

1 Title

2 Environmental influences of life history strategies in partial anadromous brown trout (*Salmo*
3 *trutta*, Salmonidae)

4

5 Running title

6 Life history of brown trout

7

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34 **Abstract**

35 This paper reviews the life history of brown trout (*Salmo trutta*, Salmonidae) and factors
36 influencing decisions to migrate. Decisions that maximize fitness appear dependent on size at
37 age. In partly anadromous populations, individuals that attain maturity at the parr stage
38 typically become freshwater resident. For individual fish, the life history is not genetically
39 fixed, and can be modified by the previous growth history and energetic state in early life.
40 This phenotypic plasticity may be influenced by epigenetic modifications of the genome.
41 Thus, factors influencing survival and growth, determine life history decisions. These are
42 intra- and interspecific competition, feeding and shelter opportunities in fresh and salt water,
43 temperature in alternative habitats and flow-conditions in running water. Male trout exhibit
44 alternative mating strategies and can spawn as a subordinate sneaker or a dominant
45 competitor. Females do not exhibit alternative mating behaviour. The relationship between
46 growth, size and reproductive success differs between sexes in that females exhibit a higher
47 tendency to migrate than males. Southern populations are sensitive to global warming. In
48 addition, fisheries, aquaculture with increased spreading of salmon lice, introduction of new
49 species, weirs and river regulation, poor water quality and coastal developments all threaten
50 trout populations. The paper summarizes life history data from six populations across Europe
51 and ends by presenting new research questions and directions for future research.

52

53 **Keywords:**

54 freshwater resident; habitat; migration; partial anadromy, Salmonidae, sex ratio

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80 *Inter-specific competition*

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82 **Influence of the marine environment on migration outcome**

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103 *Epigenetics*

104 *Management strategies*

105 **Acknowledgements**

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111 **Introduction**

112 Brown trout (*Salmo trutta*, Salmonidae) is a facultative (i.e. partly) anadromous species
113 (Lobón-Cerviá, Rasmussen, & Mortensen, 2017). It typically spawns in freshwater, but may
114 reproduce successfully in estuaries at salinities below 4 ppt, such as on the coast of Gotland
115 in the Baltic Sea (Landergren & Vallin, 1998; Limburg, Landergren, Westin, Elfman, &
116 Kristiansson, 2001). The species is partly migratory as some individuals within a population
117 may reside in or near the spawning area all year round, whereas other individuals move out of
118 this area for feeding. Migratory trout can be anadromous, feeding in the marine habitat.
119 Migrants generally return to breed with high precision to their area of origin for spawning,
120 but exceptions occur (B. Jonsson, Jonsson, & Jonsson, 2018).

121

122 Brown trout are phenotypically variable. Adult body length varies from approximately 10 to
123 100 cm (Evangelista, Boiche, Lecerf, & Cucherousset, 2014; B. Jonsson & Jonsson, 2011;
124 Sánchez-Hernández, Eloranta, Finstad, & Amundsen, 2017). The species exploit habitats
125 ranging from small brooks to rivers, lakes, estuaries and coastal sea, but are seldom found in
126 the open ocean, though recent literature indicate that some brown trout may live a more
127 pelagic life while at sea (B. Jonsson & Jonsson, 2011; Kristensen, Righton, del Villar-Guerra,
128 Baktoft, & Aarestrup, 2018). Populations adapt trophically to, and vary ecologically,
129 morphologically, behaviourally and genetically with local conditions over the distribution
130 area. This diversity complicates the systematics of the species, and makes some scientists
131 term *Salmo trutta* a species complex rather than a single species (Keller, Taverna, &
132 Seehausen, 2011; Patarnello, Bargelloni, Caldara, & Colombo, 1994; Sanz, 2017). Although
133 the systematics of brown trout have still to be resolved, the phylogeographic and the genetic
134 structure of the species were recently clarified (Sanz, 2017).

135

136 Freshwater resident populations are well described (Baglinière & Maisse, 2002; Frost &
137 Brown, 1967; Gosset, Rives, & Labonne, 2006; B. Jonsson, 1989; Maisse & Baglinière,
138 1990). More complex is the ecology of anadromous trout (Harris, 2017; Harris & Milner,
139 2006), which occur naturally along the length of the Atlantic coast of Europe from northern
140 Russia to Portugal, Iceland included, and occur as an introduced fish in North and South
141 America, Australia, New Zealand and Kerguelen Islands (Baglinière, 1999; Elliott, 1994; B.
142 Jonsson & Jonsson, 2011; Lecomte, Beall, Chat, Davaine, & Gaudin, 2013) (Figure 1). The
143 species is present along the coast of the Black and Caspian-Aral Seas in central Europe
144 (Baglinière, 1999; Elliott, 1994; B. Jonsson & Jonsson, 2011). Among all introduced
145 Salmonidae species, brown trout is the species with the highest success rate of naturalisation
146 and the largest distribution out of its original range. This is likely the result of a high adaptive
147 capacity and tolerance for habitat change (Baglinière, 1999).

148

149 Brown trout have been the focus of several books such as those by Fahy (1985), Elliott
150 (1994), Baglinière and Maisse (1999), Harris and Milner (2006), Harris (2017), Jonsson and
151 Jonsson (2011), and Lobón-Cerviá and Sanz (2017). However, some recent knowledge on
152 migration, its complexity and plasticity is not included in these books (Figure 2). This work is
153 also motivated by the desire to complement the literature review with a compilation of data
154 from six populations across Europe. Partly anadromous means that individual populations can
155 consist of both freshwater resident and anadromous individuals. In this review, we present
156 information on both these life history components, and discuss drivers of anadromy, the
157 influence of the marine environment on the migration, and effects of spawning habitat on
158 body size and sexual size dimorphism. Furthermore, we summarize knowledge on effects of
159 interspecific competitors and predators on abundance and behaviour of brown trout and
160 impacts of the parasitic sea lice on local sea trout, which constitutes one of the main threats to

161 wild populations in some areas (Thorstad et al., 2015), and which has led to significant
162 population collapses (e.g. Gargan, Poole, & Forde, 2006). Environmental constraints in
163 freshwater may stimulate migration of brown trout, including constraints from competition,
164 poor feeding and low growth opportunities. We review the effects of these, as well as
165 negative environmental impacts at sea that may select against the propensity to migrate
166 (Poole et al., 2006). Last, we present important questions for further research.

167

168 **Resident versus anadromous brown trout**

169 **Historical overview**

170 Carolus Linnaeus, in his 10th edition of *Systema Naturae* (1758), classified anadromous (sea)
171 trout (*Salmo eriox*) as a different species from river trout (*Salmo trutta*). The classification
172 was based on colouration and body form, a taxonomic classification maintained into the 19th
173 century (B. Jonsson & Jonsson, 2011). Among others, Dahl (1904) questioned the
174 classification as he observed that river trout could move downstream to sea. Furthermore,
175 Regan (1911) proposed that anadromous and non-anadromous trout could be freely
176 interbreeding fractions of a single species. Nevertheless, until the development of modern
177 genetic techniques in the 1980's, much uncertainty remained about whether or not sea trout
178 and river trout were the same or separate species (Frost & Brown, 1967).

179

180 **Two phenotypes and a single species**

181 Brown trout may have split from Atlantic salmon *Salmo salar* between 10 and 14 million
182 years ago (Crête-Lafrenière, Weir, & Bernatchez, 2012) and the five major evolutionary
183 lineages of brown trout evolved in its native Eurasian and North African range of distribution
184 with geographic isolation occurring during the Pleistocene Ice Ages and have largely
185 remained allopatric since then (Bernatchez, 2001). Their evolutionary histories have been

186 shaped by glaciations, habitat loss and varying potential for dispersal. They survived in ice-
187 free refuges during the periods of glaciation and colonized rivers as the ice cover retreated
188 (McKeown, Hynes, Duguid, Ferguson, & Prodöhl, 2010). After the last glaciation period
189 some 14000 years ago they entered rivers in the former glaciated northern areas and gradually
190 acquired their natural area we see today (Ferguson, 2006). The anadromous behaviour
191 probably existed before speciation of the salmonid family and the anadromous types, mainly
192 of the genus *Salmo*, evolved from the freshwater forms (Balon, 1980).

193

194 By origin, brown trout is chiefly a European species, but populations have been introduced to
195 areas outside their natural range they were unable to reach naturally (B. Jonsson & Jonsson,
196 2011). For instance, offspring of anadromous trout were released in some North American
197 rivers, and from these progenitors both anadromous and non-anadromous trout developed
198 (Rounsefell, 1958), proving that the two trout forms could develop from single gene pools.
199 Similar evidence was obtained from releases in the Kerguelen Islands (Davaine & Beall,
200 1997). The close connection between the two phenotypes was further highlighted by the
201 observation that offspring of a population of resident mountain living brown trout feed and
202 grow well at sea when transferred to a coastal river with free access to and from the sea (N.
203 Jonsson, Jonsson, & Hansen, 1994). They also survive and grow when they are released
204 directly into sea water as unsmoltified parr or immature brown trout (N. Jonsson, Jonsson,
205 Hansen, & Aass, 1994), although osmoregulatory performance is favoured by a progressive
206 transfer to seawater (Boeuf & Harache, 1982). Experimentally, Skrochowska (1969) and
207 Ombredane *et al.* (1996) demonstrated that anadromous as well as non-anadromous parents
208 produced both freshwater resident and sea-run migratory offspring. However, the proportion
209 of anadromous offspring was higher for anadromous than non-anadromous parents,
210 indicating a difference in gene expression between the two forms. Also, within single river

211 systems, anadromous and non-anadromous trout spawn together as has been observed in the
212 field (Charles, Guyomard, Hoyheim, Ombredane, & Baglinière, 2005; Cucherousset,
213 Ombredane, Charles, Marchand, & Baglinière, 2005; B. Jonsson, 1985; Vøllestad, 2017), but
214 the proportions of anadromous vs resident maternal origin parr will probably differ in
215 different sections of the stream (Rohtla et al., 2017). Population diversification through
216 anadromous and non-anadromous individuals is not unique to brown trout, but is also found
217 in other salmonids (e.g. rainbow trout: *Oncorhynchus mykiss*, Arctic charr *Salvelinus alpinus*)
218 and some non-salmonid species (e.g. American shad: *Alosa sapidissima*) (B. Jonsson &
219 Jonsson, 1993).

220

221 Contrast in gene expression

222 Although anadromous and non-anadromous trout are genetically similar when in sympatry
223 (Charles et al., 2005; Cross, Mills, & Williams, 1992; Hindar, Jonsson, Ryman, & Ståhl,
224 1991; Pettersson, Hansen, & Bohlin, 2001), around 50% of the variability in migration v.
225 residency, among individuals within a population, may be due to genetic variance (Ferguson,
226 Reed, Cross, McGinnity, & Prodöhl, 2019). Recent evidence suggests differences in the gene
227 expression influencing the life history of the two trout phenotypes (Giger et al., 2006;
228 Lemopoulos et al., 2018, 2017). For instance, Giger et al. (2006) demonstrated that the gene
229 expression was primarily related to the migratory trait and not to genetic relatedness, whether
230 the fish migrate to the sea or a lake. They found that migrant and freshwater resident brown
231 trout from the same area exhibited different gene expression profiles, whereas evolutionarily
232 or geographically distant populations sharing the same life histories showed similar gene
233 expression, i.e. similar levels of mRNA transcripts. For example, a resident population
234 belonging to a Mediterranean lineage that diverged more than 500 000 years ago from the
235 Atlantic lineage, exhibited a gene expression profile like that of resident Atlantic populations.

236 By contrast, migratory and resident trout from the same river had very different profiles (sets
237 of mRNAs). Migration destination (mainstream river, lake, or sea) also appears to be
238 genetically programmed (Ferguson et al., 2019). Giger et al. (2006) suggested that the genetic
239 difference between life history types of brown trout is the result of a few controlling genes
240 that determine the expression of many other genes defining the life history pattern. They
241 found that life history differences explained 45% of the total variability in gene expression
242 levels, three times more than the variability explained by genetic diversity between
243 populations. Thus, gene expression appears to be influenced by the environment and
244 interactions between genes and environment that drive life history and migration decisions.

245

246 [Phenotypic plasticity](#)

247 There is considerable variation in life history strategies among individuals and populations,
248 and in the timing and duration of marine migrations of brown trout (Aldvén & Davidsen,
249 2017; B. Jonsson, 1989; Thorstad et al., 2016). Figure 2 illustrates this diversity: after 1 to 7
250 years in freshwater, some individuals make a physiological transformation from parr to smolt
251 and migrate to sea. Young parr may also make excursions into brackish water. Downstream
252 migration usually takes place in spring and autumn (Aarestrup, Birnie Gauvin, & Larsen,
253 2017; Poole et al., 2006; Winter, Tummars, Aarestrup, Baktoft, & Lucas, 2016). Anadromous
254 trout spend from 1 up to 36 months at sea on their maiden sea sojourn. In the marine habitat,
255 they feed on polychaetes, crustaceans and small fish (Knutsen, Knutsen, Gjørseter, &
256 Jonsson, 2001), and grow more than in freshwater. Sometimes, anadromous trout perform an
257 early (premature) return, characterised by a brief incursion in brackish or freshwater, before
258 heading back to the sea, this phenomenon may be exacerbated by sea louse infestation
259 (Birkeland, 1996). In summer, autumn and even winter, mature anadromous trout return to
260 their natal river to breed. While immature anadromous trout from northern Europe may spend

261 the winter in brackish or freshwater (often not in their natal river) before moving back to the
262 sea in the following spring (Thomsen, Koed, Nielsen, & Madsen, 2007). Mature trout spawn
263 in freshwater in the autumn/winter and return to sea immediately after spawning (B. Jonsson
264 & Jonsson, 2009b; N. Jonsson & Jonsson, 2002) or in the subsequent spring (B. Jonsson,
265 1985). The former is more dominating for trout spawning in small water courses with poor
266 shelter for wintering trout (B. Jonsson, Jonsson, Brodtkorb, & Ingebrigtsen, 2001; B. Jonsson
267 et al., 2018). Survivors typically undertake a shorter sea sojourn before heading back to
268 freshwater as repeat spawners (B. Jonsson & Jonsson, 2009b). Some of the parr do not smolt
269 and remain in freshwater during their entire life. Resident and anadromous trout can
270 reproduce on sympatric spawning grounds, or spawn in separate areas of the same river
271 (Hindar et al., 1991; Rohtla et al., 2017).

272

273 Brown trout exhibit a large range of body sizes across their endemic distribution range, with
274 resident trout being on average smaller than anadromous trout (Figure 3). Within a given
275 catchment, resident trout rarely become as large as their anadromous counterparts of similar
276 age. However, older resident trout may become larger than young anadromous trout and the
277 largest resident trout can be larger than the smallest anadromous specimen within age-classes
278 (i.e. total age from birth). Large resident trout feeding on fish can grow equally large or larger
279 than anadromous trout do. Ferox trout from Scottish and Irish Lochs are examples of such
280 large resident trout (R. N. Campbell, 1979; Hughes et al., 2019).

281

282 The parameters controlling juvenile growth rate play an important role and various thresholds
283 regulate the individual's decision of life history and migration strategy. Growth rate variation
284 induces two antagonistic phenomena: sexual maturation or migration (Baglinière & Maisse,
285 1985; B. Jonsson & Jonsson, 1993; Maisse & Baglinière, 1999). The higher the growth rate,

286 the earlier the onset of maturation or migration. Presumably, the developmental threshold for
287 precocious sexual maturation appears earlier in the season than that for migration. In partly
288 anadromous populations, mature parr typically become freshwater resident, although a few of
289 them may migrate to sea in a later year (B. Jonsson & Jonsson, 2011). The characteristics of
290 these thresholds, relative to the life stage of the fish, depend on environmental factors, the
291 stage and sex of the trout, and its genotype (Baglinière, Guyomard, Héland, Ombredane, &
292 Prévost, 2001). Across its European distribution area, the age of smolt varies widely, from 1-
293 3 years in France, to 5-7 years in northern Norway (Figure 4). Within each population, the
294 size of smolts increases with age. This large-scale pattern suggests that despite phenotypic
295 plasticity and local environmental constraints, a physiological, threshold may underlie smolt
296 migration in brown trout. We may add, however, that smolt size is particularly small among
297 trout spawning in small streams, with some smolts as small as 8 cm being recorded (B.
298 Jonsson et al., 2001).

299

300 Like in the Atlantic salmon, the parr-smolt transformation takes place in the largest juvenile
301 trout of a given population (Tanguy, Ombredane, Baglinière, & Prunet, 1994) and smolting
302 occurs in spring. Silvering encompasses a peak of gill Na^+/K^+ -ATPase activity and a
303 simultaneous decrease in plasma prolactin is observed, together with morphological changes
304 (Aarestrup, Nielsen, & Madsen, 2000; Boeuf & Harache, 1982). But, compared to the
305 Atlantic salmon, no surge in growth hormone is documented (Tanguy et al., 1994). Hypo-
306 osmoregulatory ability is greatest at the time of peak gill Na^+/K^+ -ATPase activity and it
307 increases in spring in all trout, irrespective of smolt status (C. Nielsen, Aarestrup, & Madsen,
308 2006). Smolting appears less stringent in brown trout than in Atlantic salmon, and does not
309 seem to be an obligatory process for seawater adaptation in this species. The level of smolting
310 also depends on stock origin and body size, e.g. fast-growing juveniles can migrate to sea

311 without smolting (Tanguy et al., 1994). Usually, juvenile trout migrate from rivers in spring
312 (March-June in Europe) (Byrne, Poole, Dillane, Rogan, & Whelan, 2004; Flaten et al., 2016;
313 A. J. Jensen et al., 2012), but may also migrate at other times of the year, e.g. during autumn
314 (Aarestrup et al., 2017; B. Jonsson & Jonsson, 2009a; B. Jonsson et al., 2018; N. Jonsson &
315 Jonsson, 2002; Poole et al., 2006; Poole, Whelan, Dillane, Cooke, & Matthews, 1996; Taal et
316 al., 2014; Winter et al., 2016) indicating that the time of seaward migration is highly plastic.
317 There are indications that smolt run timing may be changing with migrations occurring
318 earlier in recent years (Byrne et al., 2004), a phenomenon also observed in Atlantic salmon
319 (B. Jonsson, Jonsson, & Finstad, 2014; Otero et al., 2014), possibly caused by climate
320 change.

