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1 Migration strategies of brown trout (*Salmo trutta*) in a subarctic river system as revealed by
2 stable isotope analysis

3

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13

14 Running title: Migration strategies of brown trout in a subarctic river

15

16 Abstract

17 We estimated the proportions of anadromous and freshwater-resident brown trout (*Salmo*
18 *trutta*) in different parts of the subarctic River Näätämöjoki/Neidenelva system (Finland and
19 Norway) using carbon, nitrogen, and hydrogen stable isotope analyses of archived scales as
20 identifiers of migration strategy. Our results showed that carbon stable isotope values were
21 the best predictor of migration strategy. Most individuals fell into two clearly distinct groups
22 representing anadromous (47 %) or freshwater-resident (42 %) individuals, but some fish
23 had intermediate carbon values suggesting repeated movement between freshwater and
24 the sea. The proportion of anadromous individuals decreased steadily with distance from

25 the sea forming a spatial continuum in migration strategies which is probably maintained by
26 the combination of several factors such as divergent availability of food resources, variable
27 migration costs, and genetic differences. These within-catchment differences in migration
28 strategies should be taken into account in fisheries management practices.

29

30 Keywords: anadromy, life-history strategies, residency, salmonid, partial migration

31

32 Introduction

33

34 Most salmonid stocks have declined as a result of over-exploitation, habitat modification,
35 and other human activities (e.g., Klemetsen et al., 2003). Despite considerable effort,
36 effective management of endangered stocks has proved difficult, and is complicated by the
37 variable life history strategies among salmonids (e.g., Klementsens et al., 2003; Vähä et al.,
38 2010; Chapman et al., 2012; Erkinaro et al. 2018). Brown trout (*Salmo trutta* L.) has a
39 particularly flexible life history with several identifiable strategies (e.g., Jonsson and
40 Jonsson, 1993; Elliot, 1994; Jonsson and Jonsson, 2017). A single river system can contain
41 partially migrating population with sea-migrating (anadromous), freshwater-migrating
42 (potamodromous), and freshwater-resident individuals which are able to interbreed (Elliot,
43 1994; Klementsens et al., 2003; Huusko et al., 2017).

44

45 There is increasing evidence that a wide diversity in life-history strategies (e.g., partial
46 migration) could stabilize fish populations, and buffer them from environmental variability
47 (e.g., Schindler et al., 2010; Chapman et al. 2012; Moore et al., 2014). Fishing is a strong,
48 selective evolutionary factor which could lead to unwanted changes in fish stocks (e.g., Hard

49 et al. 2008; Laugen et al., 2014; Tillotson & Quinn, 2017). Selective fishing mortality in
50 migratory routes or in non-breeding areas could severely affect fish population life-history
51 diversity by decreasing the number of migrating individuals (Thériault et al., 2008; Syrjänen
52 & Valkeajärvi, 2010). In addition, migratory strategies may vary between sexes (Klements
53 et al., 2003, Jonsson & Jonsson 2017), and fishing can be more selective towards the large,
54 highly fecund, early migrating females (like in many salmonid fish species) leading to a
55 drastic decline in reproduction and recruitment. Therefore, it is essential to know which life-
56 history strategies are present in a population, at different phases of the life cycle, and in
57 various habitats, and how harvesting is targeting fish, if partially migrating populations are
58 to be managed in a sustainable fashion.

59

60 Several methods, including scale reading, genetics, external and internal tagging, elemental
61 analysis, and muscle pigment analysis, have been used to track salmonid migrations
62 (Jonsson & Jonsson, 2002; Vähä et al., 2010; Briers et al., 2013; Ryan et al. 2016), but all
63 have limitations. Analysis of naturally occurring stable isotopes of carbon ($\delta^{13}\text{C}$) and nitrogen
64 ($\delta^{15}\text{N}$) have been widely used to resolve the proportions of anadromous individuals in fish
65 populations as there appear to be distinct differences in stable isotope values between sea
66 and freshwater (McCarthy & Waldron, 2000; Charles et al., 2004; Briers et al., 2013).

67 Hydrogen stable isotope values ($\delta^2\text{H}$) have been shown to be robust in terrestrial migration
68 studies (Hobson & Wassenaar, 2008), and distinct $\delta^2\text{H}$ values between sea and freshwater
69 (Dansgaard, 1964; Xu et al., 2012) could help in tracking migrations of anadromous fish.

70 However, effects of ambient water exchange and of metabolism related to tissue synthesis
71 among many other influencing factors (Vander Zanden et al., 2016) could complicate

72 interpretation, and the feasibility of hydrogen isotopes in aquatic migration studies is still
73 uncertain (Whitledge et al., 2006; Soto et al., 2011; Soto et al., 2013).

74

75 Fish muscle tissues, otoliths, and scales have all been used to track fish migrations using
76 stable isotopes (McCarthy & Waldron, 2000; Charles et al., 2004; Torniainen et al., 2014,
77 Torniainen et al., 2017, Orell et al., 2017). Isotope values of fish muscle tissue reflect shorter
78 (weeks to months) changes mainly due to growth and tissue turnover (Perga & Gerdaux,
79 2005). In contrast, otoliths and scales reflect long-term information regarding an individual's
80 diet and location. Otoliths offer high temporal resolution, but analyses are costly and
81 laborious, and fish must be killed for sampling (e.g., Hanson et al., 2010; Ramsay et al.,
82 2011). In contrast, fish scales are easy to collect and prepare for isotope analysis
83 (Hutchinson & Trueman, 2006), do not require the fish to be killed, and offer the particular
84 advantage that many institutes house long-term archives of fish scales (Dixon et al., 2015).

85

86 We estimated the proportions of sea-migrating and freshwater-resident brown trout in
87 different sectors of the River Näätämojoki system in northern Finland and Norway using
88 carbon and nitrogen stable isotope analysis of archived scales as identifiers of individual fish
89 migration strategy. We also assessed the value of hydrogen isotope values of scales for
90 resolving brown trout migration strategies. We then evaluated whether fish size and sex
91 vary between anadromous and resident groups, as those characteristics are often used in
92 management aiming at protecting certain groups of fish, for instance, through minimum
93 catch size limits.

