first tagging group, $n = 31$, $P = 0.70$; second tagging group, $n = 33$, $P = 0.51$). The same
263 was true for the groups of smolts released in late June and early July (Chi-square test,
264 pooled groups, survival, $n = 64$, $P = 0.80$; diurnal timing of sea entry, $n = 64$, $P = 0.95$).
265 These groups were therefore pooled in the following analyses.

266

267 **SURVIVAL RATES**

268 Overall, 75% (95% CL: 63–89%) of the post-smolts were estimated to survive during the
269 first 17 km of the fjord migration. The survival rate in the fjord depended on fish body
270 length (Table I). For post-smolts at 140 mm body length, the survival rate was estimated
271 at 99.5% per km and for post-smolts at 150 mm length 97.0% per km (Fig. 4). This
272 means that the model estimates that 92% of the 140 mm and 60% of the 150 mm post-
273 smolts survived to the second ALS array 17 km from the river mouth. The survival rate in
274 the river increased with body length and ranged from 97.5–99% per km (Fig. 4). The best
275 approximating model indicated that there was no difference in survival between the first
276 (river mouth to first array) and second fjord zone (first to second array) (Table I). There
277 was also no difference in survival between individuals from the two tagging periods
278 (period 1 and 2) or as a function of individual mass (Table I), and the registration rates at
279 the ALS arrays ('recapture rates') were not a function of any of the components included
280 in the model.

281

282 **MIGRATORY SPEED**

283 The smolts spent from 7–1309 h (mean = 113 h, S.D. = 222) migrating the 11 km
284 downstream the river from the release site to the river mouth. Mean migratory speed was
285 0.3 km h^{-1} (range $0.0\text{--}1.6 \text{ km h}^{-1}$) corresponding 0.5 bl sec^{-1} (Table II). Time spent from
286 the river mouth to the last array 31 km along the fjord varied from 11–165 h (mean = 36
287 h, S.D. = 32). The migratory speed was slower from the river mouth to the first array (1.0
288 km h^{-1} ; 1.8 bl sec^{-1}) than from the first to the second array (1.6 km h^{-1} ; 3.0 bl sec^{-1}) (*t*-test
289 (bl sec^{-1}), $n = 59$, $P = 0.005$). There was no difference in migratory speed from the first to
290 the second, and from the second to the third array (1.7 km h^{-1} ; 3.1 bl sec^{-1}) (*t*-test (bl sec^{-1}),
291 $n = 48$, $P = 0.90$) (Table II).

292

293 **EFFECTS OF ENVIRONMENTAL FACTORS ON THE MIGRATION** 294 **PATTERNS**

295 Salinity and temperature varied with location, depth (Fig. 2) and time, but salinity
296 generally increased along the fjord. Forty three (70%) of the 62 post-smolts that were
297 registered in the river mouth before the termination of the environmental measurements
298 entered the sea during high tide (24, 39%) or ebbing tide (19, 31%) (Table III). More
299 post-smolts passed the north-eastern current meter of the first ALS array on ingoing
300 currents (14) than on outgoing currents (4) (Chi-square test, $n = 18$, $P < 0.001$) (Fig. 3).
301 No such difference was found at the south-western current meter (Chi-square test, $n = 8$,
302 $P = 0.42$) (Fig. 3). The current speeds ($< 15 \text{ cm s}^{-1}$, Fig. 3) were all the time well below
303 the estimated migratory speed of post-smolts between the river mouth and first ALS array
304 (27 cm s^{-1} , Table II). The current measurements showed that the variation of current
305 direction could not be explained by the tides alone. At the north-eastern current meter, the
306 tide modulated (accelerated and retarded) the current speed, but the current direction did
307 not change with every tidal period (Fig. 3). The measurements from the south-western
308 current meter showed less regular variation. The dominating current directions were into

309 and out of the fjord at both current meter locations. The currents at the two current meters
310 did not co-vary. The currents at the two locations were flowing in opposite direction on
311 several occasions, indicating episodes with both clockwise and counter-clockwise
312 circulation in the fjord. However, periods with currents flowing in the same direction at
313 the two current meters were also recorded.

314

315 There was a clear difference in the light intensities between day (20 000–209 424 lx) and
316 night (54–20 000 lx) during the study period (26 June–18 July). There was no difference
317 in the number of smolts caught day or night in the trap in the river (Table IV). Similarly,
318 there was no difference between day and night in the time of arrival of tagged post-smolts
319 at the three ALS arrays in the fjord (Table V). However, more smolts entered the fjord
320 from the river by night (Chi-square test, $n = 39$, $P = 0.01$) (Table III). When combining
321 tidal water and time of the day, 31 (50%) of the smolts left the river mouth at high (17,
322 27%) or ebbing tide (14, 23%) during the night (Table III). A larger proportion of the
323 post-smolts that entered the sea during day (71%) than at night (59%) survived to the
324 second array (Table III). Similarly, a larger proportion of the post-smolts that entered the
325 sea at low tide (91%) than at high tide (67%) survived the same distance. The largest
326 proportion of survivors came from the groups of post-smolts that entered the sea at low
327 (100%) and high (86%) tide during day time and at low tide during night time (86%)
328 (Table III).