321

322 Post-smolt brown trout feed at sea and some immature fish return to estuarine or freshwater
323 to overwinter, whereas others remain at sea (B. Jonsson et al., 2001, 2018). Evidence of
324 unsmoltified parr making brief brackish water excursions to switch streams has also been
325 documented (Taal et al., 2018). In northern Europe, immature trout can also return to
326 freshwater in summer after a short stay at sea. Ionoregulation in sea water at low temperature
327 is arduous, but anadromous trout have been observed at sea during winter and tolerate full
328 salinity seawater at temperatures as low as 1-2°C (Eldøy et al., 2017; J. L. A. Jensen &
329 Rikardsen, 2012; Knudsen et al., 2009; Olsen, Knutsen, Simonsen, Jonsson, & Knutsen,
330 2006). In the brackish Baltic Sea, parr can migrate from the freshwater to the Baltic coastal
331 zone without undergoing smolting. There, they may experience little or no physiological cost
332 in terms of lower survival and growth from this transition (Landergren, 2005). Otoliths
333 collected from brown trout in the Baltic Sea sometimes show no evidence of a freshwater
334 history, raising the possibility of a contingent of the coastal population that does not depend
335 on riverine spawning or that the fish move to sea as fry (Limburg et al., 2001). The duration

336 and timing of marine migrations are likely governed by trade-offs between mortality risk and
337 growth opportunities in different habitats and the most beneficial strategy may vary among
338 individuals and populations. Based on life table analysis, Jonsson (1981) found that the
339 product of survival and fecundity, as a measure of fitness, was similar for freshwater resident
340 and anadromous brown trout of the same population. Possibly, the fitness of different aged
341 smolts are also similar as indicated from calculations of survival and fecundity of female
342 Atlantic salmon (B. Jonsson, Jonsson, & Albretsen, 2016).

343

344 Epigenetics

345 Divergent life history phenotypes may be the result of epigenetic modifications that link
346 environmental factors and the genome to regulate internal cues as reported from studies on
347 steelhead trout *Oncorhynchus mykiss* (Baerwald et al., 2016). The most studied epigenetic
348 effect is a consequence of DNA methylation. High methylation levels are associated with
349 silencing of gene expression, and demethylation is linked to active gene transcription (Bird,
350 2002). Evidence of an epigenetic effect on life history variation was reported by Moran and
351 Pérez-Figueroa (2011). They found a link between DNA-methylation and maturation in
352 Atlantic salmon male parr. Mature male parr exhibit reduced probability of smolting in brown
353 trout (B. Jonsson, 1985) and Atlantic salmon (Berglund, 1995). Epigenetic effects can be
354 mediated early, such as at the embryonic stage (B. Jonsson & Jonsson, 2019). For instance,
355 thermal conditions during the embryogenesis may influence later growth, as found in Atlantic
356 salmon (A. G. Finstad & Jonsson, 2012) and zebra fish (Scott & Johnston, 2012).
357 Furthermore, there is evidence of multiple differentially methylated genes between
358 anadromous and non-anadromous rainbow trout (Baerwald et al., 2016). They reported that
359 smolting of steelhead trout is associated with DNA methylation pattern. Furthermore, it has
360 been shown that salt-induced alterations in DNA methylation patterns play a role in sea water

361 adaptation in fishes (Artemov et al., 2017; Moran, Marco-Rius, Megías, Covelo-Soto, &
362 Pérez-Figueroa, 2013). One may hypothesize that early environmental factors may also
363 influence life history decisions and phenotypic plasticity in brown trout, although this has not
364 yet been investigated.

365

366 **Trade-offs between growth and survival**

367 *Habitat selection theory*

368 Mobile organisms are expected to select the most profitable feeding habitat. They should
369 choose the habitat where mortality (μ) over growth (g) (μ/g) is minimized (Werner &
370 Gilliam, 1984). These two components are main determinants of their fitness. The relative
371 value of feeding habitats in terms of survival and growth often changes seasonally, or in
372 relation to the developmental stage of the individual. Thus, selection should favour migration
373 from freshwater to the sea when this reduces the value of μ/g , and habitat choices should be
374 influenced by benefits and costs in each habitat. However, organisms only experience the
375 situation where they currently are, and do not know the profitability of moving to distant
376 feeding grounds unless this is innately determined through an epigenetic threshold type
377 response or a genetically predetermined behaviour. Sea trout must therefore rely on
378 additional cues, such as present growth or size, to bias their movements towards the
379 appropriate feeding ground (Dodson, Aubin-Horth, Thériault, & Páez, 2013). Their response
380 is fine-tuned through natural selection, although the response appears phenotypically plastic,
381 allowing the fish to cope with environmental stochasticity and variation. However, the degree
382 of plasticity is at least partly inherited and varies among populations (Fusco & Minelli, 2010).
383 There is little knowledge on the extent of epigenetic effects on behavioural decisions
384 (Baerwald et al., 2016), although Jonsson and Jonsson (2018) showed that the temperature

385 experienced by Atlantic salmon embryos influences the timing of their homing migration
386 years later, when they as adults return from the ocean to spawn in freshwater.

387

388 [Migration to improve growth](#)

389 Growth of trout depends largely on food consumption and temperature. Young trout
390 experiencing reduced growth because of food restrictions may either move to a more
391 profitable feeding habitat or attain sexual maturation at an early age to make the most of a
392 poor environment (B. Jonsson, 1985). Thus, feeding migration is a viable alternative if distant
393 habitats provide improved growth opportunities without a disproportional decrease in
394 survival (B. Jonsson & Jonsson, 1993). Growth is typically higher at sea than in freshwater.
395 For instance, length increase during the second year in freshwater is typically 6 cm in
396 Southern Norway (L’Abee-Lund et al., 1989), which is approximately half the length
397 increase obtained by immature trout spending their second year at sea (B. Jonsson & Jonsson,
398 2011; Poole et al., 1996), but growth decreases with age and sexual maturation. In Northern
399 Norway, the difference between freshwater and marine growth may be even larger (Berg &
400 Jonsson, 1990). In addition to better feeding opportunities, growth at sea may be less
401 constrained because of reduced population density and intraspecific competition in northern
402 temperate and sub-Arctic areas. In some systems, lakes may also offer better growing
403 condition than the nearby mainstream river and reduced costs of migration compared to
404 seaward migration (e.g. short migration distance, low predation). A similar pattern may hold
405 true for brown trout moving from tributaries to the mainstream, further downstream, in large
406 river systems. Distinct populations of adfluvial trout have been identified, such as the
407 Dollaghan trout in Lough Neagh, Northern Ireland, and the Croneen trout in Lough Derg on
408 the Shannon, Ireland (Ferguson, 2004). Such a trade-off may also be driving lacustrine

409 migration in landlocked trout populations, as observed in lake Geneva (Champigneulle,
410 Buttiker, Durand, & Melhaoui, 1999).

411

412 The aggregation of six datasets from across Europe allowed us to highlight some new
413 patterns (Figure 5). Within our six populations, we observe a general pattern that emerges in
414 the form of a positive correlation in body length between anadromous and resident trout. This
415 means that rivers with large resident trout also produce large anadromous trout. Moreover,
416 the relative growth gained by the sea migration (i.e. the deviation from the 1:1 line in Figure
417 5) is larger in populations of large brown trout. Apparently, for anadromy to be a viable life
418 history tactic, the growth rate of anadromous fish must be higher than that of corresponding
419 freshwater residents.

420

421 [Migration can improve survival](#)

422 Mortality is higher during the marine migration than in freshwater, with sea trout facing high
423 predation rates during early sea migration, i.e. when they are small and cross the estuarine
424 zone. For instance, precise estimates from Black Brows Beck, Lake District, England showed
425 that the instantaneous rate of survival of brown trout was about 0.88% day⁻¹ during the
426 second year in freshwater while the return rate of post-smolts at sea averages 0.25% day⁻¹
427 (Elliott, 1993). Aldvén et al. (2015) detected a significantly higher mortality rate in brown
428 trout smolts moving from the river into a shallow estuary (mortality 26 to 51 %) than in
429 smolts entering a deep fjord (17.5-29.2 %). Dieperink et al. (2002; 2001) studied avian
430 predation on emigrating wild and domesticated sea trout post-smolts in fjords of the western
431 Baltic Sea and North Sea. In total, 65% of the post-smolts were eaten by fish-eating birds,
432 and during the first two days after entering the sea, both wild and domesticated post-smolts
433 suffered a daily predation rate estimated at 20-34%. Thus, the trout appeared to experience a

434 transient period with elevated risk of predation immediately after exposure to sea water.
435 However, in other places, the early mortality is noticeably lower. Survival of smolts
436 migrating through Randers and Mariager Fjords in Denmark showed survivals between 76-80
437 % 30 days after fjord entry and in Poole Harbour in England 88% of the trout smolts entering
438 the estuary made the 12 km transition to the open sea (Aarestrup, Baktoft, Koed, del Villar-
439 Guerra, & Thorstad, 2014; del Villar-Guerra, Aarestrup, Skov, & Koed, 2013; Lauridsen et
440 al., 2017). Predation rates appear to be influenced by the time and size at migration, and sea
441 trout of the River Imsa, Norway exhibit highest survival if migrating in May (ca. 15% until
442 river return) and low survival if migrating to the sea between July and December (ca. 2%) (B.
443 Jonsson & Jonsson, 2009a). However, in Gudsø Stream, Denmark, the return rates of spring
444 and autumn migrants were similar (Birnie Gauvin & Aarestrup, 2018). This suggests
445 difference in autumn mortality between rivers. Also, one would expect that sea migration in
446 the autumn would benefit other fitness components, such as growth, and compensate for this
447 potential high initial migration cost.

448

449 By migrating, sea trout can avoid adverse environmental conditions in the home stream, such
450 as winter icing-up of streams or summer drought. For instance, in small streams regularly
451 experiencing summer drought, sea trout can migrate to sea at a small size early in life, and in
452 this way avoid poor growth and survival conditions (B. Jonsson et al., 2001; Landergren,
453 2004; Titus & Mosegaard, 1992). This pattern resembles the strategy followed by some
454 Pacific salmonids, such as pink salmon *Oncorhynchus gorbuscha* and chum salmon
455 *Oncorhynchus keta*, which both start their seaward migration early in life. Trout from streams
456 with low water level during winter may migrate to a neighbouring watercourse for
457 overwintering (Aldvén & Davidsen, 2017), or stay in marine waters (Eldøy et al., 2017; B.
458 Jonsson et al., 2018; Olsen et al., 2006).

459

460 **Improved fecundity**

461 Fecundity, or number of ova per unit length, changes between stocks (Fahy, 1985; Poole,
462 Byrne, Dillane, Whelan, & Gargan, 2002) and between stocks in different regions (N.
463 Jonsson & Jonsson, 1999; Solomon, 1997). But, with larger body size, sea trout increase their
464 gamete production and direct competitive ability on the spawning ground, and thus obtain
465 augmented reproductive success (Fleming, 1996; Gross, 1987; Hutchings & Myers, 1985).
466 For instance, mean fecundity of sea trout from Vangsvatnet Lake, Norway was 1790 eggs
467 compared to 330 eggs for non-anadromous females of similar age (i.e. < 20%; B. Jonsson,
468 1981, 1985). Egg size increases with the size of the mother, and with increasing egg size,
469 early growth and viability of offspring increases (Bagenal, 1969; Segers & Taborsky, 2011).
470 However, these relationships are dependent on the female life history, with females investing
471 in larger ova as the fish become larger and older. It seems that anadromous females had
472 smaller ova compared with freshwater-resident females of similar body size (i.e. older fish)
473 and achieved higher fecundity as they grew bigger (Acolas, Roussel, & Baglinière, 2008).
474 Another advantage for the offspring of anadromous females may come from an earlier
475 hatching date in the season, as reported in anadromous brown trout (N. Jonsson & Jonsson,
476 1999) and rainbow trout relative to sympatric resident trout (Zimmerman & Reeves, 2000). A
477 longer spawning period in resident trout may buffer this phenological difference in some
478 cases, e.g. river Oir, France (Maisse et al., 1991). Less is known about the production of male
479 milt and spermatozoa in brown trout, although differences in sperm count were observed
480 between stocks and the length of the spawning migration (B. Jonsson & Jonsson, 2006b) and
481 a negative trend was linked with size and age of males, possibly indicating a lower fertilising
482 ability of older fish within any one stock (Poole & Dillane, 1998).

483

484

485 **The energy surplus hypothesis**

486 Several studies suggest that anadromy in brown trout is triggered by energy limitation in natal
487 rivers (reviewed by Dobson *et al.* (2013)), and can be terminated if the relative advantage of
488 migration changes (Sandlund & Jonsson, 2016). Some early studies documented an
489 asymptotic size at one year, which is limited by the carrying capacity of the river (Baglinière
490 & Maisse, 1990). Thus, to meet their energy requirements and grow further, individuals
491 should change habitat and move toward a more productive habitat further downstream in the
492 watershed or at sea (Baglinière & Maisse, 2002). Brown trout appear to favour a migration
493 strategy when the energy surplus useable for growth becomes low (Forseth, Nesje, Jonsson,
494 & Hårsaker, 1999; B. Jonsson & Jonsson, 1993).

495

496 Experimentally, Davidsen *et al.* (2014) induced migration by decreasing ration size during
497 the six months prior to smolting. Similarly, Jones *et al.* (2015) demonstrated that reduced
498 winter and spring feeding increased the tendency to smoltify for lake feeding brown trout
499 from the River Klarälven, Sweden. In contrast, another experiment reported that trout facing
500 food restriction in late autumn exhibited lower rate of silvering, which is indicative of a delay
501 in smolting (Näslund, Sundström, & Johnsson, 2015). Thus, winter/beginning of spring
502 appears to be a critical period when the decision is made about whether to smolt and migrate
503 to a better feeding area. These experimental findings contrast with Thorpe & Metcalfe's
504 (1998) hypothesis that autumn is the critical time in Atlantic salmon, when decisions of
505 migration versus maturation and residency are taken. This implies that brown trout are more
506 plastic and energy intake during winter and spring may over-rule an initial decision,
507 depending on the energetic state of the fish (cf. B. Jonsson, Jonsson, & Finstad, 2013). In
508 contrast, rearing brown trout in aquaculture with optimum rations reduces the probability of

509 smolting, leads to early maturation and lowers the return rates from sea releases (Byrne,
510 Poole, Dillane, & Whelan, 2002; Mills, Piggins, & Cross, 1990).

511

512 Within brown trout populations, fast growers tend to migrate at a younger age, and typically
513 smaller size than slow growers (B. Jonsson, 1985; Økland, Jonsson, Jensen, & Hansen, 1993)
514 and within a given cohort, larger juveniles tend to undertake longer migrations (Ombredane
515 et al., 1996). Individuals with a high metabolic rate may migrate downstream earlier as their
516 energy demands more rapidly exceed those available in their current habitat than in smaller
517 trout (Ferguson, Reed, McGinnity, & Prodöhl, 2017; Forseth et al., 1999; Peiman et al.,
518 2017). Sea trout smolts have very low energy density at the time of migration (ca. 350 KJ/100
519 g wet mass), which is similar to that of resident trout after spawning (N. Jonsson & Jonsson,
520 1997a, 1998). This is due to a low lipid density (ca. 1.5 g/100 g wet mass), which may
521 contribute to the compensatory growth exhibited by sea trout during the first weeks at sea
522 (Marco-Rius, Caballero, Moran, & Leaniz, 2012). In brook trout *Salvelinus fontinalis*,
523 Morinville and Rasmussen (2003) reported that in the year before migration, migrant brook
524 trout have consumption rates 1.4 times higher than those of resident brook trout. However,
525 migrants have lower growth efficiencies (ratio of growth to consumption) than residents,
526 indicating that migrants have higher metabolic costs, and relatively less surplus energy
527 available at the time the migrations commences.

528

529 Individual growth rate better integrates the mechanisms underlying migration decision
530 whereas body size is more strongly related to survival in trout (Acolas, Labonne, Baglinière,
531 & Roussel, 2012). Intrinsic differences between individuals explain why migrants and
532 residents differ in body size in many partial migratory species (Chapman et al., 2012).

533 Improved feeding opportunities and growth is thus the main benefit of anadromy for fish
534 spawning in freshwater (Frier, 1994; Gross, Coleman, & McDowall, 1988).