94

95 Material & Methods

96

97 The River Näätamöjoki (Neidenelva in Norwegian) drains a catchment area of 2 962 km²,
98 situated mostly in northern Finland, and flows to the Arctic Ocean in Norway (Figure 1). The
99 River Näätamöjoki holds a substantial Atlantic salmon (*Salmo salar* L.) stock which supports
100 important recreational and subsistence fisheries (Orell, 2012). Another important salmonid
101 fish species in the system is brown trout, which includes both anadromous and freshwater-
102 resident individuals. Annual brown trout catches in the lower reaches in the Norwegian
103 sector have averaged 314 ± 42 (mean \pm SD) individuals (328 ± 32 kg) per year between 2007
104 and 2014 (www.scanatura.no). Salmon migrate up the river to Lake Iijärvi (surface area 37
105 km², 70 km upstream from the river mouth) but there is little information regarding the
106 range of anadromous brown trout, although they have been suggested to mostly occupy the
107 lower reaches and tributaries (Orell, 2012). Annual brown trout catches in the Finnish sector
108 have been tens to some hundred individuals in recent years, including both anadromous
109 and freshwater-resident fish (Niemelä et al., 2015).

110

111 We used archived brown trout scale samples collected by the Natural Resources Institute
112 Finland (former Finnish Game and Fisheries Research Institute) between 1983 and 2006. In
113 total, 79 fish were caught and sampled by fishermen using rod and line or gillnets from five
114 sampling areas: estuary (Neidenfjorden), Norwegian lower river reaches (Neidenelva; all
115 samples were collected from Skoltefossen, Figure 1), a tributary (River Nuortijoki), upper
116 river reaches in the Finnish sector (Näätamöjoki, from national border to Lake Iijärvi, and
117 Lake Iijärvi (Figure 1, Table 1). Sex, total fish length, and catch location were recorded at the
118 time of scale collection (Table 1). Distance from catch locations to the river mouth was
119 measured by using GIS-software. Scale samples from upper river reaches (Table 1:

120 Näätäinjoki, Finland) were collected from several sites and pooled for discriminant
121 analysis. Scale samples were collected over a long time period (23 years) which may have
122 influenced the stable isotope composition due to temporal changes in background isotope
123 baselines (e.g., changes in anthropogenic loading). However, we presumed insignificant
124 variation in background values as such changes have not been found in the Teno River
125 system (Roussel et al., 2014), the neighbouring catchment in the same near pristine
126 subarctic area with minimal human influences.

127

128 Scales for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analysis were dried for 48 hours at 60°C (Perga & Gerdaux, 2003).
129 No acidification was performed for scales as previous results indicated that influence of
130 inorganic carbon for results was minor (Roussel et al., 2014). Approximately 0.5 mg of
131 scales (1-2 whole scales or halves cut lengthwise) were weighed into tin cups and analysed
132 on a FlashEA1112 elemental analyser coupled to a Thermo Finnigan DELTA^{plus} Advantage
133 continuous flow isotope ratio mass spectrometer (Thermo Electron Corporation, Waltham,
134 MA, USA). The reference material used was an internal standard (white muscle tissue of
135 northern pike (*Esox lucius* L.)) of known relation to the international standards of Vienna
136 Pee Dee belemnite for carbon isotopes and atmospheric nitrogen for nitrogen isotopes.
137 Standard samples were run repeatedly in each sequence. Standard deviations within
138 reference samples were less than 0.2 ‰ for carbon and nitrogen in each sequence.

139

140 Scales for $\delta^2\text{H}$ analysis were lipid-extracted by soaking in a chloroform-methanol solution
141 (2:1), dried for 48 hours at 60°, and weighed (approx. 0.35 mg) into silver capsules. Weighed
142 samples and references were stored open to laboratory air for a week to equilibrate the
143 exchangeable hydrogen with ambient water vapour (Wassenaar and Hobson, 2003).

144 Samples were analysed on a vario PYRO cube elemental analyser (Elementar
145 Analysensysteme GmbH, Hanau, Germany) coupled to an Isoprime 100 isotope-ratio
146 spectrometer (Isoprime Ltd, Stockport, UK). Two keratin laboratory standards, caribou hoof
147 and kudu horn of known relation to international standards (Standard Mean Ocean Water)
148 obtained from Environment Canada, were used as internal laboratory standards (Wassenaar
149 & Hobson, 2010). Standard samples were run repeatedly in each sequence. Standard
150 deviations within $\delta^2\text{H}$ reference samples were 1.22 ‰ for caribou hoof and 3.51 ‰ for kudu
151 horn. All stable isotope analyses were performed at the Department of Biological and
152 Environmental Sciences, University of Jyväskylä. All stable isotope ratios are expressed in
153 standard δ -notations as parts per thousand (‰) deviations from international standards.

154

155 Linear discriminant analysis was used to predict the most probable life-history strategy
156 (anadromous or freshwater-resident) of individuals across five areas consisting of samples
157 collected from the estuary to the Lake Iijärvi (Figure 1, Table 1). A stepwise selection
158 method was used for variables which potentially separated groups ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$, $\delta^2\text{H}$) with
159 Wilks lambda (critical values of $F = 3.84$ in, and $F = 2.71$ out) as selection criteria.

160 We used catch area (five areas from estuary to Lake Iijärvi) as pre-defined group in our
161 analysis. If fish was predicted to belong to the Lake Iijärvi group it was considered as
162 freshwater resident, and respectively, if fish was predicted to belong to Estuary group it was
163 considered as anadromous. That assumption relies on visual inspection of stable isotope
164 results, most individuals in the Lake Iijärvi reflected a clear freshwater carbon stable isotope
165 label and individuals caught in the estuary showed a marine carbon label. Average carbon
166 and nitrogen isotope values of assigned groups were almost identical to sea and resident
167 trout values analysed by McCarthy & Waldron (2000), indicating that grouping was valid.

168 Individuals which were not assigned to either group were categorised as an intermediate
169 group.

170

171 Pearson correlation tests were used to test correlations between fish length and stable
172 isotope values. Student's T-tests were used to analyse differences in fish length between
173 anadromous and freshwater-resident fish determined by discriminant analysis and
174 differences in length between sexes. Fisher exact test was used to test migration behaviour
175 differences between sexes. The number of samples was lower for these tests (n=48) as
176 some individuals lacked sex determination. All statistical analyses were performed using
177 IBM SPSS statistics version 22 (IBM Corp., Armonk, NY, USA).