329

330 There was a tendency for the post-smolts to migrate on the north-eastern side of the fjord
331 when passing the innermost array (Spearman's rank correlation, $n = 46$, $P = 0.08$).
332 However, when passing the second ($n = 46$, $P = 0.03$) and third array ($n = 34$, $P < 0.001$),
333 the horizontal use of the fjord increased towards the western side of the fjord. The
334 horizontal distribution at the second array differed between periods with and without

335 wind. During periods with no wind (wind speeds $< 3.0 \text{ m sec}^{-1}$), the post-smolts were
336 evenly distributed across the ALS array (Chi-square test, $n = 21$, $P = 0.87$), while when
337 the wind was blowing (wind speeds: $3.0\text{--}12.5 \text{ m sec}^{-1}$) from the east (wind direction: 51--
338 140°), almost all post-smolt passed the array on the western side of the fjord ($n = 10$, $P <$
339 0.001) (Table VI). There was no difference between periods with and without wind in the
340 horizontal distribution when the post-smolts passed the first and third ALS array.

341

342

DISCUSSION

343

SURVIVAL RATES

345 The estimated post-smolt survival rate of 75% over the first 17 km through the estuary
346 and fjord indicates that post-smolts in the northern Alta Fjord had a relatively high
347 mortality during the first days after sea entry. This is particularly clear when taking into
348 consideration that the study covers only a small fraction of their 1-3 year marine period of
349 the potentially lengthy migration through the northern Atlantic and Barents Sea (Holst *et*
350 *al.*, 2000; Rikardsen *et al.*, 2008). Therefore, these results provide further support for the
351 general belief that the period of first migration to sea is critical in the overall survival of
352 salmon at sea.

353

354 The transition from freshwater in the river to saline water in the estuary and fjord may be
355 a critical period for the post-smolt. Osmotic stress is suggested to involve a less effective
356 antipredator behaviour (Handeland *et al.*, 1996) and the exposure to predators
357 immediately after sea entry is high (Hvidsten & Lund, 1988; Dieperink *et al.*, 2002). The
358 observed survival rates were higher in the north than those observed in Romsdalsfjorden,
359 southern Norway, where 35% of similarly tagged wild post-smolts survived the first 37
360 km from the river mouth (Thorstad *et al.*, 2007), but lower than in Passamaquoddy Bay in

361 Canada where 82% of 38 wild post-smolts survived the first 20 km of migration through
362 the bay (Lacroix *et al.*, 2004b). However, the mean L_F of the Passamaquoddy Bay post-
363 smolts was 187 mm, while the mean L_F of post-smolts in Romsdalsfjorden and this study
364 were only 152 and 147 mm, respectively. Negative size selective mortality has been
365 observed in several studies (Eriksson, 1994; Thorstad *et al.*, 2007), and the differences in
366 body length may be one explanation for the higher survival rate found by Lacroix *et al.*
367 (2004b).

368

369 Smaller smolts had the lowest survival rate in the river, but not in the fjord. This may be
370 due to a combination of increased predation rate and possible tagging effects, since
371 smaller smolts may be more vulnerable to the surgical implantation (Jepsen *et al.*, 2002;
372 Lacroix *et al.*, 2004a). The smolts were tagged and released 11 km upstream the river,
373 and were therefore expected to be recovered from tagging stress at the time of sea entry.
374 If survivors from the smallest size group in the river represent the best adapted smolts,
375 this may explain why the size selective mortality was observed only in the river and not
376 in the fjord, as opposed to in the studies of Eriksson (1994) and Thorstad *et al.* (2007).
377 Tagged smolts in those studies were released in the river mouth and a size selective
378 mortality occurred in the fjord. Twenty-two (18%) of the smolts in the present study were
379 never registered after release, which may be due to predatory birds bringing the smolts
380 out of the river, malfunctioning transmitters, or the smolts moving or drifting to a place
381 where the detection efficiency was low (like rapids and other places with high current
382 speeds). The present study demonstrates that northern post-smolts also seem to have a
383 relatively high mortality during migration through the estuary and fjord.

384

385 **MIGRATORY SPEED**

386 The migratory speed out of the fjord (mean 1.5 days during the first 31 km) was slightly
387 higher than in studies from more southern areas. Wild post-smolts in the south
388 Norwegian Romsdalsfjorden spent on average 5.6 days passing the first 48 km of the
389 marine migration (Thorstad *et al.*, 2007), and in the Passamaquoddy Bay in North
390 America, post-smolts migrated the first 23–36 km through the bay in 2–6 days (Lacroix
391 & McCurdy, 1996; Lacroix *et al.*, 2004b). The results are, therefore, contrary to the
392 expectations based on both the earlier hypothesis of potential prolonged fjord residency
393 of northern post-smolts due to generally better feeding conditions in the north (Rikardsen
394 *et al.*, 2004), and the results of Knudsen *et al.* (2005), who found that the high intensity of
395 trophically transmitted parasites in some of the northern post-smolts supported this
396 theory. As there is no information available on the feeding intensity of the fish in the
397 present study, it was not possible to verify if the fjord feeding affected their migratory
398 speed. It might be that the years studied by Knudsen *et al.* (2005) had a higher food
399 abundance and that some smolts prolonged their fjord feeding period due to this.
400 However, feeding in the Alta Fjord seem anyhow to be generally more extensive and less
401 variable between years than observed in the southern Norwegian fjords (Rikardsen *et al.*,
402 2004; Hvidsten *et al.*, 2009). Therefore, an assumed high initial feeding rate combined
403 with the observed fast seaward migration, may result in a reduced chance of being eaten
404 by predators and a high immediate growth rate for the survivors, thus contributing to a
405 potentially better start to the marine life for the post-smolt in the northern Alta Fjord
406 compared to the generally much longer and less productive southern Norwegian fjords.
407
408 There was a large individual variation in migratory speeds, which may indicate that the
409 individuals encountered different current speeds and directions at sea entry. Alternatively,
410 this may be an indication of individual behaviour. The fact that the mean migratory speed
411 was always higher than the measured current velocities indicates that the post-smolts had