535

536 Size may also interact with the ability of juveniles to establish and hold territories, thus
537 smaller and/ or younger parr may be forced to leave the stream by larger and/ or older
538 conspecifics (Landergren, 2004). In Atlantic salmon, some populations exhibit a bimodality
539 in size by the end of the first growing season (Baglinière & Maisse, 1985). Individuals from
540 the upper mode, i.e. large juveniles, smolt and migrate to sea the following spring (Baglinière
541 & Maisse, 1985; Thorpe, Talbot, & Villarreal, 1982). Atlantic salmon appear to smolt when
542 the young have reached a critical size, although this pattern may not be detected in slower
543 growing populations of northern Europe (Økland et al., 1993). This is probably because
544 survival at sea is strongly size dependent (Flaten et al., 2016; B. Jonsson et al., 2016). In
545 trout, it is unknown to what degree size influences age at smolting (Figure 4). Juvenile size
546 bimodality has not been detected at the end of the growth season (Baglinière, Prévost, &
547 Maisse, 1994). This suggests that the migration decision may be taken later in trout,
548 highlighting the greater flexibility of trout life history compared to Atlantic salmon
549 (Baglinière et al., 2001).

550

551 **Sex-specific response**

552 Skewed sex ratios are commonly observed within the anadromous and resident components
553 of partially migratory brown trout populations. The skewed sex ratios results from differences
554 in physiological constraints and life history trajectories in males and females. The fitness of
555 females appears more closely associated with body size than in males. Although the same
556 environmental conditions interact with threshold limits to determine individual life histories,

557 the mechanisms selecting for migration or residency differ between the sexes. This results in
558 sexually divergent thresholds and rates of anadromy (B. Jonsson et al., 2001).

559

560 [Bias in sex ratio](#)

561 Although the sex ratio of parr is even in brown trout, there appears to be a female surplus
562 among emigrating smolts (Cucherousset et al., 2005; B. Jonsson, 1985; Klemetsen et al.,
563 2003). In northern France, the percentage of females among migrating smolts varies between
564 57% and 67% (Euzenat, Fournel, & Richard, 1999; Quéméré, le Gentil, & Launey, 2011),
565 which fits well with what is found elsewhere (Table 1). Also, females typically outnumber
566 males among adults entering streams for spawning (J. S. Campbell, 1977; Euzenat, Fournel,
567 & Fagard, 2006; K. W. Jensen, 1968; B. Jonsson, 1985; Mills et al., 1990; Okumuş,
568 Kurtoglu, & Atasaral, 2006; Poole et al., 2006). On the spawning grounds, however, the
569 operational sex ratio may be skewed in favour of males because they stay longer and if
570 possible, spawn with several females (Aarestrup & Jepsen, 1998).

571

572 The size of the stream used for spawning may influence spawning success and therefore
573 indirectly the sex ratio, with male surplus reported in several small streams (B. Jonsson et al.,
574 2018; Rubin, Glimsäter, & Jarvi, 2005). The highest proportion of females among the
575 anadromous trout are found in the nutrient rich and productive streams and large rivers of the
576 Baltic and the North Sea areas (Table 1), and this bias may be larger when the high
577 proportion of repeat spawners, as post-spawning survival is greater in females than in males..
578 In small streams, males mature younger and smaller than females, and relatively more males
579 will therefore survive to adulthood (B. Jonsson, 1985; B. Jonsson & Jonsson, 2015). Where
580 there is a female surplus among the smolts, it may be evened out among anadromous adults

581 because males mature younger than females and more will therefore survive to adulthood (B.
582 Jonsson et al., 2018).

583

584 Anadromous females typically outnumber anadromous males in larger streams, and the same
585 is reported from other species of partly migratory trout and charr, such as rainbow trout
586 (McMillan, Katz, & Pess, 2007; Rundio, Williams, Pearse, & Lindley, 2012; Van Doornik,
587 Berejikian, & Campbell, 2013), Arctic charr (Nordeng, 1983), whitespotted charr *Salvelinus*
588 *leucomaenis* (Tamate & Maekawa, 2004) and some Atlantic salmon populations (N. Jonsson,
589 Jonsson, & Hansen, 1998), although exceptions occurs (Bagliniere, personal communication).
590 Dodson *et al.* (2013) noted an increase in male anadromy of brook trout towards the north.
591 This has not yet been investigated for brown trout.

592

593 [Strong size dependence in females](#)

594 Large female size is selected by natural selection as reproductive success is more strongly
595 associated with body size in females than males (B. Jonsson, 1985; Kendall et al., 2014).
596 Furthermore, body size variation is smaller in females than in males. This may be because
597 females do not exhibit alternative spawning tactics (sneaking versus fighting) as males do
598 (McLean, Bentzen, & Quinn, 2004). Furthermore, the gonad development of females requires
599 more energy (Baglinière et al., 2001; Fleming, 1996; Prouzet, Le Bail, & Heydorff, 1984).
600 Thus, females are more likely to migrate to more food rich areas, and stay there for longer
601 periods of time to grow larger before spawning (Bordeleau et al., 2018; Cucherousset et al.,
602 2005; Ferguson, 2006; Northcote, 1992). Undertaking a longer and more risky sea migration
603 may reduce survival, resulting in relatively few anadromous female trout returning as adults.
604 Higher marine mortality in females than males has been reported for anadromous
605 whitespotted charr by Tamate & Maekawa (2004), but no empirical evidence is available for

606 sea trout. On the other hand, post-spawning survival is higher in female charr (and salmon)
607 than in males, which may also hold for brown trout. Thus, sex-ratio of repeat spawners may
608 be even more skewed in favour of females (Euzenat et al., 1999).

609

610 [An alternative strategy in males](#)

611 A large male size may be favoured because of both natural and sexual selection (Young,
612 2005). Natural selection because large males have larger testes (B. Jonsson & Jonsson, 2005;
613 N. Jonsson & Jonsson, 1997b), win spawning contests more often and therefore spawn more
614 times than smaller males (Fleming et al. 1996). They are favoured by sexual selection
615 because females prefer large males as partners (Petersson et al. 1999; Serbezov et al. 2010)
616 and large males gain better access to females due to higher fighting success. On the other
617 hand, male size is not directly associated with reproductive success (Poole & Dillane, 1998)
618 even though large males do enjoy strong competitive advantages over smaller resident males
619 when fighting for mates (Bohlin, Dellefors, & Faremo, 1990). Some males may adopt an
620 alternative spawning behaviour (Dominey, 1984; Gross, 1991). While large males gain access
621 to females through fighting, small resident males effectively employ a sneaking tactic to the
622 same ends (Olsén, Järvi, Mayer, Petersson, & Kroon, 1998), avoiding the risks of migration,
623 and breeding at a younger age (Foote, Brown, & Wood, 1997). However, ‘precocious’
624 maturation is less pronounced in brown trout than in Atlantic salmon, where males can
625 mature before the age of 1 (Baglinière & Maisse, 1985). Since maturation and smolting may
626 be considered competing developments in terms of energy allocation and physiology, the
627 energy requirements for smolting after maturing may be too large to allow migration within a
628 reasonable seasonal schedule. Indeed, maturation in brown trout correlates with delayed or
629 reduced rates of smolting (Bohlin et al., 1990; Cucherousset et al., 2005; Dellefors & Faremo,
630 1988; B. Jonsson, 1985), but nevertheless does happen.

631

632 Intermediate-sized individuals, in contrast to large or small individuals, may be ineffective at
633 both fighting and sneaking mating strategies, putting them at a competitive disadvantage and
634 maintaining the separation of two distinct male phenotypes as observed within many wild
635 salmonid populations (Gross, 1985). It is possible that where intermediate-sized mature males
636 are present on spawning grounds, they utilise female mimicry in order to approach females
637 without attracting the aggression of large dominant males (Esteve, 2005). This behaviour,
638 which is associated with altered male colouration resembling that of mature females, has been
639 reported in Arctic charr, pink salmon, chum salmon and red-spotted masu salmon
640 (*Oncorhynchus masou ishikawae*) (Kano, Shimizu, & Kondou, 2006; Keenleyside & Dupuis,
641 1988; Sigurjónsdóttir & Gunnarsson, 1989).

642

643 **Environmental drivers of anadromy in juveniles**

644 Anadromy and residency in brown trout are considered alternative tactics within a single
645 strategy (Dodson et al., 2013). The decision to migrate to sea results from a trade-off between
646 mortality and growth in fresh and salt waters so that the overall fitness is maximized, and
647 individuals must use proximate cues to adopt the most appropriate life history (Kendall et al.,
648 2014). Environmental factors influencing growth in early life are probably the main cues on
649 which the decision is made (Baglinière et al., 2001; Ferguson et al., 2017; B. Jonsson &
650 Jonsson, 1993).

651

652 **Food availability**

653 Both empirical and experimental studies have reported negative correlations between the
654 proportion of migratory trout and food availability in the natal freshwater system (review in
655 Ferguson *et al.* (2017)). For instance, the migration of brown trout between a tributary where

656 they spawned and the main river, ceased when the growth opportunities in the main river
657 decreased because of damming and reduced flow in the main river (B. Jonsson & Sandlund,
658 1979; Sandlund & Jonsson, 2016). Kendall *et al.* (2014) noted that food quality, i.e. energy
659 value, may be as important as food quantity. Hence, resident trout appear to be abundant in
660 the most productive areas, with a high invertebrate biomass. Where lakes are present, a
661 lacustrine-adfluvial migration pattern often predominates (Ferguson, 2004; Ferguson *et al.*,
662 2017; Gresswell, Liss, & Larson, 1994), as some lakes may offer good growth condition with
663 a lower predation cost than sea migration. This is supported by the observation that stocking
664 well fed, juvenile hatchery trout often produces freshwater resident fish, but starving the fish
665 before release induces a migratory behaviour (Davidsen *et al.*, 2014; Larsson, Serrano, &
666 Eriksson, 2011). Thus, growth opportunities in the local habitat play an important role in the
667 decision whether to migrate (Larsson *et al.*, 2011). Also, environmental stochasticity in the
668 river, such as winter frost or summer drought, can seasonally constrain feeding opportunities
669 and initiate migration. In this case, trout may opt for migration to the marine environment,
670 which may appear more stable and protective against harsh physical conditions (Aldvén &
671 Davidsen, 2017; Ferguson *et al.*, 2017).

672

673 [Thermal condition](#)

674 Temperature is a key factor structuring freshwater ecosystems. It may influence migratory
675 decisions, with both absolute temperature and variation in temperature being important
676 (Kendall *et al.*, 2014; Morita, Tamate, Kuroki, & Nagasawa, 2014). Optimum temperature for
677 growth of juvenile 1g brown trout is found to be 13-14°C (Forseth *et al.*, 2009), but it can be
678 high if energy consumption is very high such as in piscivorous trout (Forseth & Jonsson,
679 1994), and lower if the fish are particularly large or feeding is reduced (Morita, Fukuwaka,
680 Tanimata, & Yamamura, 2010). Temperature is clearly linked to food availability, feeding

681 activity, metabolism and lipid storage (Ferguson et al., 2017). High temperature allows higher
682 food consumption but also increases maintenance costs and may accelerate energy shortages.
683 Furthermore, standard metabolic rate may be affected by the temperature experienced by the
684 yolk feeding larvae (Álvarez, Cano, & Nicieza, 2006). Thus, unless food production increases
685 by the same order of magnitude, individuals may not be able to meet their energetic
686 requirements when temperature increases. However, this pattern may be attenuated by
687 temperature itself, as abnormal temperature may also act as a physiological stressor and
688 induce migration (Peiman et al., 2017). However, an increase in temperature may fuel the
689 production of invertebrates and thereby offer improved feeding opportunities for resident
690 trout, as explained above (Morita et al., 2014; Olsson, Greenberg, Bergman, & Wysujack,
691 2006). But further projected increases in river water temperature above the optimal
692 temperature for growth will likely decrease growth, body length and age at smolting, and
693 ultimately reduce the survival of trout (Davidson, Hazlewood, & Cove, 2007; Fealy et al.,
694 2010). However, the relative contribution of temperature to trout growth compared to other
695 environmental drivers remains difficult to quantify. In Atlantic salmon, Bal *et al.* (2011)
696 reported that variation in freshwater temperature had only a small effect on the growth of
697 juveniles compared to variation in salmonid density.

698

699 Flow condition

700 In the rivers, trout are largely ambush predators, relying on the flow to bring food to them
701 although they are more active hunters than Atlantic salmon. In darkness, they can pick
702 zoobenthos on the bottom. The nursery habitat may differ between resident and anadromous
703 conspecifics as reported by Morinville and Rasmussen (2003). They studied brook trout, and
704 found that the young of migratory trout used faster running water than young resident trout,
705 and that they also fed on different food items. This pattern is expected to come from intrinsic

706 differences in metabolic requirement and is not indicative of an effect of flow condition on
707 migration decision. High flow often correlates with high availability in food resource, which
708 influences the opportunities for growth (Kendall et al., 2014; Morinville & Rasmussen,
709 2003). Furthermore, flow may have an effect on anadromy in rainbow trout, at least in
710 climate zones where summer flows are a limiting factor (Kendall et al., 2014). Flow that
711 regularly reaches zero may represent a population bottleneck for non-migratory fishes
712 (Courter, Justice, & Cramer, 2009), and low flow may explain the small size at first smolting
713 of brown trout in some small streams (Borgstrøm and Heggenes 1988; Jonsson et al. 2001).
714 More generally, unsuitable flow condition in streams is likely to drive the propensity to
715 migrate to sea, e.g. due to low flow, or highly variable flow conditions in the home stream, or
716 a reduction in suitable habitat and high keen competition from conspecifics (density
717 dependence effect).

718

719 So far, there is empirical evidences of a positive correlation between flow and the number of
720 migrating smolts in brown trout. In the Danish River Lilleaa the migration speed of wild sea
721 trout smolts was positively correlated with water discharge (Aarestrup, Nielsen, & Koed,
722 2002). But when the flow remains low, trout may wait until the temperature comes over a
723 certain level (Aarestrup et al., 2002). In a Swedish west coast stream, smolts remained in the
724 rivers during years with low precipitation until the temperature reached 10°C, and migration
725 increased thereafter irrespective of the discharge (Aldvén et al., 2015). A shift from nocturnal
726 to diurnal migration appears to occur when the water temperature is 12-13°C and is most
727 pronounced in large smolts (Haraldstad, Kroglund, Kristensen, Jonsson, & Haugen, 2017).
728 Single large temperature increases can also initiate a daytime migration (Aarestrup et al.,
729 2002). Water temperature and flow influence the phenology of the sea trout smolt migrations.
730 Temperature regulates the timing of the start and the end of the migration period whilst water

731 level, change in water flow and water temperature influence the number of smolts migrating
732 each day (Byrne et al., 2004; N. Jonsson & Jonsson, 2002).

733

734 Density-dependence

735 The food availability interacts with fish density in limiting the resources available per capita.

736 Higher competition for food and space at high density results in fewer residents, with

737 migrants maximising growth by moving into the sea (Ferguson et al., 2017; Olsson et al.,

738 2006). During periods of drought or hydropower regulation, density will increase. Stradmeyer

739 *et al.* (2008) showed how the importance of dominance status for maintaining food intake

740 increases as the polarization between the top ranked fish and others increased. As a result,

741 fewer fish will mature and become residents, thus migration may be an alternative (B.

742 Jonsson & Jonsson, 1993).

743

744 Inter-specific competition

745 Similarly, competing species may also influence the proportion of brown trout that migrate,

746 mediated through a density-dependence process (Olsson et al., 2006). Young brown trout and

747 Atlantic salmon compete for food and space in rivers, as evidenced by the spatial segregation

748 observed between the two species (B. Jonsson & Jonsson, 2011). Young Atlantic salmon are

749 mainly found in shallow, fast flowing habitats of the main river while young trout colonize

750 tributaries and headwaters (Baglinière & Arribe-Moutounet, 1985; Baglinière &

751 Champigneulle, 1982; Kalleberg, 1958). In the Shelligan Burn (Scotland), the density of

752 young Atlantic salmon was negatively correlated with that of young trout (Egglisshaw &

753 Shackley, 1982). Brown trout are territorial and very aggressive, and through interference,

754 they constrain young Atlantic salmon from shallow, slow-flowing areas (Harwood, Metcalfe,

755 Armstrong, & Griffiths, 2001; Heggenes, Baglinière, & Cunjak, 1999; Houde, Wilson, &

756 Neff, 2017; Kalleberg, 1958). This trend is accentuated by the early hatching of trout
757 (Baglinière et al., 1994), which are larger and have already established a territory by the time
758 Atlantic salmon fry emerge. Furthermore, when brown trout are removed, young Atlantic
759 salmon expand their habitat into former trout-defended areas, i.e. competitive release (Hearn,
760 1987; Kennedy & Strange, 1986). Experimentally, Gibson and Erkinaro (2009) showed that
761 brown trout were four times more aggressive than corresponding Atlantic salmon. As a result
762 of their more aggressive behaviour and larger size, brown trout have a competitive advantage
763 in slow flowing, shallow areas along stream banks and pools where they monopolize the food
764 resources (Gibson & Erkinaro, 2009; Höjesjö, Stradmeyer, Griffiths, & Armstrong, 2010).
765 Atlantic salmon, on the other hand, make more use of cover, deep pools and fast-flowing
766 riffles where food is difficult to defend. In addition, their more streamlined body shape and
767 larger pectoral fins are assumed to give young Atlantic salmon a selective advantage in
768 rapidly flowing rivers (Karlström, 1977), and they may outcompete trout in fast flowing
769 streams (Montorio, Evanno, & Nevoux, 2018). The interaction between young brown trout
770 and Atlantic salmon in rivers is adversely competitive, i.e. increased abundance of the one
771 leads to a decrease in abundance of the other. This is exemplified in formerly acidified rivers
772 treated with calcium carbonate (limestone powder). As the abundance of Atlantic salmon
773 increased with time, the density of brown trout decreased (Hesthagen, Larsen, Bolstad, Fiske,
774 & Jonsson, 2017). However, even when the abundance of Atlantic salmon increases at the
775 expense of brown trout, the total output of salmonid smolts increases (cf. Kennedy and
776 Strange, 1986).