178

179 Results

180

181 There were consistent differences in mean values of all measured stable isotope values
182 among the five study areas (Table 2). Scale $\delta^{13}\text{C}$ values separated fish into two visually
183 distinct groups (Figure 2A), fish collected from the upper river reaches of the Näätämöjoki
184 River in the Finnish sector and from the Lake Iijärvi being more ^{13}C -depleted (Table 2). $\delta^{15}\text{N}$
185 values were higher in fish collected from the estuary and lower river reaches in Norway than
186 in fish from the upper reaches (Table 2), but the grouping was not as clear as for $\delta^{13}\text{C}$ (Figure
187 2A). $\delta^2\text{H}$ values showed wide variation from -40 to -140 ‰ presumably reflecting marine
188 and freshwater labels, but no clear groups could be distinguished (Figures 2B & 2C). Carbon,
189 nitrogen, and hydrogen stable isotope values showed significant positive correlation with
190 fish length ($\delta^{13}\text{C}$: $R^2= 0.477$, $p < 0.001$; $\delta^{15}\text{N}$: $R^2= 0.569$, $p < 0.001$) being most evident in $\delta^2\text{H}$
191 ($R^2 = 0.677$, $p < 0.001$) (Figure 3).

192

193 Due to the strong correlations between measured stable isotope values (Figure 2), only the
194 $\delta^{13}\text{C}$ value of brown trout scales was selected to predict fish grouping by a stepwise process
195 in discriminant analysis. Most individuals caught in the estuary in Neidenfjorden
196 represented marine $\delta^{13}\text{C}$ carbon values, and 82 % of them were assigned by discriminant
197 analysis to one group which was defined as sea-migrating fish (Table 3). However, two
198 individuals (44.0 and 43.5 cm TL) caught from the estuary had more ^{13}C -depleted values still
199 apparently reflecting a freshwater signature. Most fish (88%) caught from the lower
200 Norwegian reaches (Neidenelva) were assigned to the migratory fish group with a distinct
201 sea carbon signature. Fish caught from the Nuortijoki tributary showed similar proportions
202 as most individuals (88%) had a clear sea signature; none were classified as freshwater-
203 residents (i.e. belonging to the Lake Iijärvi group) but two fish had intermediate carbon
204 isotope values (Table 3).

205

206 The proportion of anadromous fish determined by discriminant analysis decreased with the
207 distance from the sea (Figure 4), and in the Finnish sector of the Näätämöjoki (22 to 66 km
208 from the sea) 57 % of individuals were classified as freshwater-resident (Table 3). Most of
209 the fish (96%) caught from Lake Iijärvi had a clear freshwater-resident carbon signature
210 (Table 3). One fish had a rather higher $\delta^{13}\text{C}$ value (Figure 3 and 4) but presumably was not
211 an anadromous individual in view of its small size (267 mm).

212

213 Individuals classified as anadromous were longer (mean 53.8 cm, SD 8.7) than freshwater
214 resident fish (mean 42.2 cm, SD 13.6) ($t = 4.281$, $df = 67$, $p > 0.021$) (Figure 5A), but females
215 and males were similar in length ($t = 0.633$, $df = 46$, $p = 0.530$). However, variation in mean

216 length was higher in freshwater residents ranging from 27 cm to 72 cm (Figure 5A). Results
217 also indicate that large individuals were mostly sea-migrating and only a few freshwater-
218 residents were longer than 50 cm (Figure 5A & 5B). There seemed to be slight differences in
219 length distribution in different parts of the river system (Figure 5B), but no statistically
220 significant differences were found between sea-migrating and freshwater residents caught
221 in the Finnish sector (Näätämöjoki). However, fish caught from the Neidenfjorden estuary
222 were on average smaller and were slightly more depleted in carbon than sea-migrating fish
223 collected from the river (Figure 5B & Figure 2A). The proportions of anadromous and
224 freshwater-resident individuals were similar for females and males (Fisher's Exact test, $p =$
225 0.145).

226

227 Discussion

228

229 Our stable isotope analysis results revealed two distinct groups separating most brown trout
230 caught from the River Näätämöjoki system to anadromous or freshwater-resident
231 individuals. Although $\delta^{15}\text{N}$ and $\delta^2\text{H}$ values also showed substantial variation between
232 individuals, the carbon ($\delta^{13}\text{C}$) stable isotope value was the best indicator of individual
233 migration strategy in the River Näätämöjoki, as shown previously in other river systems
234 (e.g., McCarthy & Waldron, 2000). The scales of brown trout assigned as freshwater-
235 residents were clearly depleted in heavy carbon isotope reflecting a freshwater background
236 (McCarthy & Waldron, 2000), whereas scales of individuals caught from the estuary
237 reflected an enriched marine carbon isotope label gathered during the feeding migration in
238 the estuary and sea (e.g., Doucett et al., 1999).

239

240 In addition to individuals with evident marine or freshwater $\delta^{13}\text{C}$ carbon labels, some fish
241 had intermediate carbon values forming an own group between clearly anadromous and
242 freshwater-resident fish. Brown trout show extremely wide variation in migration strategies
243 (e.g., Chucherosset et al., 2005; Jonsson & Jonsson, 2017) and recent observations suggest
244 that patterns related to sea-migration could be more diverse than generally described (e.g.,
245 Etheridge et al., 2008; Aarestrup et al., 2017; Orell et al., 2017). In some populations, sea-
246 migrating individuals overwinter in the river and descend back to the estuary/sea for one or
247 more new growing season(s) (Jensen et al., 2017) before eventually starting the spawning
248 migration to upstream spawning areas (Orell et al., 2017). This back and forth movement
249 between river and sea could potentially cause mixing of stable isotope labels if fish feed in
250 both environments. Etheridge et al. (2008) reported a similar continuum in carbon stable
251 isotope values of muscle tissue in a Scottish brown trout population which they assumed to
252 be related to repeated movement and feeding between freshwater and sea environments.

253

254 Scales of anadromous trout could be expected to have higher $\delta^{15}\text{N}$ values compared with
255 freshwater-residents as marine food sources are enriched in heavy nitrogen isotopes (Post,
256 2002; Etheridge et al., 2008). In our data, individuals assigned as sea-migrating based on
257 carbon isotope values had consistently higher nitrogen values than freshwater-residents
258 indicating use of marine food sources. However, some fish had high nitrogen values but
259 carbon values close to freshwater values ($\delta^{13}\text{C}$ from -21 to -22.4). A positive correlation was
260 observed between $\delta^{15}\text{N}$ values and fish length which indicated that larger fish were sea-
261 migrating or freshwater residents which have fed on food sources in higher trophic levels
262 (e.g. fish) (Peterson & Fry, 1987). Despite the environment, brown trout often goes through

263 an ontogenetic shift from insectivory to piscivory after attaining a certain size (e.g., Jensen
264 et al., 2012) which could explain overlapping $\delta^{15}\text{N}$ values between 45-50 cm long sea-
265 migrating and freshwater-resident fish.