412 an active swimming behaviour, which is consistent with other observations (Thorstad *et*
413 *al.*, 2004; Økland *et al.*, 2006). Despite the individual variation, post-smolts spent a
414 significantly longer time in the inner part of the fjord than in the more saline outer parts.
415 Hoar (1988) found that post-smolts may not need a period of acclimatisation in the
416 estuary because they have previously, while still in fresh water, become modified
417 physiologically to tolerate saline conditions. However, another reason for the lower
418 migratory speed in the estuary may be due to the complexity of the Alta Fjord system,
419 which could make orientation to open waters more difficult for the post-smolts. Since the
420 smolts were captured, tagged and released in the river and on average spent two to four
421 days in the river before sea entry, short term effects from tagging and handling were not
422 expected to be the causes for the initial low migratory speed in the fjord. The findings of
423 an increased migratory speed out of the fjord are in accordance with observations at
424 Gaspé Bay, Canada, where it was found that exposure to more saline waters caused
425 increased swimming speeds, and migratory speeds were higher in the outer and more
426 saline part of an embayment (Hedger *et al.*, 2008). These findings are also consistent with
427 observations from Romsdalsfjorden, southern Norway (Finstad *et al.*, 2005; Thorstad *et*
428 *al.*, 2007) and from the River Conway, Wales (Moore *et al.*, 1995). Thus, post-smolts
429 seem to increase their fjord migratory speed the more familiar they become with their
430 habitat and the closer they get to the open ocean.

431

432 **EFFECTS OF ENVIRONMENTAL FACTORS ON THE MIGRATION**

433 **PATTERNS**

434 A majority (70%) of the post-smolts entered the sea at high or ebbing tide. Swimming in
435 outgoing tide currents speeds up the migration during the first hours through the estuary.
436 Since predation on salmonid post-smolts in the river mouth and estuary can be a major

437 mortality factor (Hvidsten & Lund, 1988; Jepsen *et al.*, 2006), a fast migration through
438 these areas may reduce the predation risk.

439

440 However, the post-smolts did not seem to continue following an outgoing tidal current at
441 the time they passed the first ALS array four km from the river mouth, since more post-
442 smolts passed the array on ingoing currents. The complex current system in the inner part
443 of the Alta Fjord may complicate the post-smolts outward migration, so they only were
444 able to take advantage of an outgoing tidal current during a short period after sea entry. It
445 may, therefore, be that the reason for the observed higher survival rate of post-smolts
446 entering the sea at low tide (91%) than at high tide (67%) was that post-smolts entering
447 the sea at high tide in this case had no, or only an initial, advantage by doing so. The
448 findings are opposite to observations from Penobscot River estuary, where hatchery-
449 reared *S. salar* post-smolts were found to passively drift on tidal currents (McCleave,
450 1978). However, this estuary is influenced by strong tidal currents with surface currents
451 exceeding 200 cm s^{-1} , which is about ten times higher than observed in the River Alta
452 estuary. The current meters used in the Alta Fjord were placed three meters below the
453 water surface, in the halocline. If the post-smolts followed the brackish water layer closer
454 to the surface, they may have experienced different current speed and directions than
455 measured. However, Davidsen *et al.* (2008) found that post-smolts during the early
456 seaward migration migrated at 1-3 meters depth, which corresponds to the depth of the
457 current meters. To fully understand the fjord water mass dynamics and the effects on the
458 post-smolt migration, current measurements are recommended to be taken at additional
459 locations and depths within a fjord.

460

461 A larger proportion of the post-smolts entered the sea during night than during day.

462 Nocturnal migration in temperate areas with dark nights is thought to be an adaptive

463 behaviour to avoid or minimize predation by visual predators (Solomon, 1982). Even
464 though the northern River Alta is situated on a latitude with midnight sun, light intensities
465 were still lower than 20 000 lx at night, in contrast to the 50 000–200 000 lx measured
466 during day time. The nocturnal migration pattern at sea entry may also be an anti-predator
467 strategy in northern areas. When combining timing of sea entry with both time of the day
468 and the tidal cycle, it was found that post-smolts entering the sea at high tide during day
469 and low tide during night had a similar survival rate (86%). Despite small sampling
470 groups, the findings indicate that the optimal strategy for timing the sea entry is far more
471 complex than only timing to tidal cycles and day light. This is supported by observations
472 from a study in the Usk Estuary, Wales, where the entrapment of smolts in the river
473 mouth showed that the largest numbers of *S. salar* smolts were caught during the day on
474 the flood tide and the least on an ebbing night tide (Aprahamian & Jones, 1997).
475 However, both Moore *et al.* (1995) and Lacroix *et al.* (2004b) found that smolts mainly
476 left the river during the night on ebbing tides. Thus, these observations may indicate that
477 the optimal timing of sea entry may vary with different environmental conditions of the
478 estuaries and with different impacts of predators.

479

480 A diurnal variation in the timing of migration was not observed in the catches in the
481 smolt trap in the river, nor in the time of arrival at the three ALS arrays in the fjord.
482 Daytime migration in northern rivers has been previously reported (Veselov *et al.*, 1998;
483 Davidsen *et al.*, 2005), but this is first time it has been demonstrated in a northern fjord.
484 The fact that the proportion of post-smolts entering the sea was larger at night than during
485 the day, while there was no diurnal variation in the migration in the river and fjord, may
486 be an adaptation to the increased predation risk immediately after sea entry (Hvidsten &
487 Lund, 1988; Jepsen *et al.*, 2006). The pattern of smolt migration both day and night in

488 northern rivers has been suggested to be a trade off between utilizing the warmer water in
489 the day and the darker hours in the night (Davidsen *et al.*, 2005).