777

778 The aggressiveness of brown trout is energetically costly. Their high-energy use is assumed
779 to be the main reason why brown trout are outcompeted by Arctic charr because of a much
780 lower growth efficiency in cold, food limited habitats (A. G. Finstad et al., 2011). In shallow,

781 temperate localities richer in food, on the other hand, brown trout outcompete Arctic charr
782 because of its higher aggressiveness. In sympatry, the two segregate spatially, with charrs
783 shifting to the pelagic or the profundal zone (Heggberget, 1984; Klemetsen et al., 2003;
784 Langeland, L'Abée-Lund, Jonsson, & Jonsson, 1991).

785

786 There is also competition between grayling *Thymallus thymallus* and brown trout. Mäki-
787 Petäys et al. (2000) suggested that competition between these species increases in streams
788 during winter when ice decreases the habitat availability. Competition between the two
789 species may be a reason for their partial segregation in rivers (Greenberg, Svendsen, &
790 Harby, 1996). However, recruitment of grayling and trout were positively associated in an
791 English chalk stream (Bašić, Britton, Cove, Ibbotson, & Gregory, 2018). Also, Alpine
792 bullhead (*Cottus poecilopus*) is a strong competitor to juvenile brown trout where these
793 species co-occur (Hesthagen & Heggenes, 2003; Holmen, Olsen, & Vøllestad, 2003). For
794 instance, Holmen *et al.* (2003) reported that brown trout density was five to 10 times higher
795 at the upper, allopatric site than in downstream areas where it lived in sympatry with the
796 Alpine bullhead. Diet composition suggested that brown trout in sympatry with Alpine
797 bullhead foraged more on invertebrate drift and surface arthropods than allopatric brown trout
798 did.

799

800 In addition, novel species that invade brown trout areas, naturally or because of human-
801 mediated releases, may influence brown trout migration and habitat use. Brown trout living in
802 sympatry with brook trout consumed more terrestrial prey, had smaller home ranges, and a
803 stouter body shape (Závorka et al., 2017). Sympatric brown trout also had lower specific
804 growth rates, suggesting a lower fitness. Other introduced species, such as rainbow trout
805 affect brown trout negatively. Blanchet *et al.* (2007) found by use of laboratory and field

806 studies that rainbow trout significantly affected native brown trout habitat selection and
807 apparent survival. In contrast, Baran *et al.* (1995) demonstrated a competition advantage of
808 the brown trout in mountainous rivers when the two species live in sympatry. The more
809 similar the ecology of the interacting species, the greater the impact of competition is.

810

811 There are examples of rivers where Atlantic salmon and resident trout co-exist, but little or no
812 sea trout run is observed, as in Ireland and Brittany (France). In the Irish systems, the
813 presence of lakes and running river sections may promote habitat segregation and reduce
814 inter-specific competition while in large salmon rivers, the occurrence of sea trout is often
815 restricted to the lower stretches and to small tributaries close to or directly entering an estuary
816 (Fahy, 1985; K. F. Whelan, 1989). Similarly, the tree-like shape of the watersheds in
817 Brittany, characterized by many small tributaries, may maximise segregation and reduce
818 competition between the two species (Baglinière *et al.*, 1994).

819

820 It is still unclear whether interspecific competition in freshwater influences the tendency to
821 migrate to the sea. However, one may hypothesize that brown trout will exhibit a stronger
822 tendency to migrate if their resource use in freshwater is constrained by competing species, as
823 shown for increased competition from conspecifics (Olsson *et al.*, 2006). Montorio *et al.*
824 (2018) provided empirical evidence for inter-specific competition-exclusion relationship.
825 They found a negative effect of trout density on growth and survival in juveniles, but a
826 positive effect of Atlantic salmon density on the probability of migration in young trout. They
827 reported that in years following a high recruitment in salmon, the propensity of trout leaving
828 the stream was high. Atlantic salmon may be a main competitor in temperate areas and Arctic
829 charr in sub-Arctic and Arctic areas.

830

831 **Predation**

832 The role of predators in shaping patterns of partial migration has been historically neglected
833 (Chapman et al., 2012). However, if the decision to migrate is a balance between growth
834 opportunities and mortality risk, increased predation in freshwater should select for anadromy
835 in trout. Predation risk may constrain habitat use and thereby reduce individual growth
836 (Johnsson, Rydeborg, & Sundström, 2004). Alternatively, high predation in freshwater may
837 offer more resource per capita to the remaining individuals with an opposite effect on the
838 opportunity for growth.

839

840 Predation is expected to be particularly high during the smolt run and in the first few days
841 after the smolts reach sea water (Dieperink et al., 2002; Thorstad et al., 2016). If there are
842 alternative prey, such as Atlantic salmon smolts migrating to sea at the same time, this may
843 reduce the mortality and increase the fitness of sea trout (B. Jonsson & Jonsson, 2009b), or it
844 may stimulate the aggregation of predators (Jepsen, Holthe, & Økland, 2006). Thus, although
845 effects of predation on the life history strategy of trout is not well studied, this does not mean
846 that predation is unimportant in this respect.

847

848 **Influence of the marine environment on migration outcome**

849 The decision to migrate is a trade-off between benefit and cost. Costs associated with sea
850 migrations include energy used for swimming and increased probability of death, e.g. owing
851 to predation, parasitism and diseases, but also the physiological adjustments for salt excretion
852 (Gross et al., 1988a). Distance to the coast and deep sea areas may limit the distribution of
853 sea trout. It is generally assumed that most anadromous brown trout feed in shallow waters
854 within 100 km from the river mouth (B. Jonsson & Jonsson, 2011; Thorstad et al., 2016).
855 Nevertheless, there are some evidences of large within and between population variations in

856 marine migration distance (B. Jonsson & Jonsson, 2014; Kristensen et al., 2018; Potter,
857 Campbell, Sumner, & Marshall, 2017; Prodöhl et al., 2017).

858

859 Growth potential

860 Growth levels off with age and spawning history, but the difference in size between resident
861 and anadromous trout increases with age (Figure 6, left panel). This suggests that the best
862 growth strategy in brown trout would be to leave early and stay longer at sea. In the
863 Burrishoole River (Ireland) and the River Bresle (France), fish with the combination of smolt
864 age and sea age that results in the highest growth gain are well represented among the
865 returning anadromous trout (Figure 6, right panel). However, some of these strategies are
866 represented by a low proportion of trout. Data support a mismatch between the age-specific
867 additional growth and the age-structure of the anadromous trout in River Vosso (Norway),
868 River Tamar (England) and River Oir (France). In these populations, data show a shorter
869 marine sojourn and/ or an older age at smolting than expected under the hypothesis of growth
870 maximisation. We argue that strong constraints in the marine environment, in terms of
871 mortality, may select against growth maximisation strategies. For instance, young smolts may
872 be too small to escape length-biased predation, thus favouring late runners. Furthermore,
873 marine survival may be too low to support long marine sojourns, i.e. very few two sea winter
874 sea trout may survive until spawning.

875

876 By driving the level of mortality and growth in trout that initiate seaward migration, the
877 marine environment influences the balance between the cost and benefit of the time at sea. If
878 the costs of feeding at sea exceeds the gains, selection should favour freshwater residency
879 (Gross et al., 1988a). In only a few generations, altered environmental conditions can
880 terminate the tendency to migrate (Olsson et al., 2006; Sandlund and Jonsson, 2016). The

881 marine environment acts as a selective filter on anadromy, and any increase in mortality at
882 sea is likely to contribute to the reduction in sea trout abundance over space and time.

883

884 Seascape

885 Quéméré et al. (2016) explored effect of seascape, e.g. the marine landscape, on the
886 connectivity of brown trout populations between rivers, and how the seascape influences the
887 life history of brown trout across northern France. They found two genetically distinct
888 populations which strongly differ in terms of migratory propensity and stock characteristics.
889 Western populations mainly produce freshwater resident trout and small sea trout (finnock,
890 i.e. post-smolt returning in the same year as they went to sea for the first time), while eastern
891 populations produce large sea trout that perform long sea-sojourns. They hypothesised that
892 such a pattern may be driven by the spatial arrangement and feeding opportunities of marine
893 habitats, which promotes a clinal variation in migratory behaviour. In the highly productive
894 Eastern basin of the English Channel, anadromous trout can achieve very large size and long
895 sea sojourn, which may favor dispersal and gene flow among neighbouring streams. In the
896 Western basin, marine feeding opportunities are poor and trout have evolved mainly a
897 freshwater resident life history (Quéméré et al., 2016). The dispersal barrier may act as a
898 forcing factor for a distinct life history (Richardson, Urban, Bolnick, & Skelly, 2014). On the
899 other hand, the rivers appear different, and habitat characteristics may also add to the
900 variation observed. Fahy (1985) also observed differences in trout size, growth and condition
901 between trout returning from different regions, such as the Irish Sea compared to the Irish
902 west coast and even from different bays along the west coast (Poole, unpublished).

903

904 [Sea lice](#)

905 The sea lice *Lepeophtheirus salmonis* and *Caligus elongatus* are natural parasites of sea trout
906 that can propose major threats to trout in the marine environment. During the last 30 years,
907 salmon farming has increased the abundance of sea lice (B. Finstad & Bjørn, 2011; Fjørtoft et
908 al., 2017; Thorstad & Finstad, 2018; Thorstad et al., 2015; Tully, Poole, & Whelan, 1993;
909 Tully, Poole, Whelan, & Merigoux, 1993) in some areas. Sea lice induce ionoregulatory
910 dysfunction, physiological stress, anaemia, reduced feeding and growth, changes in post-
911 smolt behaviour, increased susceptibility to secondary infections, reduced disease resistance
912 and ultimately mortality of individual sea trout (B. Finstad & Bjørn, 2011; ICES, 1997;
913 Poole, Nolan, & Tully, 2000). Wild adult sea trout in farm-free areas exhibit relatively low
914 sea lice levels (Gargan, Tully, & Poole, 2003; Schram, Knutsen, Heuch, & Mo, 1998). On the
915 other hand, in farm-intensive areas, sea lice levels on wild sea trout are typically higher
916 (Gargan et al., 2003; I. Moore et al., 2018; Tully, Poole, Whelan, et al., 1993; Tully &
917 Whelan, 1993). Sea lice infestations in these areas regularly exceed more than 0.35 lice per
918 gram of fish mass, initiating physiological disturbance to the trout with weight range from
919 16-70 gram (Wells et al., 2006, 2007). At higher lice levels mortality may occur (Taranger et
920 al., 2015). The sea lice levels on wild sea trout are particularly high within 30 km of salmon
921 farms, but elevated lice infestations extend beyond this distance (Gargan et al., 2003; I.
922 Moore et al., 2018; Serra-Llinares, Bjørn, Finstad, Nilsen, & Asplin, 2016; Serra-Llinares et
923 al., 2014; Tully, Gargan, Poole, & Whelan, 1999). Therefore, sea lice in intensively farmed
924 areas negatively impact wild sea trout through a suite of primary and secondary impacts
925 reducing marine growth and survival of sea run fish (Halttunen et al., 2018; S Shephard,
926 MacIntyre, & Gargan, 2016). Quantification of these impacts remains a challenge, although
927 population-level effects have been quantified in Atlantic salmon using field experiments
928 (Krkošek et al., 2013; Skilbrei et al., 2013; Vollset et al., 2016), showing higher survival in

929 groups of anti-parasitically treated fish relative to non-treated control groups. Reduced
930 growth and increased mortality in the marine environment decrease the benefits of marine
931 migration for sea trout (Halttunen et al., 2018), and high sea lice levels might select against
932 anadromy. In some populations, immature anadromous trout return frequently to rivers
933 during the growth season. Such ‘premature returning’ may be an early warning signal of
934 heavy salmon lice infections (Halttunen et al., 2018; Maisse et al., 1991). Sea lice-induced
935 effects on sea trout may in extreme cases lead to local loss of anadromous trout and a
936 transition to entirely resident trout populations (discussed in Poole *et al.* (2006) with
937 reference to the Burrishoole sea trout stock). However, recent studies showed the complexity
938 of the relationship between brown trout and sea lice infections in the wild (relationship
939 between size of trout and distance of farm cage) and emphasised the requirement of further
940 research to quantify these effects (I. Moore et al., 2018).

941

942 **Influence of the spawning habitat on reproduction outcome**

943 Marine migration is a strategy that allows brown trout to escape from, or reduce the influence
944 of, density dependence and resource limitation in freshwater, and by that maximize
945 reproductive output (B. Jonsson & Jonsson, 2006b; Lobón-Cerviá, 2007; Marco-Rius,
946 Caballero, Moran, & Leaniz, 2013). But to reproduce, trout must return to freshwater and
947 compete for access to suitable spawning sites and mates. Intense spawning competition may
948 introduce both density and frequency dependant pressures (Berejikian et al., 2010; Foote et
949 al., 1997; Gross, 1985), where body size is important for determining reproductive success
950 (Serbezov, Jorde, Bernatchez, Olsen, & Vøllestad, 2012). Interference competition generally
951 favours large individuals (Olsén et al., 1998), however, in small shallow tributaries, small
952 resident trout may have higher fitness because these habitats are less accessible for large
953 individuals. In populations dominated by individuals with short sea sojourns, there is larger

954 spatial overlap between the spawning grounds of resident and anadromous trout than in
955 populations dominated by longer sea sojourn. Interbreeding between the two phenotypes
956 (Charles, Roussel, Lebel, Baglinière, & Ombredane, 2006) produces fertile offspring
957 (Ombredane et al., 1996), but these offspring have reduced migration probability because the
958 migratory strategy is partly inherited (Baglinière et al., 2001; B. Jonsson, 1982). Size-specific
959 spawning success of both sexes is influenced by habitat characteristics as well as the
960 competitive ability and density of the competitors, although contrasting selective mechanisms
961 operate on males and females (B. Jonsson & Jonsson, 2015). Hence, the effect of each of
962 these selective variables is sex-specific and determined by both the environment and the
963 population structure (Young, 2005). Thus, spawning requirements play an important role in
964 determining the frequency, abundance, and sex ratio of anadromous brown trout (B. Jonsson
965 & Jonsson, 2015).

966

967 [Habitat suitability](#)

968 In order to breed successfully, female brown trout require a specific combination of
969 hydrological conditions and substrate composition (Baglinière, Champigneulle, & Nihouarn,
970 1979; Gauthey et al., 2015; Montgomery, Buffington, Peterson, Schuett-Hames, & Quinn,
971 1996; Tappel & Bjornn, 1983). In many circumstances, the availability of habitat that
972 adequately meets these conditions represents the primary factor limiting the size of salmonid
973 populations (Buffington, Montgomery, & Greenberg, 2004; Kondolf & Wolman, 1993).

974

975 Despite their difference in body size, the specific spawning habitat requirements of
976 anadromous trout versus freshwater resident trout have hardly been studied (Nika, Virbickas,
977 & Kontautas, 2011; Walker & Bayliss, 2007). It seems clear, however, that growth associated

978 with anadromy will represent differing reproductive advantages depending on the nature of
979 available spawning habitat.

980

981 The extra energy expenditure of migrating a longer distance is indicated by the gradual
982 decrease in the condition factor of anadromous brown trout with increasing migratory
983 distance inland. The gonadosomatic index of males ($I = \text{mass of gonads} / \text{somatic mass}$)
984 decreases with migratory distance (B. Jonsson & Jonsson, 2006a). Bohlin et al. (2001)
985 hypothesized that the fitness of migrants is negatively related to the altitude of the spawning
986 area because of migratory costs, and in support of this they found that anadromous trout were
987 replaced by non-anadromous conspecifics at an altitude of ca. 150 m in southern Sweden.
988 More than distance itself, it is the energetic demand required to reach the spawning ground
989 that matters. As such, the cumulative effect of barriers (natural or artificial) can greatly
990 impede sea trout migration inland in fragmented rivers.

991

992 [Flow condition and scouring risk](#)

993 Prior to spawning, female salmonids flex their flanks and tail fin to excavate depressions
994 (nests) in the streambed into which eggs are deposited. Due to the allometric relationship
995 between fish length and caudal thrust, salmonid females can construct their nests in gravel
996 where the median particle diameter does not exceed 10% of their fork length (Kondolf &
997 Wolman, 1993). Thus, nest sizes and depths are positively correlated with body size (Crisp &
998 Carling, 1989; Elliott, 1984; Gauthey et al., 2015). The depths of gravel mobilized during
999 high flow events are influenced by the strength of the stream flow, stream gradient and
1000 substrate composition (Harrison, Legleiter, Wyzdga, & Dunne, 2011). Within water courses
1001 prone to such riverbed 'scour', individual scour events are likely to kill trout eggs located
1002 above the maximum scour depth, thereby exerting a strong selective pressure for a locally-

1003 determined minimum female body size (Montgomery et al., 1996). Thus, due to their ability
1004 to dig deeper nests and move heavier gravel, large anadromous females may enjoy a distinct
1005 advantage over small resident females as scour depth and gravel particle size increase. This
1006 size-dependent mechanism may interfere with habitat selection in trout within a river basin,
1007 leading to positive correlation between female body size and river size at the spawning area.