266

267 Recently there has been much interest in the use of hydrogen isotopes as a complimentary
268 isotope tracer in aquatic studies (e.g., Soto et al., 2013; Vander Zanden et al., 2016). Our
269 data showed that the utility of hydrogen isotope values for separating sea-migrating and
270 freshwater-resident brown trout was limited in the River Näätamöjoki system. We found
271 wide variation (from -40 to -140 ‰) in hydrogen isotope values evidently reflecting marine
272 and freshwater backgrounds (Post, 2002; Xu et al., 2012) but no clear groupings were
273 detected. Instead, measured values formed a continuum between proposed freshwater and
274 marine background values.

275

276 H stable isotope pathways in organisms are not as straightforward and predictable as those
277 for carbon and nitrogen isotopes (e.g., Vander Zanden et al., 2016; Soto et al., 2017).

278 Freshwater animals incorporate H isotopes from both diet and ambient water, and it is
279 widely assumed that the isotopic composition of the diet often has a stronger influence (
280 Soto et al., 2013). Therefore, we presumed that the observed variation in brown trout
281 hydrogen stable isotope values was related mainly to different migration strategies as
282 discussed above. We are aware that results could be influenced by exchangeable hydrogen
283 between tissues and environmental water after tissue formation (Vander Zanden et al.,
284 2016). However, as we compared hydrogen isotope values between similar tissues which
285 were analysed following a similar procedure, we expected differences mainly to stem from
286 differences in migration strategies (i.e., influence of exchangeable water proportion is

287 rather similar in all samples). In the future, more detailed studies are needed to unravel the
288 questions related to H isotope routing and effects of exchange with ambient water in fish
289 scales if it is used to study fish migrations.

290

291 Our results revealed that the number of sea-migrating individuals decreased constantly with
292 distance from the sea in accordance with the results based on scale readings (Niemelä et al.,
293 2015) forming a spatial continuum in migration strategies (Cucherousset et al., 2005). In the
294 River Näätamöjoki, brown trout spawn mainly in smaller tributaries which have higher
295 juvenile densities than in the main river (Niemelä et al., 2015). The most important
296 spawning areas for sea-migrating brown trout are believed to be in tributaries in the middle
297 part of river system (e.g., River Sillisjoki), and in the Nuortijoki tributary (Niemelä et al.
298 2015).

299

300 Migration costs are expected to be one of the main drivers of life-history variability in brown
301 trout populations as costs increase (e.g., energy, predation risk) with distance to the feeding
302 area and could lead to reduced fitness finally leading to loss of migratory strategy (Bohlin et
303 al., 2001; Klemetsen et al., 2003). In addition to distance, high altitude or migration barriers
304 such as strong rapids and waterfalls could restrict the migration tendency (L'Abée-Lund,
305 1991; Bohlin et al., 2001). Skoltefossen rapid, ca. 10 kilometres upstream from the
306 Neidenfjorden estuary, slows down salmon and brown trout migration in the Näätamöjoki,
307 especially during high discharges (Orell, 2012). A fish ladder was built in 1968 to assist
308 salmon and brown trout upstream migration. In a video monitoring study, Orell (2012)
309 found that brown trout passed the rapid mainly through the fish ladder from which we
310 presume that Skoltefossen rapid does not any longer restrict upstream migration.

311

312 All brown trout caught from Lake Iijärvi, which is the source of River Nääämöjoki, were
313 classified as freshwater residents. Lake Iijärvi together with slow flowing, large lake like pool
314 sections of the river below Iijärvi most probably offers a good feeding area for trout as a
315 favourable alternative to a long migration to sea (Jonsson & Jonsson, 2004). According to
316 Niemelä et al. (2015) potamodromous (from river to lake) migration occurs between Iijärvi
317 and Nääämöjoki and other small rivers flowing to Iijärvi. However, it was not possible to
318 separate freshwater-migratory individuals from residents in our data as no detailed $\delta^{13}\text{C}$
319 baseline data was available across tributaries.

320

321 Sexual size dimorphism is often observed in brown trout populations where migratory and
322 resident forms are present (Jonsson & Jonsson, 2004). Females are found to be more often
323 migratory as they are supposed to benefit more from migration due to increased fecundity
324 and thereby reproduction success which stems from better growth rates in the sea or in the
325 lakes (Jonsson & Jonsson, 1993; Jonsson & Jonsson, 1997; Solomon, 2004). In our study,
326 individuals assigned as anadromous were on average more than 10 cm longer than
327 freshwater residents which was concordant with earlier observations. The largest individuals
328 were mostly assigned as anadromous but two exceptionally large freshwater residents (> 70
329 cm) showed that under favourable conditions the Nääämöjoki brown trout can also grow
330 well in freshwater. Females often dominated the migratory component of the population
331 (Klemetsen et al., 2003), but we found no clear differences between sexes in migration
332 strategies.

333

334 In the current data set, the average size of fish caught from the Neidenfjorden estuary was
335 smaller than in sea-migrating fish collected from the river. This is likely a result of sampling
336 feeding fish, including immature individuals, in the estuary, whereas the river sample of
337 anadromous fish consisted mostly of mature spawners.

338

339 The River Näätamöjoki system supports brown trout sub-populations with various migration
340 strategies which vary spatially along the gradient from sea to freshwater sources. Such
341 variability in migration strategies is a great challenge for conservation and fisheries
342 management. Although the Näätamöjoki trout clearly exhibit partial migration within the
343 river continuum, the tendency to migrate seems to gradually disappear towards
344 headwaters. This indicates that management of trout population could be carried out in two
345 separate spatial units. Although not fully explicit, division into two migration strategies,
346 from partially migrating to resident populations, takes place roughly at 35 – 50 km from the
347 river mouth. Results indicated that some anadromous brown trout were present up to Lake
348 Opukasjärvi (Fig. 1), but trout were mostly residents farther upstream. Lake Opukasjärvi
349 (1.53 km²; 50 km from the river mouth) forms a natural break in river continuum and may
350 therefore form a natural division for two management units. However, we had only a few
351 samples between lakes Opukasjärvi and Iijärvi; hence, more spatial coverage would be
352 needed for defining management areas.