490

491 The significant relationship between wind direction and horizontal distribution of the
492 post-smolts in the second ALS array shows that the migration routes in this part of the
493 fjord were influenced by the wind-induced surface currents. The relationship between
494 horizontal distribution and wind speed and direction found in the second ALS array, but
495 not in the first or third, can be explained by the relevant fetch length being longer in the
496 broad and open part of the fjord, where the second ALS array was positioned.

497

498 In conclusion, as with southern populations of *S. salar*, this study shows that the start of
499 the marine migration of the northern post-smolts may be a bottleneck where they
500 experience low survival rates compared to the rest of their marine phase. The migratory
501 speed was high in the Alta Fjord compared with southern populations, and more smolts
502 entered the sea at night at high or ebbing tide, which may be a strategy to reduce the
503 predatory risk. The high migratory speed in combination with earlier observations of a
504 higher immediate fjord feeding rate of northern compared to southern post-smolts, may
505 indicate that they have a potentially better start to the oceanic feeding migration than their
506 southern conspecifics. In years with an earlier or later migration period than observed in
507 this study, survival rates and migratory behaviour may differ due to differences in
508 temperature regimes and other environmental factors. However, the high variance in
509 migration patterns, both in river and fjord, might indicate that individuals in stochastic
510 estuarine and marine environments are exposed to highly variable selection regimes
511 resulting in different responses to environmental factors on both temporal and spatial
512 scales.