1008

1009 Furthermore, female brown trout show a marked preference for spawning in previously
1010 utilized nests containing incubating eggs (Gortázar, Alonso, & Jalón, 2012). This behaviour,
1011 known as redd superimposition, includes a period of excavation that leads to high mortality
1012 rates amongst eggs deposited by earlier spawners (McNeil, 1964; Nomoto et al., 2010). This
1013 behaviour has also been reported where brown trout and Atlantic salmon share the same
1014 spawning ground (Baglinière et al., 1979). The intensity of redd superimposition depends on
1015 the density of spawners, the size of the spawning area, the duration of the spawning period
1016 and the distribution of spawners within the river system. As with environmentally-based
1017 scour, the survival of eggs depends on whether they are deposited below the depth of gravel
1018 mobility during subsequent excavations. As a result, the ability of large (i.e. anadromous)
1019 females to construct deeper nests than smaller freshwater resident females may represent a
1020 distinct inter-specific and intra-specific advantage where population density is high or where
1021 suitable spawning habitat is in short supply.

1022

1023 [Thermal condition and spawning phenology](#)

1024 In some populations, freshwater residents appear to spawn later in the spawning period than
1025 their anadromous counterparts (N. Jonsson & Jonsson, 1999). The asynchronous spawning of
1026 anadromous and resident females may lead to the eggs of anadromous females hatching
1027 earlier than those of resident females, potentially conferring a competitive advantage on the

1028 progeny of anadromous females through early growth opportunities. But this different
1029 temporal spawning pattern between resident and anadromous trout does not exist everywhere.
1030 In France the spawning period of sea trout (mid-December to late January) occurs within the
1031 larger spawning period of resident trout (late November to mid-February) (Baglinière, Pers.
1032 com.).

1033

1034 The efficiency of yolk conversion to body tissue declines as water temperature increases
1035 (Fleming & Gross, 1990), meaning that rising water temperatures during spring are likely to
1036 have a more pronounced negative impact on the growth performance of eggs spawned later in
1037 the breeding period. It is possible that the higher energy density found in the eggs of resident
1038 females relative to those of anadromous females from the same population (N. Jonsson &
1039 Jonsson, 1997b, 1999) represents an adaptation which mitigates the competitive
1040 disadvantages that result from late spawning. Possibly, thermal differences between eggs
1041 fertilized early or late during the spawning period may also influence later growth and
1042 reproductive allocations, as they appear to do in Atlantic salmon (A. G. Finstad & Jonsson,
1043 2012; B. Jonsson & Jonsson, 2014, 2018).

1044

1045 [Oxygen and siltation](#)

1046 In addition to benefitting from increased fecundity, large anadromous females, which tend to
1047 accumulate high somatic mass during marine feeding, are likely to produce larger eggs than
1048 smaller resident females (Hendry & Day, 2003; N. Jonsson & Jonsson, 1999). While
1049 increased redd depth is beneficial in protecting eggs from washout during scour events, the
1050 threat of egg asphyxiation due to sedimentation or weakly oxygenated water increases with
1051 burial depth (Haury, Ombredane, & Baglinière, 1999). Einum *et al.* (2002) found that the
1052 fitness of brown trout eggs at differing oxygen levels is size-dependant, with larger eggs

1053 exhibiting significantly higher survival than small eggs when the oxygen concentration is
1054 low, possibly as a result of their increased surface area which facilitates diffusion. Laboratory
1055 experiments with brown trout embryos suggest that sublethal stress in the gravel nest caused
1056 by hypoxia can alter the behaviour and survival of trout during the early juvenile period
1057 (Roussel, 2007). It follows that the nature of local scour regimes, dissolved oxygen levels,
1058 siltation rates and riverbed gravel composition may all influence the relative fitness and
1059 frequency of differing adult female phenotypes. These factors should select for increased
1060 body size and egg mass associated with anadromy where scour is deep, gravel particles are
1061 large, and siltation or deoxygenation represent a significant threat to egg survival.

1062

1063 [Male mating strategies: frequency dependence, density dependence and shelter](#)

1064 There is strong regional and local variation in age at maturity and freshwater residency rates
1065 of males, indicating that populations are locally adapted with regard to body size and
1066 migratory strategy (Bohlin et al., 1990; Dellefors & Faremo, 1988). Where the habitat
1067 permits, small males may safely remain close to spawning females by utilising crevices,
1068 rocks, debris, or shallow areas as refuges where the aggression of large males is avoided
1069 (Gross, 1985). Thus, the availability of appropriate refuge habitats near spawning sites may
1070 be a factor influencing the fitness and, consequently, the proportion of male brown trout that
1071 forego marine migration or mature at a small size (B. Jonsson & Jonsson, 2011).

1072

1073 While the abiotic characteristics of spawning habitat and local hydrological regimes are likely
1074 to influence the relative fitness of anadromous and freshwater resident phenotypes in brown
1075 trout, direct competition on spawning grounds may exert density-dependent selection on
1076 these phenotypes. But also, polymorphism amongst mature males appears to be maintained
1077 by frequency-dependent selection during spawning that increases the relative fitness of the

1078 rarer phenotype and promotes the co-occurrence of both mating strategies (Berejikian et al.,
1079 2010; Foote et al., 1997; Gross, 1985; Hutchings & Myers, 1985). For instance, in Atlantic
1080 salmon, aggressive competition for mates between large males occupies much of their focus,
1081 allowing young and small males to go unnoticed and successfully employ their sneaking
1082 tactic when courting females. As the density of large males increases, this alternative mating
1083 behaviour may confer a greater mating success, balanced against the risk of getting killed by
1084 a large male. Conversely, the fitness of large males is likely to be reduced by competition for
1085 mates as the frequency of large males increases (Engqvist & Taborsky, 2016). Similarly, as
1086 the frequency of precocious males increases, their individual genetic contribution is likely to
1087 diminish due to increased competition from other precocious males (Hutchings & Myers,
1088 1994). In brown trout, males do not mature as early and small as in salmon, but the contrast
1089 between small resident and large migrant individuals provides a similar framework.

1090

1091 It has been argued that the development and maintenance of an evolutionarily stable
1092 alternative male reproductive strategy requires a strong underlying genetic basis, although the
1093 expression of these strategies is conditional, in the sense that environmental conditions
1094 associated with growth and survival interact with genetically based threshold responses to
1095 determine individual strategy (Engqvist & Taborsky, 2016; Tomkins & Hazel, 2007).
1096 However, one cannot rule out epigenetic mechanisms, which might provide a rapid response
1097 to changing environmental conditions (Moran & Pérez-Figueroa, 2011). Hutchings and
1098 Myers (1994) suggested that within a given trout population, an evolutionarily stable
1099 continuum of strategy frequencies is maintained by polygenic thresholds (which are likely to
1100 differ significantly between sexes as well as between individuals) of environmentally
1101 controlled traits (primarily associated with growth). In this sense, the polyphenic mating
1102 strategies employed by male brown trout may be regarded as both locally adapted and

1103 phenotypically plastic, resulting from the interplay between genotype, environmental
1104 conditions and both frequency and density dependent pressures. While density dependent
1105 pressures are likely to lead to high rates of migration and anadromy where feeding
1106 opportunities are poor in the home river, frequency dependent pressures largely maintain
1107 alternative mating strategies and associated polyphenism through intrasexual competition on
1108 the spawning beds (Forseth et al., 1999; Landergren, 2001; Wysujack, Greenberg, Bergman,
1109 & Olsson, 2009).

1110

1111 **Human impacts on sea trout**

1112 **Climate change**

1113 Possible effects of climate change on sea trout populations have been extensively reviewed
1114 (Elliott & Elliott, 2010; Graham & Harrod, 2009; B. Jonsson & Jonsson, 2009a; Lassalle &
1115 Rochard, 2009). The expected climate change in the Atlantic region is for warmer, drier
1116 spring and summer seasons, and for milder and wetter winters, with more precipitation falling
1117 as rain and less as snow, shorter ice-covered periods, and more frequent periods of extreme
1118 weather, including droughts, heavy rain events and strong spates. A shorter ice-covered
1119 period may increase the activity and energy use of trout in rivers and decrease production
1120 unless feeding opportunities increase to a similar extent (Watz et al., 2015).

1121

1122 Climate change may also be responsible for increased rates of land erosion, which is
1123 reinforced by land-use change in agriculture and forestry practices. As a result, an increase in
1124 river sediment is likely. Suspended sediment affects trout behaviour and survival directly.
1125 Sediment loads clog gravel beds impeding brown trout from spawning and reducing
1126 recruitment success (Scheurer, Alewell, Bänninger, & Burkhardt-Holm, 2009). Invertebrate
1127 communities and growth opportunities for trout are also affected by increasing sediment input

1128 (J. I. Jones et al., 2012). An increase in water temperature, notably during the spawning
1129 period, is likely to impact reproductive behaviour and egg mortality as observed in
1130 experimental conditions in Atlantic salmon (Beall & De Gaudemar, 1999), ultimately leading
1131 to a drastic reduction in the species distribution. Overall, Jonsson and Jonsson (2009a)
1132 predicted a north and northeastward movement of the distributional range of sea trout, with
1133 decreased production and population extinction in the southern regions and invasion of new
1134 spawning and nursery rivers and feeding areas in the north.

1135

1136 Fisheries

1137 Trout are exploited through fishing both in freshwater and marine habitats. Overexploitation,
1138 i.e., when a population is exploited to the extent that the optimal recruitment cannot be
1139 maintained due to a lack of spawners and thereby insufficient egg deposition, leads to
1140 population declines, and/ or a shift the balance between anadromous and freshwater resident
1141 compartments of populations. Because brown trout are iteroparous, the impact of exploitation
1142 is cumulative on older and larger fish (Solomon & Czerwinski, 2007). Catch statistics, as
1143 well as information on catch per unit effort and catch rates, are important for the monitoring
1144 of sea trout and assessments of levels of exploitation. In the Burrishoole catchment, fishing
1145 effort was found to be the most important determinant of catch with a weaker but significant
1146 relationship between catch and stock (Mills, Mahon, & Piggins, 1986). The quality of catch
1147 statistics for trout is adequate in some fisheries and countries, but needs improvement in
1148 others (Milner et al., 2007). The extent of illegal sea trout fishing is unknown, but can be
1149 significant in some countries.

1150

1151 [Aquaculture](#)

1152 Salmon farming affects sea trout by spreading infectious diseases caused by viruses, bacteria,
1153 fungi and parasites, as well as often functioning as a barrier to migration (Aarestrup & Koed,
1154 2003). Such diseases may affect both the freshwater and marine stages of the sea trout life
1155 cycle. Although numerous studies document the impact of salmon lice (see previous section
1156 on sea lice), little knowledge and monitoring is available on other effects of fish farming on
1157 wild brown trout populations (Bakke & Harris, 1998). However, considering the importance
1158 of the parasitism impact on wild salmonids in Norway, an operational salmon lice model has
1159 been developed to provide an improved monitoring system for risk assessment (Myksvoll et
1160 al., 2018) as well as the implemented “traffic light system” for a sustainable fish farming in
1161 Norway (Vollset et al., 2018). In Ireland, Single Bay Management (Anon, 2008) was
1162 implemented in the early 1990s which included close monitoring and advice for to harvest or
1163 treat lice, especially in the immediate months before and during the wild smolt runs.

1164

1165 [Degradation of water quality](#)

1166 Water acidification, pollution (e.g. from agriculture, sewage treatment works, roads and
1167 mining), hydropower developments, flow regulation, water abstraction, migratory barriers,
1168 and habitat alterations as diverse as high diffuse organic load or clearing riffles of stones for
1169 passing logs through, affect trout populations negatively (reviewed by Thorstad et al., 2014;
1170 K. F. Whelan & Poole, 1993).

1171

1172 Freshwater acidification arising from industrial emissions of sulphur dioxide and nitrogen
1173 oxides to the atmosphere, and subsequent acid precipitation wiped out trout populations in
1174 southern Fennoscandia during the last century. Although emissions were reduced after 1990,
1175 many rivers in this area are still affected by chronic or episodic acidification (e.g. Hesthagen

1176 et al., 2017; Kroglund et al., 2007; Rosseland & Kroglund, 2010). Brown trout are vulnerable
1177 to acidification, although to a lesser degree than Atlantic salmon (Henrikson & Brodin,
1178 1995). Hence it is likely that any liming strategy adopted specifically for Atlantic salmon
1179 may also restore water to a quality suitable for sea trout. However, liming strategies can still
1180 be optimised to improve conditions for sea trout in tributaries and small streams that
1181 presently are not included in the liming programme of the main stem of rivers. Furthermore,
1182 competition with more acid sensitive species than brown trout, such as Atlantic salmon,
1183 seems to increase as a consequence of liming and reduce the abundance of trout in acidified
1184 waters treated with calcium carbonate (Hesthagen et al., 2017).

1185

1186 Contaminants derived from intensive agriculture, afforestation, mining and other industries
1187 impact sea trout negatively, both as a consequence of direct and indirect effects in freshwater
1188 (B. Jonsson, Jonsson, & Ugedal, 2011). High nitrite concentrations are lethal for embryos,
1189 this impact being higher when dissolved oxygen concentrations are low (Massa, Baglinière,
1190 Prunet, & Grimaldi, 2000). Livestock grazing contributes to river eutrophication due to
1191 runoff from livestock manure. Interestingly, intensive agriculture systems relying on a large
1192 quantity of nutrients led to an increase in productivity in river Scorff, France (Roussel et al.,
1193 2013). This coincided with an increase in growth performance in juvenile Atlantic salmon
1194 and a decrease in mean age at smolting (Rivot et al., 2009). However, this positive effect on
1195 fish may only hold within a reasonable level of eutrophication. In the Burrishoole, Ireland,
1196 land use
1197 change was found to have no significant impact on the freshwater survival of either salmon or
1198 trout (de Eyto et al., 2016). Nevertheless, contaminants also alter the parr-smolt
1199 transformation, and influence the run-timing and survival of smolts once they enter sea water
1200 (S. D. McCormick, Hansen, Quinn, & Saunders, 1998; Rosseland & Kroglund, 2010).

1201 Contaminants may damage fish gills and thereby compromise the ionoregulatory capacity of
1202 smolts (Kroglund et al., 2007; S. D. McCormick et al., 1998; A. Moore, Lower, Mayer, &
1203 Greenwood, 2007). Sublethal exposure to contaminants during smolting may therefore have
1204 implications for the survival for trout at sea and their tendency to migrate. Livestock
1205 trampling of stream bank may induce direct destruction of eggs and fry (Gregory & Gamett,
1206 2009), potentially leading to population decline, as illustrated in a cutthroat trout model
1207 (Peterson, Rieman, Young, & Brammer, 2010). Stream bank trampling also increases
1208 siltation sedimentation of salmonids redds, which limits the interchange of surface and
1209 intragravel water and, therefore, the supply of dissolved oxygen to the embryo (Heywood &
1210 Walling, 2007). Stock exclusion from watercourses using riparian fencing and limited pool
1211 excavation has the potential to preserve and enhance wild trout populations in headwaters
1212 (Summers, Giles, & Stubbing, 2008). This rehabilitation work has become a widely
1213 recommended fisheries management practice (Summers, Giles, & Willis, 1996).

1214

1215 Road and railway activities contribute to freshwater pollution, but there is little available
1216 information on effects for trout. Meland *et al.* (2010) suggested that traffic-related
1217 contaminants, especially those emanating from contaminated tunnel wash water, reduce
1218 growth of juvenile trout. In winter, salt from the roads may also be an issue. In addition, poor
1219 water quality in rivers may be responsible for various skin diseases. For instance, UDN-like
1220 (Ulcerative Dermal Necrosis) disappeared from Europe in the 1970s, but in 1993, Roberts
1221 wrote: “it seems likely that UDN is a cyclical disease (...). It can therefore be expected to
1222 return again before the middle of the 21th century” (Roberts, 1993). Currently, a UDN-like
1223 disease is becoming an important driver of adult mortality in Baltic salmonids, this disease
1224 has been detected in Latvia, Poland, Germany and Sweden (ICES, 2018).

1225

1226 Threat to connectivity

1227 Hydropower stations, dams and weirs may all comprise major obstacles to migratory trout
1228 and cause marked alteration of riverine habitats. Building of roads, railways, bridges and
1229 other installations may incur migratory barriers for sea trout. In some cases, migrations may
1230 be completely blocked, whereas in others, culverts or other constructions may not be
1231 sufficiently well-designed to enable or facilitate fish passage (Larinier, 2002). River flow
1232 regulation for irrigation, freshwater fish hatcheries, channel modification to facilitate boat
1233 traffic (e.g. locks) and the building of infrastructure along rivers all pose challenges to
1234 migratory fish like those from hydropower regulation. There are numerous studies on
1235 restoration of spawning habitats, changes in overwintering environmental conditions, fish
1236 stranding due to rapid flow decreases, migration barriers, turbine mortality and the effects of
1237 flow and temperature regimes on juvenile growth, behaviour and recruitment of trout (e.g.
1238 (Aarestrup & Koed, 2003; Alonso-González, Gortázar, Sanz, & De Jalón, 2008; Pulg,
1239 Barlaup, Sternecker, Trepl, & Unfer, 2013; Saltveit, Halleraker, Arnekleiv, & Harby, 2001)).
1240 Also, passages through hydrological barriers and temperature changes affect energy
1241 expenditure and decrease the fitness gain of migration. Furthermore, recent studies show that
1242 the presence of many dams negatively affect the energetic status of sea trout kelts during their
1243 seaward migration, reducing iteroparity (Haraldstad et al., 2018).