353

354 The wide suite of migration strategies (anadromous, potamodromous, and resident) in
355 Näätamöjoki is probably maintained by the combination of several factors such as divergent
356 availability of resources, variable migration costs, and genetic differences (Bohlin et al.,
357 2001; Klemetsen et al., 2003; Jonsson & Jonsson, 2004; Wysujack et al. 2009;

358 Jonsson & Jonsson, 2017). A clear, distinct genetic structure has been detected in many
359 brown trout populations even between tributaries of a single river system (e.g., Lehtonen et
360 al., 2009; Swatdipong et al., 2010). However, some studies have shown significant gene flow
361 between migratory and resident brown trout forms (Charles et al., 2006). Further studies
362 are needed to couple genetic and ecological patterns for effective management and
363 preservation of brown trout populations with diverse life-history strategies.

364

365 References

366

367 Aarestrup, K., Birnie-Gauvin, K. & Larsen, M.H. (2017). Another paradigm lost? Autumn
368 downstream migration of juvenile brown trout: Evidence for a presmolt migration. *Ecology*
369 *of freshwater fish*, doi:10.1111/eff.12335

370

371 Briers, R. A., Waterman, J.O., Galt, K. & Campbell, R.N.B. (2013). Population differentiation
372 and temporal changes of carotenoid pigments and stable isotope ratios in the offspring of
373 anadromous and non-anadromous trout *Salmo trutta*. *Ecology of Freshwater Fish*, 22: 137-
374 144. doi: 10.1111/eff.12011

375

376 Charles, K., Roussel, J.-M. & Cunjak, R.A. (2004). Estimating the contribution of sympatric
377 anadromous and freshwater resident brown trout to juvenile production. *Marine and*
378 *Freshwater Research*, 55: 185-191. doi:10.1071/MF03173

379

380 Chapman, B.B., Hulthen, K., Brodersen, J., Nilsson, P.A., Skov, C., Hansson, L.A., Brönmark, C.
381 (2012). Partial migration in fishes: causes and consequences. *Journal of Fish Biology*, 81:
382 456-478.

383

384 Chucherousset, J., Ombredane, D., Charles, K., Marchand, F. & Baglinière, J. (2005). A
385 continuum of life history tactics in a brown trout (*Salmo trutta*) population. *Canadian*
386 *Journal of Fisheries and Aquatic Sciences*, 62: 1600-1610. doi: 10.1139/f05-057

387

388 Dansgaard, W. (1964). Stable isotopes in precipitation. *Tellus*, 16:436–468. doi:
389 10.3402/tellusa.v16i4.8993

390

391 Dixon, H. J., Dempson, J. B., & Power, M. (2015). Assessing the use of different marine
392 growth zones of adult Atlantic salmon scales for studying marine trophic ecology with stable
393 isotope analysis. *Fisheries Research*, 164: 112–119

394

395 Doucett, R.R., Booth, R.K., Power, G. & McKinley, R.S. (1999). Effects of the spawning
396 migration on the nutritional status of anadromous Atlantic salmon (*Salmo salar*): insights
397 from stable-isotope analysis. *Canadian Journal of Fisheries and Aquatic Sciences*, 56 (11):
398 2172-2180.

399

400 Elliot, D.M. (1994). *Quantitative Ecology and the Brown Trout.*, NY, Oxford University Press.

401

402 Erkinaro, J., Czorlich, Y., Orell, P., Kuusela, J., Lämsman, M., Falkegård, M., Pulkkinen, H.,
403 Primmer, C. & Niemelä, E. (2018). Life history variation across four decades in a diverse

404 population complex of Atlantic salmon in a large subarctic river. Canadian Journal of
405 Fisheries and Aquatic Sciences. 10.1139/cjfas-2017-0343
406
407 Etheridge, E.C., Harrod, C., Bean, C. & Adams, C.E. (2008) Continuous variation in the pattern
408 of marine v. freshwater foraging in brown trout *Salmo trutta* L. from Loch Lomond, Scotland.
409 Journal of Fish Biology, 73: 44–53. doi: 10.1111/j.1095-8649.2008.01905.x
410
411 Hard, J.J., Gross, M.R., Heino, M., Hilborn, R., Kope, R.G., Law, R., Reynolds, J.D. 2008.
412 Evolutionary consequences of fishing and their implications for salmon. Ecological
413 Applications, 1: 388-408. doi:10.1111/j.1752-4571.2008.00020.x
414
415 Hanson, N.N., Wurster, C.M., EIMF & Todd, C.D. (2010). Comparison of secondary ion mass
416 spectrometry and micromilling/continuous flow isotope ratio mass spectrometry techniques
417 used to acquire intra-otolith $\delta^{18}\text{O}$ values of wild Atlantic salmon (*Salmo salar*). Rapid
418 Communications in Mass Spectrometry, 24: 2491-2498. doi: 0.1002/rcm.4646
419
420 Hobson, K.A. (1999). Tracing origins and migration of wildlife using stable isotopes: a review.
421 Oecologia, 120: 314-326.
422
423 Hobson, K.A. & Wassenaar, L.I. (2008). Tracking animal migration with stable isotopes.
424 Oxford, Academic Press, Elsevier.
425

426 Hutchinson, J.J. & Trueman, C.N. (2006). Stable analysis of collagen in fish scales: limitations
427 set by scale architecture. *Journal of Fish Biology*, 69: 1874–1880. doi: 10.1111/j.1095-
428 8649.2006.01234.x

429

430 Huusko, A., Vainikka A., Syrjänen, J.T., Orell, P., Louhi, P. & Vehanen T. (2017). Life-history of
431 the adfluvial brown trout (*Salmo trutta* L.) in eastern Fennoscandia. In: Lobón-Cerviá, J. &
432 Sanz, N (ed.) *Brown Trout: Biology, Ecology and Management*. Wiley.

433

434 Jensen, A.J., Finstad, B. & Fiske, B. (2017). Evidence for the linkage of survival of
435 anadromous Arctic char and brown trout during winter to marine growth during the
436 previous summer. *Canadian Journal of Fisheries and Aquatic Sciences*,
437 <https://doi.org/10.1139/cjfas-2017-0077>

438

439 Jonsson, B. & Jonsson, N. (1993). Partial migration: niche shift versus sexual maturation in
440 fishes. *Reviews in Fish Biology and Fisheries*, 3: 348–365.