513

514

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524

525

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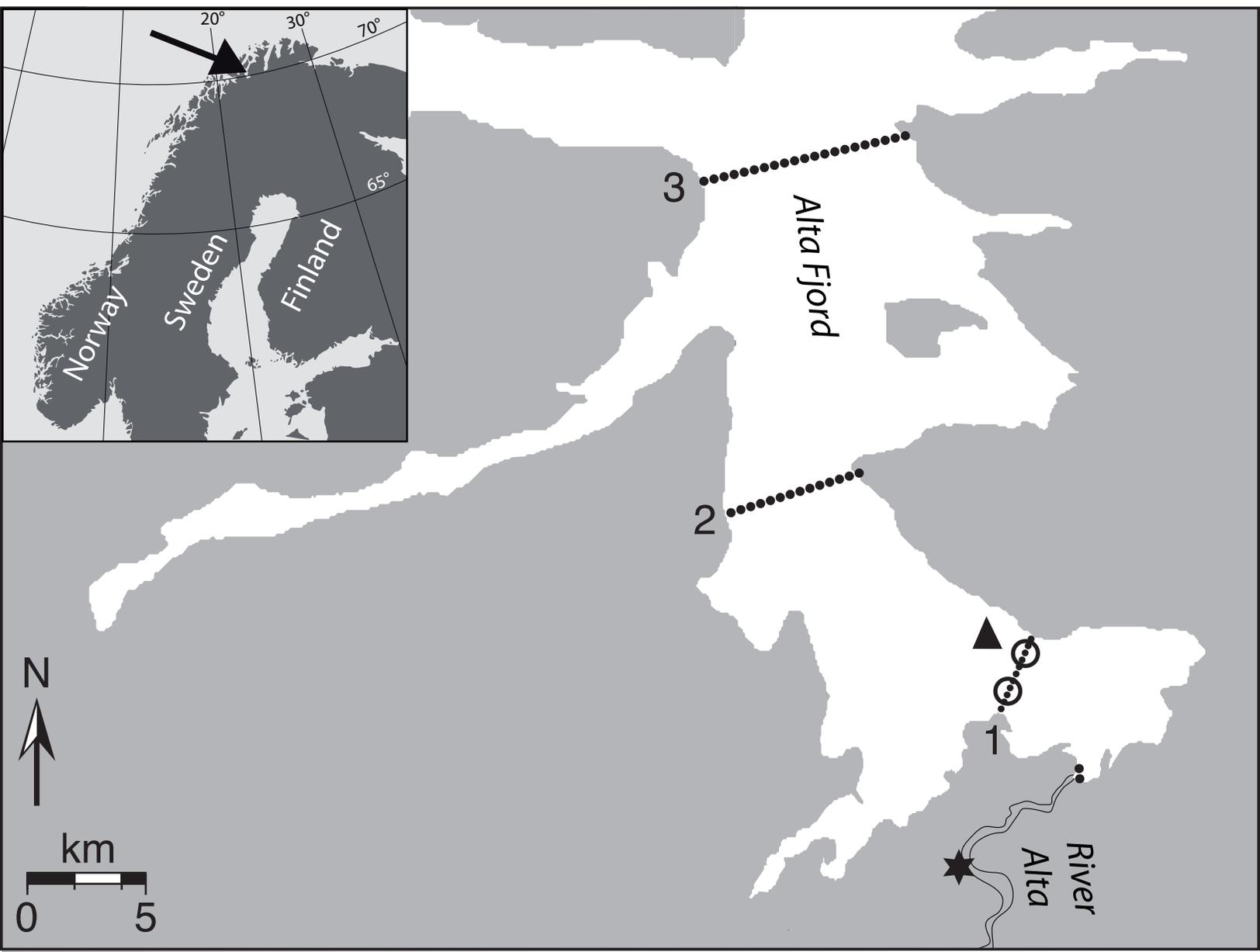
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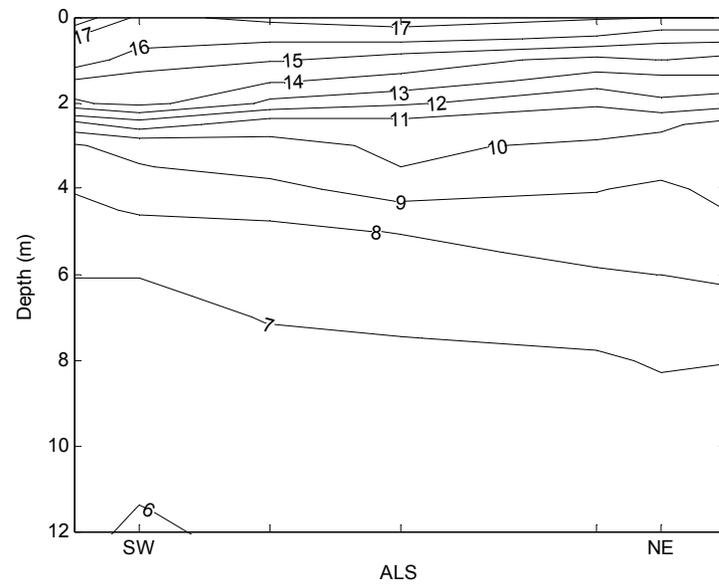
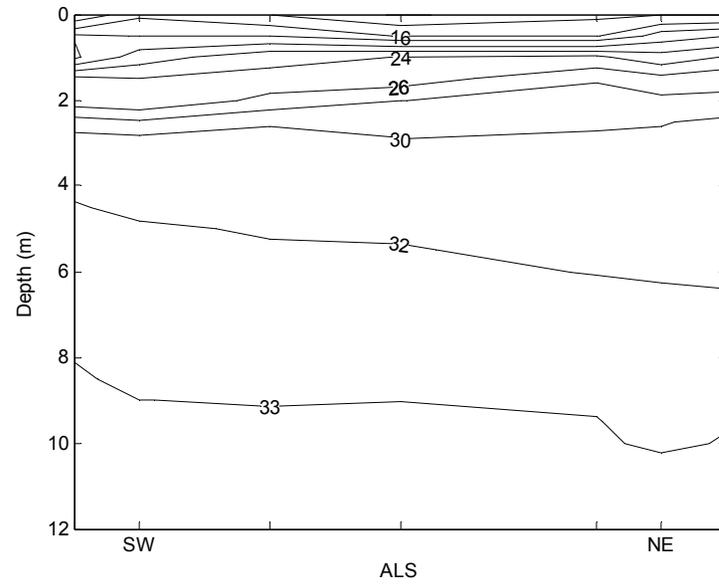
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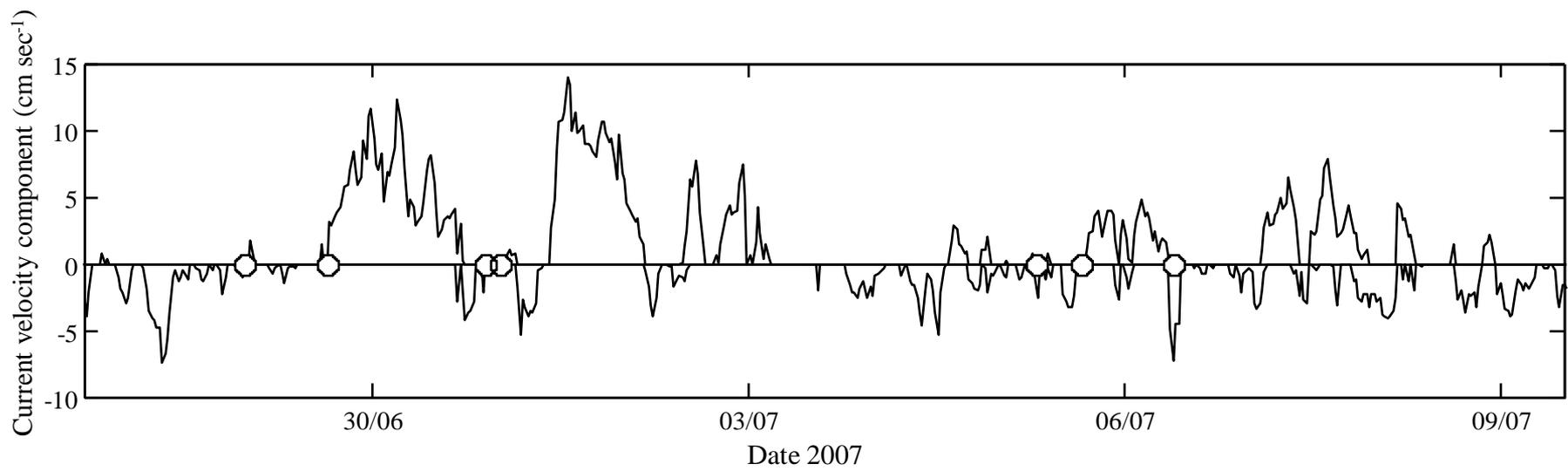
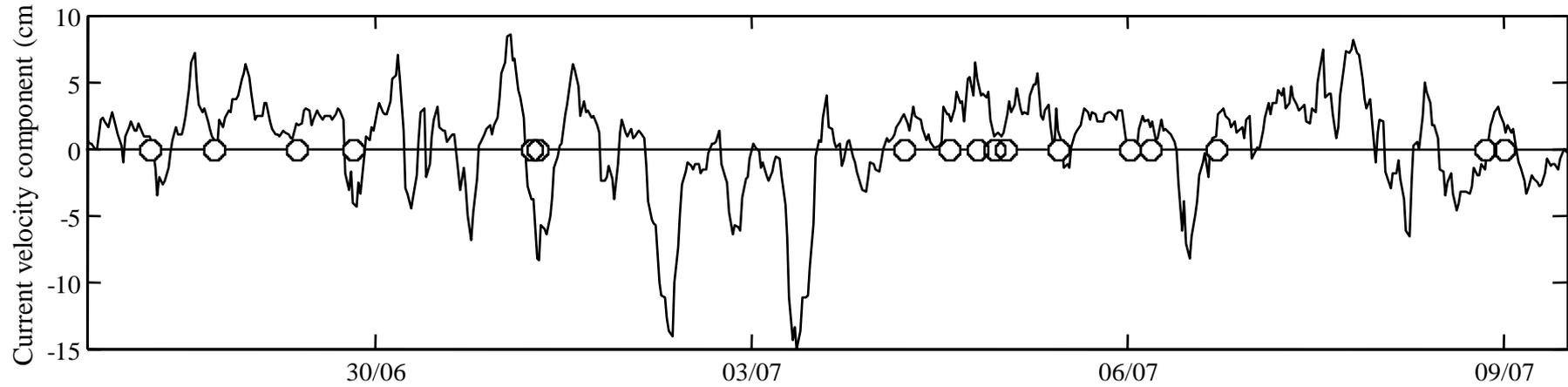
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Figure