1244

1245 Coastal development

1246 There is little information on how anthropogenic factors and increased human development
1247 activity in coastal areas affect sea trout survival and movements. It is not known how
1248 harbours, piers, bridges, fish farms, or industrial developments and deposits from mining
1249 activity in coastal areas affect sea trout. This is compounded by the construction of port
1250 facilities with piers or tethering systems that extend far offshore, as necessitated by the

1251 increasing size of ocean-going vessels. The construction of tidal power turbines is currently
1252 widely debated but the indirect impact of habitat changes associated with necessary damming
1253 and the direct impact of the spinning blades could be substantial for migratory species like
1254 trout. An increasing portion of rivers and the ocean is also now being illuminated at night. It
1255 is not known how such facilities impact sea trout, but negative effects of light pollution have
1256 been demonstrated on salmon migratory behaviour (Riley, Bendall, Ives, Edmonds, &
1257 Maxwell, 2012) and may be expected to exert the same negative effects on trout.

1258

1259 Interactions among impact factors

1260 Often, several anthropogenic factors impact trout populations simultaneously, but studies of
1261 synergistic effects of anthropogenic disturbances on fish populations are often complicated
1262 and expensive to conduct, and very few such studies on any species exist. Synergistic effects
1263 of two or more impact factors are complex, non-linear and unpredictable, and certainly not
1264 apparent from combining knowledge of the effects of single factors studied in isolation. As
1265 one example Finstad *et al.* (2012, 2007) investigated effects of salmon lice and acidification
1266 on Atlantic salmon post-smolt survival. These studies showed that smolts exposed to
1267 freshwater acidification were subsequently more vulnerable to salmon lice than were control
1268 groups held in good quality freshwater before migrating to sea. Vulnerability to salmon lice
1269 was, however, reduced if there was a recovery period following the acidification episode and
1270 prior to exposure to salmon lice. The interaction between higher temperature and reduced sea
1271 louse generation time has been implicated in exacerbating the farm lice sea trout impact
1272 (Tully, 1992) in a context of global warming. The interaction between run timing of sea trout
1273 smolts and the point in time at which those smolts gain a sea louse burden has been
1274 demonstrated to lead to additional stress on those smolts (Poole *et al.*, 2000). Therefore, we
1275 conclude that in years when environmental conditions are less favourable for sea trout

1276 transition from freshwater to saltwater and a high abundance of sea lice is present in the area,
1277 the combined impact on trout will be greater than in more “normal” years or locations.

1278

1279 **Research Questions and future directions**

1280 *Assessment of partial anadromy*

1281 In brown trout, partial anadromy is driven by complex interactions between intrinsic and
1282 extrinsic factors, leading to a wide variety of life history patterns. In particular, partial
1283 migration is influenced by juvenile growth in freshwater, largely determined by temperature
1284 and feeding opportunities (B. Jonsson, 1981) and resulting in a continuum of life history
1285 strategies in brown trout (Cucherousset et al., 2005). However, there are few empirical data
1286 sets available because studies rarely consider simultaneously sea trout and resident trout from
1287 the same population. The development of passive integrated transponder (PIT) tag monitoring
1288 programs across Europe is promising but currently limited to small to medium coastal
1289 streams or tributaries and do rarely encompass catchment or population level surveys. Scale
1290 samples and the relative concentrations of strontium (Sr) and calcium (Ca) in the otoliths can
1291 be used as proxies of movement of anadromous fish between freshwater and salt water. Also,
1292 investigations of nutritional status which differs between freshwater resident and anadromous
1293 fish or spawning ground surveys of types of spawners may offer alternative methods to study
1294 partial anadromy. In parallel, future research should explicitly incorporate both resident and
1295 anadromous individuals (and possibly all intermediate life histories), and use these in
1296 population models to improve our understanding of the complex dynamics within partly
1297 anadromous population. For instance, a recent meta-analysis highlighted that partial
1298 migration may confer a selective advantage in a stochastically varying environment (Gilroy,
1299 Gill, Butchart, Jones, & Franco, 2016). Thus, investigating whether partial anadromy under

1300 chronic global change may promote a greater resilience in the brown trout compared to
1301 anadromous fish, should be an important issue for ecologists and managers.

1302

1303 Responses to climate change

1304 By influencing metabolic rate, growth and feeding opportunities, temperature is considered a
1305 key driver of migration decisions in brown trout. With climate change, temperature tends to
1306 increase more rapidly in rivers than in the ocean, but the effect of temperature on growth
1307 opportunities depends on whether it is above or below some optimal temperature. If
1308 temperature increases above the optimal temperature for growth, we hypothesize that the
1309 degree of anadromy will increase, provided that the risk of mortality in fresh relative to
1310 marine waters remains similar. If the temperature in freshwater is below the optimal
1311 temperature for growth, freshwater residency should be favoured as the temperature
1312 increases. The latter is the case in masu salmon, where the proportion of resident fish
1313 increases with temperature increase in freshwater (Morita et al., 2014). Furthermore, flow
1314 conditions are likely to interact with temperature, by either accentuating or attenuating the
1315 impact of temperature on brown trout depending on the situation. But surely, expected
1316 changes in flow regime would increase environmental stochasticity in freshwater. As a result,
1317 we predict that the influence of climate change on anadromy rates will differ from northern to
1318 southern populations in brown trout. The flexibility of partial anadromy is an issue for future
1319 research.

1320

1321 Climate also influences the phenology of fish species (Anderson, Gurarie, Bracis, Burke, &
1322 Laidre, 2013; B. Jonsson, Jonsson, & Jonsson, 2017). In a warmer climate, eggs may hatch
1323 earlier (Alp, Erer, & Kamalak, 2010), the length of the growth season may increase until a
1324 certain point (Elliott & Hurley, 1998), smolts should migrate earlier to sea (B. Jonsson &

1325 Ruud-Hansen, 1985; Otero et al., 2014) and adults return later for spawning (Alm, 1950),
1326 thereby increasing the duration of the sea-sojourn. In rivers, water flow appears to influence
1327 time of freshwater entry and upstream migration, especially in small streams (B. Jonsson et
1328 al., 2001, 2018). Furthermore, the tendency to spend the winter at sea may increase when the
1329 sea water temperature increases (Olsen et al., 2006). The spawning period in southern
1330 populations may be prolonged as observed in Spain (Larios-López, de Figueroa, Galiana-
1331 García, Gortázar, & Alonso, 2015). Investigations of latitudinal gradients in phenological and
1332 life history traits will help anticipate how climate change will influence sea trout in the future.
1333 However, because migratory distances to the home rivers differ, such gradient studies do not
1334 give direct evidence of changes in traits affected by migratory costs. Therefore, experimental
1335 research involving model species may also be helpful in studies of future phenology and life
1336 history of sea trout.

1337

1338 In a future warmer climate, age at smolting throughout much of the brown trout's distribution
1339 should decrease because of higher growth rate in freshwater; however, the opposite may be
1340 the case in the southern part of their distribution, as optimum temperature for growth will be
1341 exceeded more frequently. Whether smolt size will change or not, depends not only on
1342 growth rate, but selection for optimal size depending on size-specific mortality at sea (B.
1343 Jonsson et al., 2016). If mortality of small smolts increases more than that of large smolts,
1344 selection will favour larger smolts and high survival at sea, and vice versa if mortality
1345 increases most for large smolts. Furthermore, the ability to osmoregulate may be impaired at
1346 higher temperatures (S. D. McCormick, Shrimpton, & Zydlewski, 1996) with possible full
1347 loss of anadromy in southern areas, similar to Arctic charr.

1348

1349 Flow conditions in rivers will change in the future climate. With increasing flow in small
1350 streams, the size of both residents, smolts as well as adult trout may increase, and vice versa
1351 if the flow decreases (B. Jonsson et al., 2001). Furthermore, more water may influence the
1352 relative size of males and females. Apparently, males need more water than similar sized
1353 females to be reproductively successful because of their high activity. Therefore, males may
1354 be smaller than females in small streams, and less so when stream size increases (B. Jonsson
1355 & Jonsson, 2015). Conversely, predicted increase in the frequency of extreme summer
1356 drought is likely to jeopardize juvenile survival and growth.

1357

1358 Mean male size relative to mean female size of the anadromous trout may increase towards
1359 the north (B. Jonsson & Jonsson, 2015). This might be because conditions in freshwater make
1360 freshwater residency less favourable in the north. However, the mechanism determining the
1361 sex ratio of freshwater resident versus anadromous trout is still unknown and open for
1362 research, as the proportion of the two varies among rivers (Table 1).

1363

1364 Epigenetics

1365 Increased winter temperature might influence embryo development and in this century,
1366 winter temperatures are expected to increase more than summer temperatures (IPCC, 2013).
1367 Heritable variation in phenotypic plasticity suggests that although increasing temperatures are
1368 likely to affect some populations negatively, they may have the potential to adapt to changing
1369 temperature regimes (L. F. Jensen et al., 2008). The mechanism of this flexibility is, however,
1370 unknown, but appears to involve a change in gene expression, possibly caused as an
1371 epigenetic response to early thermal conditions (B. Jonsson & Jonsson, 2014, 2016). There is
1372 still little knowledge about epigenetic influence on phenotypically plastic traits (B. Jonsson &
1373 Jonsson, 2019).

1374

1375 **Management strategies**

1376 Stock assessments for brown trout are generally lacking across Europe. Little is known about
1377 productivity and recruitment in brown trout, as well as river specific carrying capacities. Data
1378 are lacking to quantify the mortality induced by fisheries at sea, in freshwater and as potential
1379 bycatch. There is also lack of information on sea trout stocks regarding human impacts (e.g.
1380 aquaculture and spread of diseases and parasites, pollution and water quality, agriculture,
1381 road, railway activities etc.). Estimates of straying among watercourses are sometimes large
1382 (Quéméré et al., 2016), but variable, possibly influenced by the size of the river and presence
1383 of lakes where trout spend the winter in a protected habitat. If straying between neighbouring
1384 populations is high, they may be managed together as meta-populations (Meier, Hansen,
1385 Bekkevold, Skaala, & Mensberg, 2011). However, in the future climate, autumn and winter
1386 precipitation may increase and thereby reduce the rate of straying with effects on the size of
1387 the management unit. As brown trout are partly anadromous, a future management program
1388 should be coordinate with data collection programs across Europe. To aid in its
1389 implementation, data collection suitable for supporting management of sea trout stocks
1390 should be cheap, easy and pragmatic, such as the Length Based Indicator (LBI) system
1391 proposed in Shephard et al. (2018).

1392

1393 In many countries, sea trout management is viewed as a by-product of Atlantic salmon
1394 management, and this is completely disconnected from resident trout management. Thus,
1395 there is an urgent need to develop new recommendations dedicated to brown trout ecology
1396 and plasticity to promote the conservation of this iconic species. Because trout are only partly
1397 anadromous, more research is needed to define the relative contribution of sea trout and
1398 resident trout to population dynamics, as well as more general data comparing sea survival

1399 and growth in populations across the native distribution area. Preferably, this should be done
1400 using individual tagged fish (such as PIT tagged) in order to directly couple life history to
1401 individual parameters (and avoid problems with straying, age reading etc.). Future research
1402 should define relevant management units and provide recommendations for dedicated
1403 management actions able to account for the large plasticity in individual life history
1404 trajectories in trout.

1405

1406 **Acknowledgements**

1407 This work is part of the ICES working group on sea trout WGTRUTTA. We thank Rafał
1408 Bernaś, Rasmus Lauridsen, Alan Walker, Steig Peterson, Jean-Luc Baglinière, Arne Johan
1409 Jensen and Kjell Leonardsson for their valued suggestions. We are extremely grateful to all
1410 the organisations that provided data: the Marine Institute, the Environmental Agency, the
1411 Norwegian Institute for Nature Research, the company Vattenfall Vattenkraft AB, the AFB
1412 and INRA as part of the Observatoire de Recherche en environnement DiaPFC. The
1413 contribution from MN was supported by INRA and European program Interreg France-
1414 Channel-England (project: SAMARCH); BF, JD and BJ were supported by the Norwegian
1415 Environmental Agency, and JD was also funded by the Research Council of Norway (Project:
1416 CHASES); RP was supported by the Marine Institute, Ireland; RF was supported by a Marine
1417 Institute Cullen Fellowship Grant. QJ was funded by the French Agency for Biodiversity.

1418

1419 **Data Availability Statement**

1420 The data that support the findings of this study are available from the corresponding author
1421 upon reasonable request.

1422

1423 **References**

- 1424 Aarestrup, K., Baktoft, H., Koed, A., del Villar-Guerra, D., & Thorstad, E. B. (2014).
1425 Comparison of the riverine and early marine migration behaviour and survival of wild
1426 and hatchery-reared sea trout *Salmo trutta* smolts. *Marine Ecology Progress Series*,
1427 496, 197–206. <https://doi.org/10.3354/meps10614>
- 1428 Aarestrup, K., Birnie Gauvin, K., & Larsen, M. H. (2017). Another paradigm lost? Autumn
1429 downstream migration of juvenile brown trout: Evidence for a presmolt migration.
1430 *Ecology of Freshwater Fish*, 27(1), 513–516. <https://doi.org/10.1111/eff.12335>
- 1431 Aarestrup, K., & Jepsen, N. (1998). Spawning migration of sea trout (*Salmo trutta* (L)) in a
1432 Danish river. In *Advances in Invertebrates and Fish Telemetry* (pp. 275–281).
1433 Springer.
- 1434 Aarestrup, K., & Koed, A. (2003). Survival of migrating sea trout (*Salmo trutta*) and Atlantic
1435 salmon (*Salmo salar*) smolts negotiating weirs in small Danish rivers. *Ecology of*
1436 *Freshwater Fish*, 12(3), 169–176.
- 1437 Aarestrup, K., Nielsen, C., & Koed, A. (2002). Net ground speed of downstream migrating
1438 radio-tagged Atlantic salmon (*Salmo salar* L.) and brown trout (*Salmo trutta* L.)
1439 smolts in relation to environmental factors. *Hydrobiologia*, 483(1), 95–102.
1440 <https://doi.org/10.1023/A:1021306907338>
- 1441 Aarestrup, K., Nielsen, C., & Madsen, S. S. (2000). Relationship between gill Na⁺,K⁺-
1442 ATPase activity and downstream movement in domesticated and first-generation
1443 offspring of wild anadromous brown trout (*Salmo trutta*). *Canadian Journal of*
1444 *Fisheries and Aquatic Sciences*, 57(10), 2086–2095. <https://doi.org/10.1139/f00-164>
- 1445 Acolas, M.-L., Labonne, J., Baglinière, J.-L., & Roussel, J. M. (2012). The role of body size
1446 versus growth on the decision to migrate: a case study with *Salmo trutta*.
1447 *Naturwissenschaften*, 99(1), 11–21. <https://doi.org/10.1007/s00114-011-0861-5>

- 1448 Acolas, M.-L., Roussel, J.-M., & Baglinière, J.-L. (2008). Linking migratory patterns and diet
1449 to reproductive traits in female brown trout (*Salmo trutta* L.) by means of stable
1450 isotope analysis on ova. *Ecology of Freshwater Fish*, 17(3), 382–393.
1451 <https://doi.org/10.1111/j.1600-0633.2007.00290.x>
- 1452 Aldvén, D., & Davidsen, J. (2017). Marine migrations of sea trout (*Salmo trutta*). In G.
1453 Harris (Ed.), *Sea Trout: Science & Management: Proceedings of the 2nd*
1454 *International Sea Trout Symposium* (pp. 267–276). Dundalk, Ireland: Troubador
1455 Publishing Ltd.
- 1456 Aldvén, D., Hedger, R., Økland, F., Rivinoja, P., & Höjesjö, J. (2015). Migration speed,
1457 routes, and mortality rates of anadromous brown trout *Salmo trutta* during outward
1458 migration through a complex coastal habitat. *Marine Ecology Progress Series*, 541,
1459 151–163.
- 1460 Alm, G. (1950). The sea-trout population in the Ava Stream. *Ann. Rep. Inst. Freshwater Res.*,
1461 *Drottningholm*, 31, 26–51.
- 1462 Alonso-González, C., Gortázar, J., Sanz, D. B., & De Jalón, D. G. (2008). Dam function rules
1463 based on brown trout flow requirements: design of environmental flow regimes in
1464 regulated streams. *Hydrobiologia*, 609(1), 253–262.
- 1465 Alp, A., Erer, M., & Kamalak, A. (2010). Eggs incubation, early development and growth in
1466 fry of brown trout (*Salmo trutta macrostigma*) and black sea trout (*Salmo trutta*
1467 *labrax*). *Turkish Journal of Fisheries and Aquatic Sciences*, 10(3).
- 1468 Álvarez, D., Cano, J. M., & Nicieza, A. G. (2006). Microgeographic variation in metabolic
1469 rate and energy storage of brown trout: countergradient selection or thermal
1470 sensitivity? *Evolutionary Ecology*, 20(4), 345–363. [https://doi.org/10.1007/s10682-](https://doi.org/10.1007/s10682-006-0004-1)
1471 [006-0004-1](https://doi.org/10.1007/s10682-006-0004-1)