441

442 Jonsson, N. & Jonsson, B. (2002). Migration of anadromous brown trout *Salmo trutta*
443 in a Norwegian river. *Freshwater Biology*, 47: 1391-1401. doi: 10.1046/j.1365-
444 2427.2002.00873.

445

446 Jonsson, N. & Jonsson, B. (2004). Life History of the Anadromous Trout
447 *Salmo trutta*. In: Harris, G. & Milner, N. (eds.) *Sea trout: biology, conservation and*
448 *management, Proceedings of the First International Sea Trout Symposium*.

449

450 Jonsson B., Jonsson, N. (2017). Habitat as template for life-histories. In: Lobón-Cerviá, J. &
451 Sanz, N (ed.) *Brown Trout: Biology, Ecology and Management*. Wiley.

452

453 Klemetsen, A., Amundsen, P.-A., Dempson, J.B., Jonsson, B., Jonsson, N., O'Connell, M.F.,
454 Mortensen, E. (2003). Atlantic salmon *Salmo salar* L., brown trout *Salmo trutta* L. and Arctic
455 charr *Salvelinus alpinus* (L.): a review of aspects of their life histories. *Ecology of Freshwater*
456 *Fish*, 12: 1–59. doi: 10.1034/j.1600-0633.2003.00010.x

457

458 Laugen, A. T., Engelhard, G. H., Whitlock, R., Arlinghaus, R., Dankel, D., Dunlop E.S., Eikeset
459 A.M., Enberg, K., Jørgensen, C., Matsura, S., Nussle, S., Urbach, D., Baulier, L., Boukal, D.S.,
460 Ernande, B., Johnston, F.D., Mollet, F., Pardoe, H., Therkildsen, N.O., Uusi-Heikkilä, S.,
461 Vainikka, A., Heino, M., Rijnsdorp, A.D., Dieckmann, U. (2014). Evolutionary impact
462 assessment: accounting for evolutionary consequences of fishing in an ecosystem approach
463 to fisheries management. *Fish and Fisheries*, 15: 65–96. doi: 10.1111/faf.12007

464

465 Lehtonen, P. K., Tonteri, A., Sendek, D., Titov, S., Primmer, C.R. (2009). Spatio-temporal
466 genetic structuring of brown trout (*Salmo trutta* L.) populations within the River Luga,
467 northwest Russia. *Conservation Genetics*, 10: 281-289. doi: 10.1007/s10592-008-9577-2

468

469 McCarthy, I.D. & Waldron, S. (2000). Identifying migratory *Salmo trutta* using carbon and
470 nitrogen stable isotope ratios. *Rapid Communications in Mass Spectrometry*, 14: 1325-1331.
471 doi: 10.1002/1097-0231(20000815)14:15<1325::AID-RCM980>3.0.CO;2-A
472

473 Moore, J. W., Yeakel, J.D., Peard, D. Lough, J. & Beere, M. (2014). Life-history diversity and its
474 importance to population stability and persistence of a migratory fish: steelhead in two
475 large North American watersheds. *Journal of Animal Ecology*, 83: 1035–1046. doi:
476 10.1111/1365-2656.12212
477
478 Niemelä, E., Lämsä, M., Hassinen, E., Kuusela, J., Kylmäaho, J., Haantie, J., Arvola, K.M. &
479 Kalske, T.H. (2015). Näätämojoen vesistöalueen meritaimenen ekologia, vaelluksen
480 ajoittuminen ja saaliit. Näätämojoen moninaiskäyttösuunnitelma, 102 pp.
481
482 Orell, P. (2012). Video monitoring of the River Neidenelva salmon and sea-trout migrations
483 in 2006-2011. Working papers of the Finnish Game and Fisheries Institute 8/2012.
484
485 Orell, P., Erkinaro, J., Kanninen, T., Kuusela, J. (2017). Migration behavior of sea trout
486 (*Salmo trutta*, L.) in a large sub-arctic river system: evidence of a two-year spawning
487 migration. In: Harris, G.S. (ed) *Sea trout: Science & Management*. Proceedings of 2nd
488 International Sea Trout Symposium, October 2015, Dundalk, Ireland., pp 396–410.
489
490 Orell, P., Erkinaro, J., Kiljunen, M., Tornainen, J., Sutela, T., Jaukkuri, M., & Mäki-Petäys,
491 A. Short sea migration and precocious maturation in reared Atlantic salmon postsmolts
492 in the northern Baltic Sea. *ICES Journal of Marine Science*, fsx213,
493 <https://doi.org/10.1093/icesjms/fsx213>
494
495 Perga, M. E. & Gerdeaux, D. (2003). Using the $\delta^{13}C$ and $\delta^{15}N$ of whitefish scales for
496 retrospective ecological studies: changes in isotope signatures during the restoration of Lake

497 Geneva, 1980–2001. *Journal of Fish Biology*, 63: 1197–1207. doi: 10.1046/j.1095-
498 8649.2003.00239.x
499
500 Perga, M.E. & Gerdaux, D. (2005). Are fish what they eat' all year round? *Oecologia*, 144:
501 598-606.
502
503 Post, D.M. (2002). Using stable isotopes to estimate trophic position: Models, methods, and
504 assumptions. *Ecology*, 83(3), 703-718. doi: 10.1890/0012-
505 9658(2002)083[0703:USITET]2.0.CO;2
506
507 Peterson, B.J. & Fry, B. (1987). Stable isotopes in ecosystem studies. *Annual Review of*
508 *Ecology and Systematics*, 18,292 – 320.
509
510 Ramsay, A. L., Milner, N.J., Hughes, R.N., McCarthy, I. D. (2011). Comparison of the
511 performance of scale and otolith microchemistry as fisheries research tools in a small
512 upland catchment. *Canadian Journal of Fisheries and Aquatic Sciences*, 68: 823-833.
513 doi:10.1139/F2011-027
514
515 Roussel, J.-M., Perrier, C., Erkinaro, J., Niemelä, E., Cunjak, R.A., Huteau, D. & Riera, P.
516 (2014). Stable isotope analyses on archived fish scales reveal the long-term effect of
517 nitrogen loads on carbon cycling in rivers. *Global Change Biology*, 20: 523-530. doi:
518 10.1111/gcb.12293