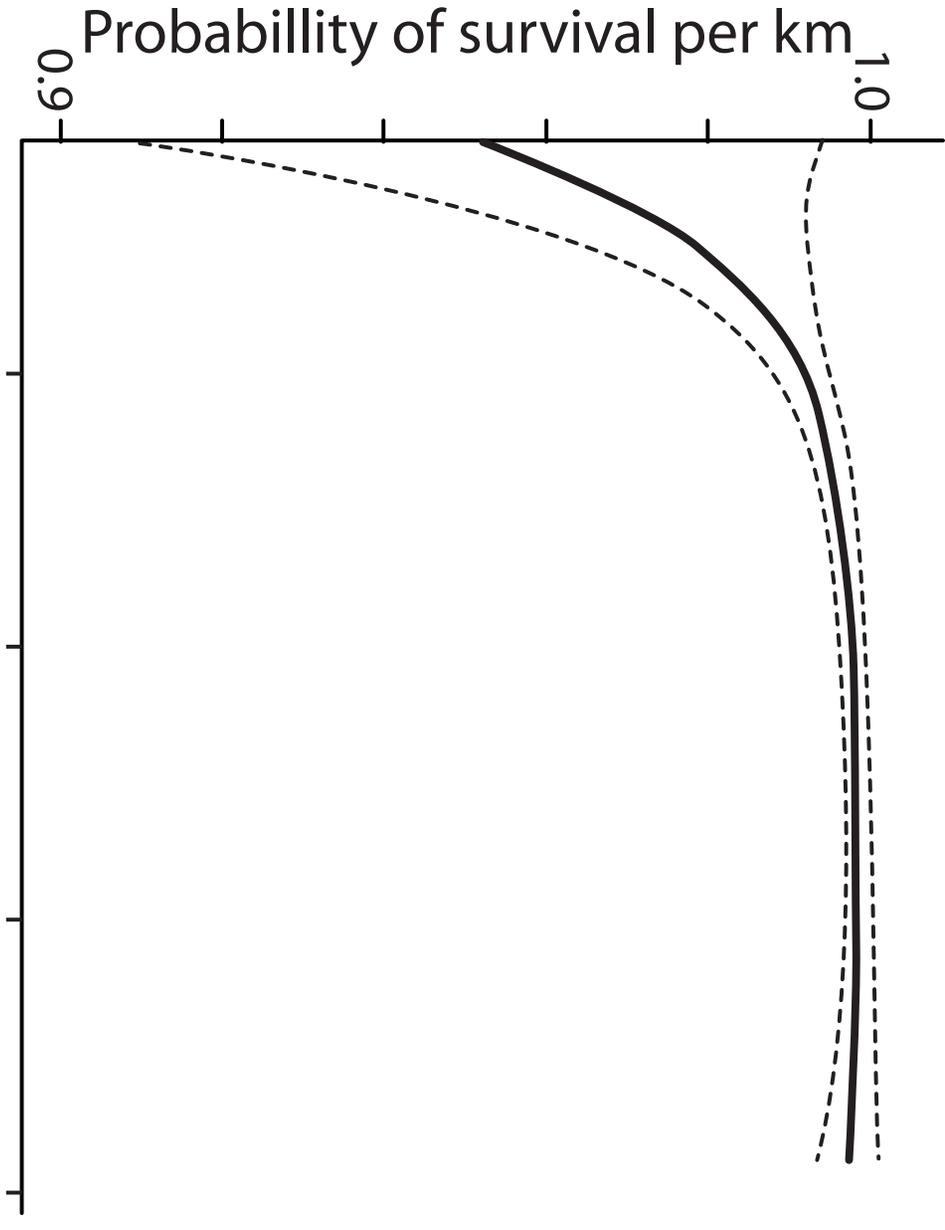
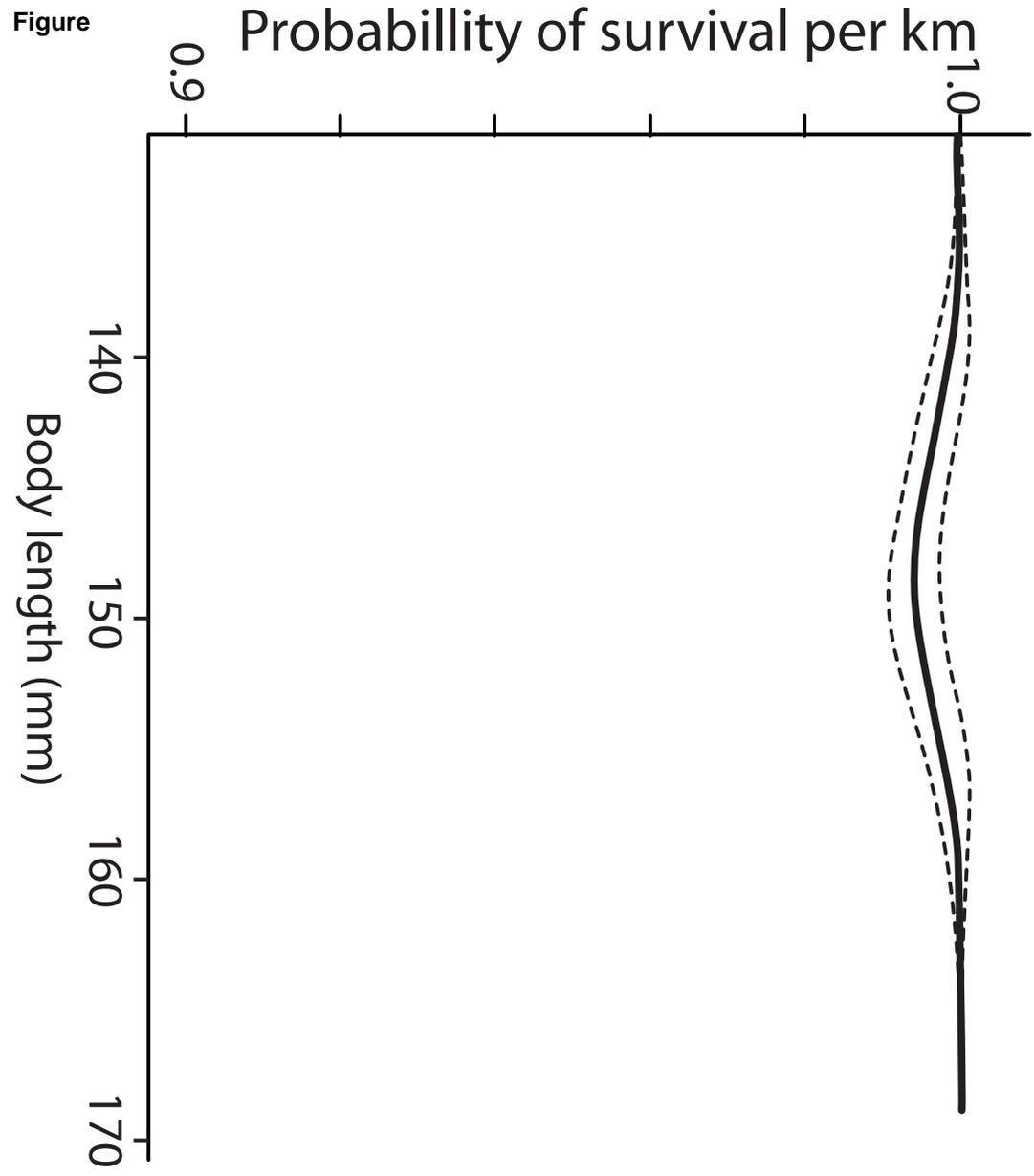