- 1472 Anderson, J. J., Gurarie, E., Bracis, C., Burke, B. J., & Laidre, K. L. (2013). Modeling
1473 climate change impacts on phenology and population dynamics of migratory marine
1474 species. *Ecological Modelling*, *264*, 83–97.
- 1475 Anon. (2008). *A strategy for improved pest control on Irish salmon farms* (p. 56pp). Dublin,
1476 Ireland: Department of Agriculture, Fisheries and Food.
- 1477 Artemov, A. V., Muge, N. S., Rastorguev, S. M., Zhenilo, S., Mazur, A. M., Tsygankova, S.
1478 V., ... Prokhortchouk, E. B. (2017). Genome-Wide DNA Methylation Profiling
1479 Reveals Epigenetic Adaptation of Stickleback to Marine and Freshwater Conditions.
1480 *Molecular Biology and Evolution*, *34*(9), 2203–2213.
1481 <https://doi.org/10.1093/molbev/msx156>
- 1482 Baerwald, M. R., Meek, M. H., Stephens, M. R., Nagarajan, R. P., Goodbla, A. M., Tomalty,
1483 K. M. H., ... Nichols, K. M. (2016). Migration-related phenotypic divergence is
1484 associated with epigenetic modifications in rainbow trout. *Molecular Ecology*, *25*(8),
1485 1785–1800. <https://doi.org/10.1111/mec.13231>
- 1486 Bagenal, T. B. (1969). Relationship between egg size and fry survival in brown trout *Salmo*
1487 *trutta* L. *Journal of Fish Biology*, *1*(4), 349–353.
- 1488 Baglinière, J.-L. (1999). Introduction: The brown trout (*Salmo trutta* L.)—its origin,
1489 distribution and economic and scientific significance. In J.-L. Baglinière & G. Maisse
1490 (Eds.), *Biology and Ecology of the Brown and Sea Trout* (pp. 1–12).
1491 https://doi.org/10.1007/978-1-4471-0775-0_1
- 1492 Baglinière, J.-L., & Arribe-Moutounet, D. (1985). Microrépartition des populations de truite
1493 commune (*Salmo trutta* L.) de juvenile de saumon atlantique (*Salmo salar* L.) et des
1494 autres espèces présentes dans la partie haute du Scorff (Bretagne). *Hydrobiologia*,
1495 *120*(3), 229–239. <https://doi.org/10.1007/BF00045166>

- 1496 Baglinière, J.-L., & Champigneulle, A. (1982). Densité des populations de truite commune
1497 (*Salmo trutta* L.) et de juvéniles de saumon atlantique (*Salmo salar* L.) sur le cours
1498 principal du Scorff (Bretagne): préférendums physiques et variations annuelles (1976-
1499 1980). *Acta Oecologica: Oecologia Applicata*.
- 1500 Baglinière, J.-L., Champigneulle, A., & Nihouarn, A. (1979). La fraie du saumon atlantique
1501 (*Salmo salar* L.) et de la truite commune (*Salmo trutta* L.) sur le bassin du Scorff.
1502 *Cybium*, 3(7), 75–96.
- 1503 Baglinière, J.-L., Guyomard, R., Héland, M., Ombredane, D., & Prévost, E. (2001). Ecologie
1504 des populations de Poissons des cours d'eau à Salmonidés. *L'eau Dans l'espace*
1505 *Rural. Vie et Milieux Aquatiques*, A. Neveu, C. Riou, R. Bonhomme, P. Chassin, F.
1506 Papy (Eds), 31–49.
- 1507 Baglinière, J.-L., & Maisse, G. (1985). Precocious maturation and smoltification in wild
1508 Atlantic salmon in the Armorican massif, France. *Aquaculture*, 45(1), 249–263.
1509 [https://doi.org/10.1016/0044-8486\(85\)90274-1](https://doi.org/10.1016/0044-8486(85)90274-1)
- 1510 Baglinière, J.-L., & Maisse, G. (1990). La croissance de la truite commune (*Salmo trutta* L.)
1511 sur le bassin de Scorff. *Bulletin Français de la Pêche et de la Pisciculture*, (318), 89–
1512 101. <https://doi.org/10.1051/kmae:1990012>
- 1513 Baglinière, J.-L., & Maisse, G. (1999). *Biology and ecology of the brown and sea trout*.
1514 Chichester, UK: Springer Praxis publishing Chichester.
- 1515 Baglinière, J.-L., & Maisse, G. (2002). La biologie de la truite commune (*Salmo trutta* L.)
1516 dans la rivière Scorff, Bretagne : une synthèse des études de 1972 à 1997. *Productions*
1517 *Animales* 5 (15), 319-331. (2002).
- 1518 Baglinière, J.-L., Prévost, E., & Maisse, G. (1994). Comparison of population dynamics of
1519 Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) in a small tributary of

- 1520 the River Scorff (Brittany, France). *Ecology of Freshwater Fish*, 3(1), 25–34.
- 1521 <https://doi.org/10.1111/j.1600-0633.1994.tb00104.x>
- 1522 Bakke, T. A., & Harris, P. D. (1998). Diseases and parasites in wild Atlantic salmon (*Salmo*
1523 *salar*) populations. *Canadian Journal of Fisheries and Aquatic Sciences*, 55(S1),
1524 247–266.
- 1525 Bal, G., Rivot, E., Prévost, E., Piou, C., & Baglinière, J.-L. (2011). Effect of water
1526 temperature and density of juvenile salmonids on growth of young-of-the-year
1527 Atlantic salmon *Salmo salar*. *Journal of Fish Biology*, 78(4), 1002–1022.
1528 <https://doi.org/10.1111/j.1095-8649.2011.02902.x>
- 1529 Balon, E. K. (1980). Early ontogeny of the lake char, *Salvelinus (Cristivomer) namaycush*.
1530 In *Chaaars: Salmonid fishes of the genus Salvelinus* (pp. 475–685). The Hague,
1531 Netherlands: Dr. W. Junk Publishers.
- 1532 Baran, P., Delacoste, M., Lascaux, J. M., Bauba, F., & Segura, G. (1995). La compétition
1533 interspécifique entre la truite commune (*Salmo trutta* L.) et la truite arc-en-ciel
1534 (*Oncorhynchus Mykiss* Walbaum) : influence sur les modèles d’habitat. *Bulletin*
1535 *Français de la Pêche et de la Pisciculture*, (337-338–339), 283–290.
1536 <https://doi.org/10.1051/kmae:1995032>
- 1537 Bašić, T., Britton, J. R., Cove, R. J., Ibbotson, A., & Gregory, S. D. (2018). Roles of
1538 discharge and temperature in recruitment of a cold-water fish, the European grayling
1539 *Thymallus thymallus*, near its southern range limit. *Ecology of Freshwater Fish*,
1540 27(4), 940–951. <https://doi.org/10.1111/eff.12405>
- 1541 Beall, E., & De Gaudemar, B. (1999). Plasticity of reproductive behaviour in Atlantic salmon
1542 *Salmo salar* (Salmonidae) in relation to environmental factors. *Cybiurn*, 23(1), 9–28.
- 1543 Berejikian, B. A., Van Doornik, D. M., Endicott, R. C., Hoffnagle, T. L., Tezak, E. P.,
1544 Moore, M. E., & Atkins, J. (2010). Mating success of alternative male phenotypes and

- 1545 evidence for frequency-dependent selection in Chinook salmon, *Oncorhynchus*
1546 *tshawytscha*. *Canadian Journal of Fisheries and Aquatic Sciences*, 67(12), 1933–
1547 1941. <https://doi.org/10.1139/F10-112>
- 1548 Berg, O. K., & Jonsson, B. (1990). Growth and survival rates of the anadromous trout, *Salmo*
1549 *trutta*, from the Vardnes River, northern Norway. *Environmental Biology of Fishes*,
1550 29(2), 145–154.
- 1551 Berglund, I. (1995). Effects of size and spring growth on sexual maturation in 1+ Atlantic
1552 salmon (*Salmo salar*) male parr: interactions with smoltification. *Canadian Journal of*
1553 *Fisheries and Aquatic Sciences*, 52(12), 2682–2694. <https://doi.org/10.1139/f95-857>
- 1554 Bernatchez, L. (2001). The Evolutionary History of Brown Trout (*Salmo trutta* L.) Inferred
1555 from Phylogeographic, Nested Clade, and Mismatch Analyses of Mitochondrial Dna
1556 Variation. *Evolution*, 55(2), 351–379. [https://doi.org/10.1111/j.0014-](https://doi.org/10.1111/j.0014-3820.2001.tb01300.x)
1557 [3820.2001.tb01300.x](https://doi.org/10.1111/j.0014-3820.2001.tb01300.x)
- 1558 Bird, A. (2002). DNA methylation patterns and epigenetic memory. *Genes & Development*,
1559 16(1), 6–21. <https://doi.org/10.1101/gad.947102>
- 1560 Birkeland, K. (1996). Consequences of premature return by sea trout (*Salmo trutta*) infested
1561 with the salmon louse (*Lepeophtheirus salmonis* Krøyer): migration, growth, and
1562 mortality. *Canadian Journal of Fisheries and Aquatic Sciences*, 53(12), 2808–2813.
- 1563 Birnie Gauvin, K., & Aarestrup, K. (2018). A call for a paradigm shift: Assumed-to-be
1564 premature migrants actually yield good returns. *Ecology of Freshwater Fish*, 0(0).
1565 <https://doi.org/10.1111/eff.12431>
- 1566 Blanchet, S., Loot, G., Grenouillet, G., & Brosse, S. (2007). Competitive interactions
1567 between native and exotic salmonids: a combined field and laboratory demonstration.
1568 *Ecology of Freshwater Fish*, 16(2), 133–143.

- 1569 Boeuf, G., & Harache, Y. (1982). Criteria for adaptation of salmonids to high salinity
1570 seawater in France. *Aquaculture*, 28(1), 163–176. <https://doi.org/10.1016/0044->
1571 8486(82)90019-9
- 1572 Bohlin, T., Dellefors, C., & Faremo, U. (1990). Large or small at maturity—theories on the
1573 choice of alternative male strategies in anadromous salmonids. *Annales Zoologici*
1574 *Fennici*, 139–147. JSTOR.
- 1575 Bohlin, T., Pettersson, J., & Degerman, E. (2001). Population density of migratory and
1576 resident brown trout (*Salmo trutta*) in relation to altitude: evidence for a migration
1577 cost. *Journal of Animal Ecology*, 70(1), 112–121.
- 1578 Bordeleau, X., Davidsen, J. G., Eldøy, S. H., Sjørnsen, A. D., Whoriskey, F. G., & Crossin, G.
1579 T. (2018). Nutritional correlates of spatiotemporal variations in the marine habitat use
1580 of brown trout (*Salmo trutta*) veteran migrants. *Canadian Journal of Fisheries and*
1581 *Aquatic Sciences*, 75, 1744–1754. <https://doi.org/10.1139/cjfas-2017-0350>
- 1582 Borgstrøm, R., & Jan, H. (1988). Smoltification of sea trout (*Salmo trutta*) at short length as
1583 an adaptation to extremely low summer stream flow. *Polskie Archwum Hydrobiologii*,
1584 35, 375–384.
- 1585 Buffington, J. M., Montgomery, D. R., & Greenberg, H. M. (2004). Basin-scale availability
1586 of salmonid spawning gravel as influenced by channel type and hydraulic roughness
1587 in mountain catchments. *Canadian Journal of Fisheries and Aquatic Sciences*, 61(11),
1588 2085–2096. <https://doi.org/10.1139/f04-141>
- 1589 Byrne, C. J., Poole, R., Dillane, M., Rogan, G., & Whelan, K. F. (2004). Temporal and
1590 environmental influences on the variation in sea trout (*Salmo trutta* L.) smolt
1591 migration in the Burrishoole system in the west of Ireland from 1971 to 2000.
1592 *Fisheries Research*, 66(1), 85–94.

- 1593 Byrne, C. J., Poole, W. R., Dillane, M. G., & Whelan, K. F. (2002). The Irish sea trout
1594 enhancement programme: an assessment of the parr stocking programme into the
1595 Burrishoole catchment. *Fisheries Management and Ecology*, *9*(6), 329–341.
1596 <https://doi.org/10.1046/j.1365-2400.2002.00314.x>
- 1597 Campbell, J. S. (1977). Spawning characteristics of brown trout and sea trout *Salmo trutta* L.
1598 in Kirk Burn, River Tweed, Scotland. *Journal of Fish Biology*, *11*(3), 217–229.
- 1599 Campbell, R. N. (1979). Ferox trout, *Salmo trutta* L., and charr, *Salvelinm alpinus* (L.), in
1600 Scottish lochs. *Journal of Fish Biology*, *14*(1), 1–29. [https://doi.org/10.1111/j.1095-](https://doi.org/10.1111/j.1095-8649.1979.tb03491.x)
1601 [8649.1979.tb03491.x](https://doi.org/10.1111/j.1095-8649.1979.tb03491.x)
- 1602 Champigneulle, A., Buttiker, B., Durand, P., & Melhaoui, M. (1999). Main characteristics of
1603 the biology of the trout (*Salmo trutta* L.) in Lake Léman (Lake Geneva) and some of
1604 its tributaries. In J.-L. Baglinière & G. Maisse (Eds.), *Biology and Ecology of the*
1605 *Brown and Sea Trout* (pp. 147–174). https://doi.org/10.1007/978-1-4471-0775-0_6
- 1606 Chapman, B. B., Hulthén, K., Brodersen, J., Nilsson, P. A., Skov, C., Hansson, L.-A., &
1607 Brönmark, C. (2012). Partial migration in fishes: causes and consequences. *Journal of*
1608 *Fish Biology*, *81*(2), 456–478. <https://doi.org/10.1111/j.1095-8649.2012.03342.x>
- 1609 Charles, K., Guyomard, R., Hoyheim, B., Ombredane, D., & Baglinière, J.-L. (2005). Lack of
1610 genetic differentiation between anadromous and resident sympatric brown trout
1611 (*Salmo trutta*) in a Normandy population. *Aquatic Living Resources*, *18*(1), 65–69.
1612 <https://doi.org/10.1051/alr:2005006>
- 1613 Charles, K., Roussel, J.-M., Lebel, J.-M., Baglinière, J.-L., & Ombredane, D. (2006). Genetic
1614 differentiation between anadromous and freshwater resident brown trout (*Salmo trutta*
1615 L.): insights obtained from stable isotope analysis. *Ecology of Freshwater Fish*, *15*(3),
1616 255–263. <https://doi.org/10.1111/j.1600-0633.2006.00149.x>

- 1617 Courter, I., Justice, C., & Cramer, S. (2009). *Flow and temperature effects on life history*
1618 *diversity of Oncorhynchus mykiss in the Yakima River basin*. Gresham, Oregon.
- 1619 Crête-Lafrenière, A., Weir, L. K., & Bernatchez, L. (2012). Framing the Salmonidae Family
1620 Phylogenetic Portrait: A More Complete Picture from Increased Taxon Sampling.
1621 *PLOS ONE*, 7(10), e46662. <https://doi.org/10.1371/journal.pone.0046662>
- 1622 Crisp, D. T., & Carling, P. A. (1989). Observations on siting, dimensions and structure of
1623 salmonid redds. *Journal of Fish Biology*, 34(1), 119–134.
- 1624 Cross, T. F., Mills, C. P. R., & Williams, M. de C. (1992). An intensive study of allozyme
1625 variation in freshwater resident and anadromous trout, *Salmo trutta* L., in western
1626 Ireland. *Journal of Fish Biology*, 40(1), 25–32. [https://doi.org/10.1111/j.1095-](https://doi.org/10.1111/j.1095-8649.1992.tb02550.x)
1627 [8649.1992.tb02550.x](https://doi.org/10.1111/j.1095-8649.1992.tb02550.x)
- 1628 Cucherousset, J., Ombredane, D., Charles, K., Marchand, F., & Baglinière, J.-L. (2005). A
1629 continuum of life history tactics in a brown trout (*Salmo trutta*) population. *Canadian*
1630 *Journal of Fisheries and Aquatic Sciences*, 62(7), 1600–1610.
1631 <https://doi.org/10.1139/f05-057>
- 1632 Dahl, K. (1904). A study on trout and young salmon. *Nyt Magazin for Naturvidenskaberne*,
1633 42, 221–338.
- 1634 Davaine, P., & Beall, E. (1997). Introduction de salmonidés en milieu vierge (Îles Kerguelen,
1635 Subantarctique) : enjeux, résultats, perspectives. *Bulletin Français de la Pêche et de*
1636 *la Pisciculture*, (344–345), 93–110. <https://doi.org/10.1051/kmae:1997013>
- 1637 Davidsen, J. G., Daverdin, M., Sjørnsen, A. D., Rønning, L., Arnekleiv, J. V., & Koksvik, J. I.
1638 (2014). Does reduced feeding prior to release improve the marine migration of
1639 hatchery brown trout *Salmo trutta* smolts? *Journal of Fish Biology*, 85(6), 1992–2002.
1640 <https://doi.org/10.1111/jfb.12485>

- 1641 Davidson, I. C., Hazlewood, M. S., & Cove, R. J. (2007). Predicted Growth of Juvenile Trout
1642 and Salmon in Four Rivers in England and Wales Based on Past and Possible Future
1643 Temperature Regimes Linked to Climate Change. In *Sea Trout: Biology,
1644 Conservation and Management* (pp. 401–416).
1645 <https://doi.org/10.1002/9780470996027.ch28>
- 1646 de Eyto, E., Dalton, C., Dillane, M., Jennings, E., McGinnity, P., O’Dwyer, B., ... Taylor, D.
1647 (2016). The response of North Atlantic diadromous fish to multiple stressors,
1648 including land use change: a multidecadal study. *Canadian Journal of Fisheries and
1649 Aquatic Sciences*, 73(12), 1759–1769. <https://doi.org/10.1139/cjfas-2015-0450>
- 1650 del Villar-Guerra, D., Aarestrup, K., Skov, C., & Koed, A. (2013). Marine migrations in
1651 anadromous brown trout (*Salmo trutta*). Fjord residency as a possible alternative in
1652 the continuum of migration to the open sea. *Ecology of Freshwater Fish*, 23(4), 594–
1653 603. <https://doi.org/10.1111/eff.12110>
- 1654 Dellefors, C. (1996). *Smoltification and sea migration in wild and hatchery-reared brown
1655 trout, Salmo trutta* (Ph.D. thesis). University of Göteborg, Göteborg.
- 1656 Dellefors, C., & Faremo, U. (1988). Early sexual maturation in males of wild sea trout, *Salmo
1657 trutta* L., inhibits smoltification. *Journal of Fish Biology*, 33(5), 741–749.
- 1658 Dieperink, C., Bak, B. D., Pedersen, L.-F., Pedersen, M. I., & Pedersen, S. (2002). Predation
1659 on Atlantic salmon and sea trout during their first days as postsmolts. *Journal of Fish
1660 Biology*, 61(3), 848–852.
- 1661 Dieperink, C., Pedersen, S., & Pedersen, M. I. (2001). Estuarine predation on radiotagged
1662 wild and domesticated sea trout (*Salmo trutta* L.) smolts. *Ecology of Freshwater Fish*,
1663 10(3), 177–183.