519 Ryan, D., Shephard, S., Kelly, F.L. (2016). Temporal stability and rates of post-depositional
520 change in geochemical signatures of brown trout *Salmo trutta* scales. *Journal of Fish*
521 *Biology*, 89: 1704–1719. doi:10.1111/jfb.13081
522

523 Schindler, D.E. , Hilborn, R. , Chasco, B. , Boatright, C.P., Quinn, T.P., Rogers, L.A. & Webster,
524 M.S. (2010). Population diversity and the portfolio effect in an exploited population. *Nature*,
525 465: 609-613. doi:10.1038/nature09060
526

527 Soto, D.X., Wassenaar, L.I., Hobson, K. A.& Catalan, J. (2011). Effects of size and diet on
528 stable hydrogen isotope values (δD) in fish: implications for tracing origins of individuals and
529 their food sources. *Canadian Journal of Fisheries and Aquatic Sciences*, 68: 2011-2019. doi:
530 10.1139/f2011-112
531

532 Soto, D.X., Wassenaar, L.I. & Hobson, K.A. (2013). Stable hydrogen and oxygen isotopes in
533 aquatic food webs are tracers of diet and provenance. *Functional Ecology*, 27: 535–543. doi:
534 10.1111/1365-2435.12054
535

536 Swatdipong, A., Vasemägi A., Niva, T., Koljonen, M.L. & Primmer C.R. (2010). High level of
537 population genetic structuring in lake-run brown trout, *Salmo trutta*, of the Inari Basin,
538 northern Finland. *Journal of Fish Biology*, 77: 2048-2071. doi:10.1111/j.1095-
539 8649.2010.02784.x
540

541 Syrjänen, J. & Valkeajärvi, P. (2010). Gillnet fishing drives lake-migrating brown trout to

542 near extinction in the Lake Päijänne region, Finland. *Fisheries Management and Ecology*, 17:
543 199-208. doi: 10.1111/j.1365-2400.2010.00738.x

544

545 Thériault, V., Dunlop, E.S., Dieckmann, U., Bernatchez, L. & Dodson, J.J. (2008). The impact
546 of fishing-induced mortality on the evolution of alternative life-history tactics in brook charr.
547 *Evolutionary Applications*, 1: 409-423. doi: 10.1111/j.1752-4571.2008.00022.x

548

549 Tillotson, M.D. & Quinn, T.P. (2017). Selection on the timing of migration and breeding: A
550 neglected aspect of fishing-induced evolution and trait change. *Fish and Fisheries*. doi:
551 10.1111/faf.12248

552

553 Torniainen, J., Vuorinen P. J., Jones, R. I., Keinänen, M., Palm, S., Vuori, K. A. M. & Kiljunen,
554 M. (2014). Migratory connectivity of two Baltic Sea salmon populations: retrospective
555 analysis using stable isotopes of scales. *ICES Journal of Marine Science*.
556 doi:10.1093/icesjms/fst153

557

558 Torniainen, J., Lensu, A., Vuorinen, P.J., Sonninen, E., Keinänen, M., Jones R.I., Patterson, W.
559 P. & Kiljunen M. (2017). Oxygen and carbon isoscapes for the Baltic Sea: Testing their
560 applicability in fish migration studies. *Ecology and Evolution*, 1–13. DOI: 10.1002/ece3.2841

561

562 Wassenaar, L.I. & Hobson, K.A. (2003). Comparative equilibration and online technique for
563 determination of non-exchangeable hydrogen of keratins for use in animal migration
564 studies. *Isotopes in Environmental and Health Studies*, 39:211–217. doi:
565 10.1080/1025601031000096781

566 Wassenaar, L.I. & Hobson, K.A. (2010). Two new keratin standards ($\delta^2\text{H}$, $\delta^{18}\text{O}$) for daily
567 laboratory use in wildlife and forensic isotopic studies. The 7th International Conference on
568 Applications of Stable Isotope Techniques to Ecological Studies. University of Alaska,
569 Fairbanks, Alaska, USA.

570

571 Whitley, G.W. & Johnson, B.M.(2006). Stable hydrogen isotope composition of fishes
572 reflects that of their environment. Canadian Journal of Fisheries and Aquatic Sciences, 63:
573 1746-1751. doi: 10.1139/f06-076

574

575 Wysujack, K., Greenberg, L.A., Bergman, E., Olsson, I.C. (2009). The role of the environment
576 in partial migration: food availability affects the adoption of a migratory tactic in brown
577 trout *Salmo trutta*. Ecology of Freshwater Fish, 18: 52-59. doi: 10.1111/j.1600-
578 0633.2008.00322.x

579

580 Vähä, J.P., Erkinaro, J., Niemelä, E., Primmer, C.R., Saloniemi, I., Johansen, M., Svehlik, M. &
581 Brørs, S. 2010. Temporally stable population-specific differences in run timing of one-sea-
582 winter Atlantic salmon returning to a large river system. Evolutionary Applications, 4: 39-53.
583 doi: 10.1111/j.1752-4571.2010.00131.x

584

585 Xu, X., Werner, M., Butzin, M. & Lohmann, G. 2012. Water isotope variations in the global
586 ocean model MPI-OM, Geoscientific Model Development, 809-818. doi: 10.5194/gmd-5-
587 809-2012

588

589 Vander Zanden, H.B., Soto, D.X., Bowen, G.J. & Hobson, K.A. (2016). Expanding the isotopic
590 toolbox: applications of hydrogen and oxygen stable isotope ratios to food web studies.
591 *Frontiers in Ecology and Evolution*. doi: 10.3389/fevo.2016.00020

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600

601 Authors' Contributions Statement

602

603 Conceived and designed the investigation: TJR, MK, OS, EV, PO, JE, RIJ

604 Performed laboratory work and stable isotope analysis: TJR, MK, OS, EV

605 Analyzed the data: TJR, MK

606 Wrote the paper: TJR, MK, PO, JE, RIJ

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613 Table 1. Number of brown trout scale samples collected from five sampling areas of the
 614 River Näätamöjoki, mean total length (min-max) of fish, and distance of the area from the
 615 river mouth.

Area	n	Length (cm)		Distance to river mouth (km)
		mean	min - max	
Lake Iijärvi	22	36.6	26.7 - 74.2	70-88
Näätamöjoki, Finland	21	53.1	31.0 - 72.0	22-66
Nuortijoki, tributary	8	53.0	45.0 - 62.0	16-25
Neidenelva, Norway	17	52.6	40.0 - 79.0	0-22
Neidenfjorden, estuary	11	48.2	37.0 - 59.0	0
All	79	47.9	26.7- 79.0	

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621 Table 2. The mean (S.D. and CV) $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and $\delta^2\text{H}$ stable isotope values of brown trout
 622 scales collected from different sampling areas of the Näätamöjoki River system.