Figure



Figure

Figure



1 FIG. 1. Map of the lower part of River Alta and the Alta Fjord showing the release site
2 (★), the two ALSs in the river mouth (*), the three ALS arrays in the fjord (•••••), the
3 two current meters in the first ALS array (○) and the weather station (▲).

4

5

6 FIG. 2. Salinity (upper panel) and temperature (° C) (lower panel) distribution recorded at
7 0–12 m depth across the first ALS array in the Alta Fjord on 6 July 2007.

8

9

10 FIG. 3. Water current velocity at 3 m depth at the north-eastern (upper panel) and south-
11 western (lower panel) side of the Alta Fjord at the first ALS array. The current velocity
12 components were computed for the dominating current directions. Positive values are the
13 velocity components towards the fjord head and negative values are towards the fjord
14 mouth. ○ indicates time at post-smolt passage.

15

16

17 FIG. 4. *S. salar* smolt survival rates in the lower part of the River Alta (upper panel) and
18 post-smolt survival rates in the Alta Fjord (lower panel) as a function of body length.

19 Dotted lines show 95% confidence intervals.

1 TABLE I. Model selection for estimating survival of acoustically tagged *S. salar* post-smolts through the Alta Fjord. The table shows all 14 tested models. The
 2 models estimate survival (Surv) and recapture rates (Recapt) and include tagging groups (G), distance dependency (D), effects of the river and the fjord including
 3 three different fjord zones and the individual length and mass of the post-smolts. AICc is the score based on Akaike's information criterium adjusted for small
 4 sample bias.