Site	$\delta^{13}\text{C}$			$\delta^{15}\text{N}$			$\delta^2\text{H}$		
	Mean	S.D.	CV	Mean	S.D.	CV	Mean	S.D.	CV
Lake Iijärvi	-23.1	0.9	3.9	8.9	0.5	5.7	-91.4	18.9	20.7
Näätamöjoki, Finland	-20.4	2.6	12.6	10.9	1.6	14.7	-83.2	20.2	24.3
Nuortijoki, tributary	-17.3	1.5	8.7	12.2	0.5	4.5	-	-	-
Neidenelva, Norway	-17.5	1.2	6.6	12.1	0.8	7.0	-70.1	12.7	18.1
Neidenfjorden, estuary	-18.0	0.6	3.2	12.3	0.6	4.6	-64.8	9.9	15.3

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624

625 Table 3. Life-history strategies of the River Näätamöjoki brown trout predicted by
 626 discriminant analysis based on $\delta^{13}\text{C}$ values of scales collected from the different sampling
 627 areas.

	n	Migratory	Resident	Intermediate	Migratory %	Resident %	Intermediate %
Lake Iijärvi	22	0	21	1	0	95	5
Näätamöjoki, Finland	21	6	12	3	29	57	14
Nuortijoki, tributary	8	7	0	1	88	0	13
Neidenelva, Norway	17	15	0	2	88	0	12
Neidenfjorden, estuary	11	9	0	2	82	0	18
	79	37	33	9	47	42	11

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643 Figure legends

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645 Figure 1. Map of the River Näätamöjoki system showing the different sampling areas:
646 estuary (Neidenfjorden), Norwegian lower river reaches (Neidenelva), a tributary (River
647 Nuortijoki), upper river reaches in Finland (Näätamöjoki), and the Lake Iijärvi.

648

649 Figure 2. Scale $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values (A), $\delta^2\text{H}$ and $\delta^{13}\text{C}$ values (B), and $\delta^{15}\text{N}$ and $\delta^2\text{H}$ values (C)
650 for brown trout collected from the Näätamöjoki river system. Sampling areas of fish are
651 marked with different symbols and colours.

652

653 Figure 3. Relationship between brown trout length and stable isotope values of $\delta^{13}\text{C}$, $\delta^{15}\text{N}$,
654 and $\delta^2\text{H}$ of scales collected from the Näätamöjoki river system.

655

656 Figure 4. Relationship between brown trout scale $\delta^{13}\text{C}$ ratio and distance from the river
657 mouth in the Näätamöjoki river system. Proposed migration categories were assigned from
658 discriminant analysis. Sea-migrating fish are indicated with open circles, intermediate fish
659 with grey circles, and freshwater-resident fish with black circles.

660

661 Figure 5. A) Total length (cm) of sea-migrating, intermediate, and freshwater-resident brown
662 trout in the Näätamöjoki river system. B) Total length (cm) of sea-migrating, intermediate,
663 and freshwater-resident brown trout in different areas of the Näätamöjoki river system.

664 Proposed migration categories were assigned from discriminant analysis. Sea-migrating fish
665 are indicated with open circles, intermediate fish with grey circles, and freshwater-resident
666 fish with black circles.

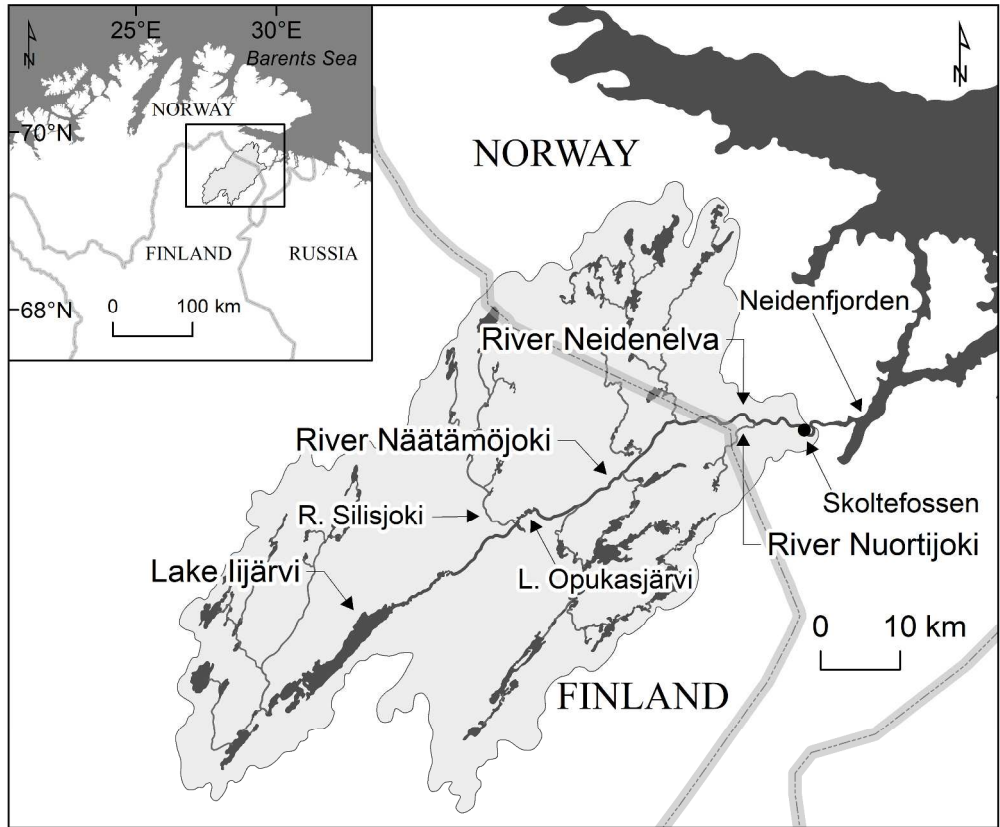


Figure 1. Map of the River Näätmöjoki system showing the different sampling areas: estuary (Neidenfjorden), Norwegian lower river reaches (Neidenelva), a tributary (River Nuortijoki), upper river reaches in Finland (Näätmöjoki), and the Lake Iijärvi.