Model	AICc	Delta AICc	AICc weights	Model Likelihood	Number of parameters	Deviance
[Surv(*D)Recapt(*.)River effect, no fjord zone effect, indiv. length quadratic std.]	574.32	0	0.88232	1	7	559.90
[Surv(*D)Recapt(*.)River effect, no fjord zone effect, indiv. length]	579.86	5.54	0.05517	0.0625	5	569.64
[Surv(*D)Recapt(*.)River effect, no fjord zone effect, indiv. length linear std.]	579.86	5.54	0.05517	0.0625	5	569.64
[Surv(*D)Recapt(*.)River effect, fjord zones, indiv. length]	584.88	10.56	0.00449	0.0051	9	566.20
[Surv(*)Recapt(*.)River effect]	588.02	13.71	0.00093	0.0011	2	583.98
[Surv(*D)Recapt(*.)River effect]	588.69	14.37	0.00067	0.0008	3	582.60
[Surv(*D)Recapt(*.)indiv. length]	589.49	15.18	0.00045	0.0005	6	577.18
[Surv(*D)Recapt(*.)]	589.64	15.33	0.00041	0.0005	5	579.42
[Surv(*D)Recapt(*.)indiv. mass]	591.27	16.96	0.00018	0.0002	6	578.96
[Surv(*D)Recapt(*D)]	591.30	16.98	0.00018	0.0002	7	576.88
[Surv(G*D)Recapt(*.)]	595.41	21.10	0.00002	0	9	576.74
[Surv(G*D)Recapt(*D)]	597.19	22.88	0.00001	0	11	574.19
[Surv(G*D)Recapt(G*D)indiv. length]	599.25	24.93	0	0	16	565.15
[Surv(G*D)Recapt(G*D)]	603.23	28.92	0	0	14	573.62

5

6 TABLE II. Migratory speeds of acoustically tagged *S. salar* smolts in the River Alta and
 7 different parts of the Alta Fjord.

Receiver site	Distance (km)	Number of smolts recorded	Mean \pm S.D. time (h) (range)	Mean \pm S.D. migratory speed	
				(km h ⁻¹) (range)	(bl s ⁻¹) (range)
Release site–River mouth	11	64	113.0 \pm 222.4 (6.7–1308.7)	0.3 \pm 0.3 (0.0–1.6)	0.5 \pm 0.5 (0.0–3.2)
River mouth–array 1	4	33	5.8 \pm 4.2 (1.6–19.8)	1.0 \pm 0.5 (0.2–2.5)	1.8 \pm 1.0 (0.4–4.2)
Array 1–array 2	13	26	12.5 \pm 9.2 (3.2–36.4)	1.6 \pm 1.0 (0.4–4.1)	3.0 \pm 2.0 (0.7–7.3)
Array 2–array 3	14	22	11.9 \pm 9.0 (4.0–38.7)	1.7 \pm 0.8 (0.4–3.5)	3.1 \pm 1.6 (0.6–6.7)

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10 TABLE III. Comparisons of the number and proportions of *S. salar* post-smolts entering the sea during 1)
 11 day and night, 2) at different stages of the tidal cycle, and 3) for different combinations of day and night
 12 and different stages of the tidal cycle. The number and proportions of post-smolts from each group
 13 surviving from the river mouth to the second array 17 km outward the fjord are also given, and differences
 14 in proportions of survivors among groups are compared with Chi-square tests and the *P*-value are given. *
 15 indicate groups having the significantly highest proportion of “time at sea entry”. ** indicate groups
 16 having the significantly highest proportion of “survivors to the second array”.

	Timing of sea entry			Survival from the river mouth to the second array in the fjord		
	Number of fish (<i>n</i> = 62)	%	<i>P</i> -value	Number of fish (<i>n</i> = 39)	%	<i>P</i> -value
Day time	21	34		15	71**	
Night time	41*	66	0.01	24	59	0.003
High tide	24*	39		16	67	
Ebbing tide	19	31		10	53	
Low tide	11	18		10	91**	
Flooding tide	8	13	0.02	3	38	< 0.001
High tide day time	7	11		6	86	
High tide night time	17*	27		10	59	
Ebbing tide day time	5	8		2	40	
Ebbing tide night time	14	23		8	57	
Low tide day time	4	6		4	100**	
Low tide night time	7	11		6	86	
Flooding tide day time	5	8		3	60	
Flooding tide night time	3	5	0.002	0	0	< 0.001

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18 TABLE IV. Catch per hour (CPH) of *S. salar* smolts during day (0800–2000 hours) and
19 night (2000–0800 hours) in a smolt trap operated in the River Alta during 2004–2006. *t*-
20 tests were used to test for significant differences between day and night.

Year	Day (CPH)	Night (CPH)	Number of days of trapping	<i>P</i> -value
2004	5.1	7.1	25	0.53
2005	5.1	5	22	0.97
2006	1.4	1.7	19	0.61

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23 TABLE V. Number and proportion of *S. salar* post-smolts arriving at each of the three
 24 ALS arrays in the Alta Fjord at day (0800–2000 hours) and night (2000–0800 hours).
 25 Chi-square tests were used to test for significant differences between the proportions.

Time of the day	Array 1	Array 2	Array 3
Day	21 (41%)	26 (49%)	20 (56%)
Night	30 (59%)	27 (51%)	16 (44%)
P-value	0.21	0.89	0.51

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28 TABLE VI. Numbers of *S. salar* post-smolts registered at the western, central or eastern
 29 side of the ALS arrays in the Alta Fjord at different wind directions. Chi-square tests
 30 were used to test for significant differences in the horizontal distribution between periods
 31 with and without wind (wind speeds < 3.0 m sec⁻¹). * indicates if a part of the fjord had a
 32 significantly different high proportion of post-smolts registered during a certain wind
 33 direction.

Wind directions (Degrees)	Side of the fjord (Number of post-smolts)			<i>P</i> -value
	South-west	Central	North-east	
First array				
No wind	6	6	13	
51–140	3	2	3	0.63
141–230	0	1	5	0.26
231–320	0	0	0	
321–50	2	4	1	0.075
Second array	West	Central	East	
No wind	7	6	8	
51–140	9*	0	1	< 0.001
141–230	5	4	2	0.39
231–320	0	0	0	
321–50	1	0	3	0.27
Third array	West	Central	East	
No wind	7	4	4	
51–140	6	4	1	0.41
141–230	4	1	0	0.27
231–320	0	0	0	

321-50	3	0	0	0.18
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