- 1664 Dodson, J. J., Aubin-Horth, N., Thériault, V., & Páez, D. J. (2013). The evolutionary ecology
1665 of alternative migratory tactics in salmonid fishes. *Biological Reviews of the*
1666 *Cambridge Philosophical Society*, 88(3), 602–625. <https://doi.org/10.1111/brv.12019>
- 1667 Dominey, W. J. (1984). Alternative mating tactics and evolutionarily stable strategies.
1668 *American Zoologist*, 24(2), 385–396.
- 1669 Egglshaw, H. J., & Shackley, P. E. (1982). Influence of water depth on dispersion of juvenile
1670 salmonids, *Salmo salar* L. and *S. trutta* L., in a Scottish stream. *Journal of Fish*
1671 *Biology*, 21(2), 141–155. <https://doi.org/10.1111/j.1095-8649.1982.tb03995.x>
- 1672 Einum, S., Hendry, A. P., & Fleming, I. A. (2002). Egg-size evolution in aquatic
1673 environments: does oxygen availability constrain size? *Proceedings of the Royal*
1674 *Society of London B: Biological Sciences*, 269(1507), 2325–2330.
- 1675 Eldøy, S. H., Davidsen, J. G., Thorstad, E. B., Whoriskey, F. G., Aarestrup, K., Naesje, T. F.,
1676 ... Arnekleiv, J. V. (2017). Marine depth use of sea trout *Salmo trutta* in fjord areas of
1677 central Norway: marine depth use of *salmo trutta*. *Journal of Fish Biology*, 91, 1268–
1678 1283. <https://doi.org/10.1111/jfb.13463>
- 1679 Elliott, J. M. (1984). Numerical changes and population regulation in young migratory trout
1680 *Salmo trutta* in a Lake District stream, 1966-83. *The Journal of Animal Ecology*, 327–
1681 350.
- 1682 Elliott, J. M. (1993). A 25-year study of production of juvenile sea-trout, *Salmo trutta*, in an
1683 English Lake District stream. *Canadian Special Publication of Fisheries and Aquatic*
1684 *Sciences*, 109–122.
- 1685 Elliott, J. M. (1994). *Quantitative Ecology and the Brown Trout*. Oxford University Press,
1686 USA.
- 1687 Elliott, J. M., & Elliott, J. A. (2010). Temperature requirements of Atlantic salmon *Salmo*
1688 *salar*, brown trout *Salmo trutta* and Arctic charr *Salvelinus alpinus*: predicting the

- 1689 effects of climate change. *Journal of Fish Biology*, 77(8), 1793–1817.
- 1690 <https://doi.org/10.1111/j.1095-8649.2010.02762.x>
- 1691 Elliott, J. M., & Hurley, M. A. (1998). Predicting fluctuations in the size of newly emerged
1692 sea-trout fry in a Lake District stream. *Journal of Fish Biology*, 53(5), 1120–1133.
- 1693 Engqvist, L., & Taborsky, M. (2016). The evolution of genetic and conditional alternative
1694 reproductive tactics. *Proc. R. Soc. B*, 283(1825), 20152945.
- 1695 Esteve, M. (2005). Observations of spawning behaviour in Salmoninae: *Salmo*,
1696 *Oncorhynchus* and *Salvelinus*. *Reviews in Fish Biology and Fisheries*, 15(1–2), 1–21.
- 1697 Euzenat, G., Fournel, F., & Fagard, J. L. (2006). Population dynamics and stock–recruitment
1698 relationship of sea trout in the River Bresle, upper Normandy, France. In *Sea Trout.*
1699 *Biology, Conservation and Management* (pp. 307–323).
- 1700 Euzenat, G., Fournel, F., & Richard, A. (1999). Sea trout (*Salmo trutta* L.) in Normandy and
1701 Picardy. In J.-L. Baglinière & G. Maise (Eds.), *Biology and Ecology of the Brown*
1702 *and Sea Trout* (pp. 175–203). https://doi.org/10.1007/978-1-4471-0775-0_7
- 1703 Evangelista, C., Boiche, A., Lecerf, A., & Cucherousset, J. (2014). Ecological opportunities
1704 and intraspecific competition alter trophic niche specialization in an opportunistic
1705 stream predator. *Journal of Animal Ecology*, 83(5), 1025–1034.
- 1706 <https://doi.org/10.1111/1365-2656.12208>
- 1707 Fahy, E. (1985). *Child of the Tides: a sea trout handbook*. Glendale Press.
- 1708 Fealy, R., Allot, N., Borderick, C., deEyto, E., Dillane, M., Erdil, R. M., ... White, J. (2010).
1709 *RESCALE: Review and Simulate Climate and Catchment Responses at Burrishoole*.
1710 Retrieved from <https://oar.marine.ie/handle/10793/31>
- 1711 Ferguson, A. (2004). The Importance of Identifying Conservation Units: Brown Trout and
1712 Pollan Biodiversity in Ireland. *Biology and Environment: Proceedings of the Royal*
1713 *Irish Academy*, 104B(3), 33–41.

- 1714 Ferguson, A. (2006). Genetics of Sea Trout, with Particular Reference to Britain and Ireland.
1715 In *Sea Trout: Biology, Conservation and Management* (pp. 155–182).
1716 <https://doi.org/10.1002/9780470996027.ch12>
- 1717 Ferguson, A., Reed, T., Cross, T. F., McGinnity, P., & Prodöhl, P. (2019). Anadromy,
1718 potamodromy and residency in brown trout *Salmo trutta*: the role of genes and the
1719 environment. *Journal of Fish Biology*. <https://doi.org/10.1111/jfb.14005>
- 1720 Ferguson, A., Reed, T., McGinnity, P., & Prodöhl, P. (2017). *Anadromy in brown trout*
1721 *(Salmo trutta): A review of the relative roles of genes and environmental factors and*
1722 *the implications for management and conservation*.
- 1723 Finstad, A. G., Forseth, T., Jonsson, B., Bellier, E., Hesthagen, T., Jensen, A. J., ... Foldvik,
1724 A. (2011). Competitive exclusion along climate gradients: energy efficiency
1725 influences the distribution of two salmonid fishes. *Global Change Biology*, *17*(4),
1726 1703–1711.
- 1727 Finstad, A. G., & Jonsson, B. (2012). Effect of incubation temperature on growth
1728 performance in Atlantic salmon. *Marine Ecology Progress Series*, *454*, 75–82.
- 1729 Finstad, B., & Bjørn, P. A. (2011). Present status and implications of salmon lice on wild
1730 salmonids in Norwegian coastal zones. *Salmon Lice: An Integrated Approach to*
1731 *Understanding Parasite Abundance and Distribution*, 279–305.
- 1732 Finstad, B., Kroglund, F., Bjørn, P. A., Nilsen, R., Pettersen, K., Rosseland, B. O., ... Salbu,
1733 B. (2012). Salmon lice-induced mortality of Atlantic salmon postsmolts experiencing
1734 episodic acidification and recovery in freshwater. *Aquaculture*, *362*, 193–199.
- 1735 Finstad, B., Kroglund, F., Strand, R., Stefansson, S. O., Bjørn, P. A., Rosseland, B. O., ...
1736 Salbu, B. (2007). Salmon lice or suboptimal water quality—Reasons for reduced
1737 postsmolt survival? *Aquaculture*, *273*(2–3), 374–383.

- 1738 Fjørtoft, H. B., Besnier, F., Stene, A., Nilsen, F., Bjørn, P. A., Tveten, A.-K., ... Glover, K.
1739 A. (2017). The Phe362Tyr mutation conveying resistance to organophosphates occurs
1740 in high frequencies in salmon lice collected from wild salmon and trout. *Scientific*
1741 *Reports*, 7(1), 14258. <https://doi.org/10.1038/s41598-017-14681-6>
- 1742 Flaten, A. C., Davidsen, J. G., Thorstad, E. B., Whoriskey, F., Rønning, L., Sjørnsen, A. D., ...
1743 Arnekleiv, J. V. (2016). The first months at sea: marine migration and habitat use of
1744 sea trout *Salmo trutta* post-smolts. *Journal of Fish Biology*, 89(3), 1624–1640.
1745 <https://doi.org/10.1111/jfb.13065>
- 1746 Fleming, I. A. (1996). Reproductive strategies of Atlantic salmon: ecology and evolution.
1747 *Reviews in Fish Biology and Fisheries*, 6(4), 379–416.
1748 <https://doi.org/10.1007/BF00164323>
- 1749 Fleming, I. A., & Gross, M. R. (1990). Latitudinal Clines: A Trade-Off between Egg Number
1750 and Size in Pacific Salmon. *Ecology*, 71(1), 1. <https://doi.org/10.2307/1940241>
- 1751 Foote, C. J., Brown, G. S., & Wood, C. C. (1997). Spawning success of males using
1752 alternative mating tactics in sockeye salmon, *Oncorhynchus nerka*. *Canadian Journal*
1753 *of Fisheries and Aquatic Sciences*, 54(8), 1785–1795. <https://doi.org/10.1139/f97-080>
- 1754 Forseth, T., & Jonsson, B. (1994). The Growth and Food Ration of Piscivorous Brown Trout
1755 (*Salmo trutta*). *Functional Ecology*, 8(2), 171–177. <https://doi.org/10.2307/2389900>
- 1756 Forseth, T., Larsson, S., Jensen, A. J., Jonsson, B., Näslund, I., & Berglund, I. (2009).
1757 Thermal growth performance of juvenile brown trout *Salmo trutta*: no support for
1758 thermal adaptation hypotheses. *Journal of Fish Biology*, 74(1), 133–149.
1759 <https://doi.org/10.1111/j.1095-8649.2008.02119.x>
- 1760 Forseth, T., Nesje, T. F., Jonsson, B., & Hårsaker, K. (1999). Juvenile migration in brown
1761 trout: a consequence of energetic state. *Journal of Animal Ecology*, 68(4), 783–793.
1762 <https://doi.org/10.1046/j.1365-2656.1999.00329.x>

- 1763 Frier, J. O. (1994). Growth of Anadromous and Resident Brown Trout with Different Life
1764 Histories in a Danish Lowland Stream. *Nordic Journal of Freshwater Research*, 64,
1765 58–70.
- 1766 Frost, W. E., & Brown, M. E. (1967). *The Trout*. HarperCollins Publishers Limited.
- 1767 Fusco, G., & Minelli, A. (2010). Phenotypic plasticity in development and evolution: facts
1768 and concepts. *Philosophical Transactions of the Royal Society of London B:*
1769 *Biological Sciences*, 365(1540), 547–556. <https://doi.org/10.1098/rstb.2009.0267>
- 1770 Gargan, P. G., Poole, W. R., & Forde, G. P. (2006). A Review of the Status of Irish Sea Trout
1771 Stocks. In *Sea Trout: Biology, Conservation and Management* (pp. 25–44).
1772 <https://doi.org/10.1002/9780470996027.ch3>
- 1773 Gargan, P. G., Tully, O., & Poole, W. R. (2003). Relationship between sea lice infestation,
1774 sea lice production and sea trout survival in Ireland, 1992–2001. *Salmon at the Edge*,
1775 10, 119–135.
- 1776 Gauthey, Z., Lang, M., Elozegi, A., Tentelier, C., Rives, J., & Labonne, J. (2015). Brown
1777 trout spawning habitat selection and its effects on egg survival. *Ecology of*
1778 *Freshwater Fish*, 26(1), 133–140. <https://doi.org/10.1111/eff.12262>
- 1779 Gibson, R. J., & Erkinaro, J. (2009). The influence of water depths and inter-specific
1780 interactions on cover responses of juvenile Atlantic salmon. *Ecology of Freshwater*
1781 *Fish*, 18(4), 629–639.
- 1782 Giger, T., Excoffier, L., Day, P. J. R., Champigneulle, A., Hansen, M. M., Powell, R., &
1783 Largiadèr, C. R. (2006). Life history shapes gene expression in salmonids. *Current*
1784 *Biology: CB*, 16(8), R281-282. <https://doi.org/10.1016/j.cub.2006.03.053>
- 1785 Gilroy, J. J., Gill, J. A., Butchart, S. H., Jones, V. R., & Franco, A. M. (2016). Migratory
1786 diversity predicts population declines in birds. *Ecology Letters*, 19(3), 308–317.

- 1787 Gortázar, J., Alonso, C., & Jalón, D. G. de. (2012). Brown trout redd superimposition in
1788 relation to spawning habitat availability. *Ecology of Freshwater Fish*, 21(2), 283–292.
1789 <https://doi.org/10.1111/j.1600-0633.2011.00546.x>
- 1790 Gosset, C., Rives, J., & Labonne, J. (2006). Effect of habitat fragmentation on spawning
1791 migration of brown trout (*Salmo trutta* L.). *Ecology of Freshwater Fish*, 15(3), 247–
1792 254. <https://doi.org/10.1111/j.1600-0633.2006.00144.x>
- 1793 Graham, C. T., & Harrod, C. (2009). Implications of climate change for the fishes of the
1794 British Isles. *Journal of Fish Biology*, 74(6), 1143–1205.
- 1795 Greenberg, L., Svendsen, P., & Harby, A. (1996). Availability of microhabitats and their use
1796 by brown trout (*Salmo trutta*) and grayling (*Thymallus thymallus*). *Regulated Rivers:
1797 Research and Management* 12: 287-303, 12, 287–303.
- 1798 Gregory, J. S., & Gamett, B. L. (2009). Cattle Trampling of Simulated Bull Trout Redds.
1799 *North American Journal of Fisheries Management*, 29(2), 361–366.
1800 <https://doi.org/10.1577/M08-020.1>
- 1801 Gresswell, R. E., Liss, W. J., & Larson, G. L. (1994). Life-history organization of
1802 Yellowstone cutthroat trout (*Oncorhynchus clarki bouvieri*) in Yellowstone Lake.
1803 *Canadian Journal of Fisheries and Aquatic Sciences*, 51(S1), 298–309.
- 1804 Gross, M. R. (1985). Disruptive selection for alternative life histories in salmon. *Nature*,
1805 313(5997), 47–48. <https://doi.org/10.1038/313047a0>
- 1806 Gross, M. R. (1987). Evolution of diadromy in fishes. *American Fisheries Society
1807 Symposium*, 1, 14–25.
- 1808 Gross, M. R. (1991). Evolution of alternative reproductive strategies: frequency-dependent
1809 sexual selection in male bluegill sunfish. *Phil. Trans. R. Soc. Lond. B*, 332(1262), 59–
1810 66.

- 1811 Gross, M. R., Coleman, R. M., & McDowall, R. M. (1988). Aquatic Productivity and the
1812 Evolution of Diadromous Fish Migration. *Science*, 239(4845), 1291–1293.
1813 <https://doi.org/10.1126/science.239.4845.1291>
- 1814 Halttunen, E., Gjelland, K.-Ø., Hamel, S., Serra-Llinares, R.-M., Nilsen, R., Arechavala-
1815 Lopez, P., ... Finstad, B. (2018). Sea trout adapt their migratory behaviour in
1816 response to high salmon lice concentrations. *Journal of Fish Diseases*, 41(6), 953–
1817 967. <https://doi.org/10.1111/jfd.12749>
- 1818 Haraldstad, T., Höglund, E., Kroglund, F., Lamberg, A., Olsen, E. M., & Haugen, T. O.
1819 (2018). Condition-dependent skipped spawning in anadromous brown trout (*Salmo*
1820 *trutta*). *Canadian Journal of Fisheries and Aquatic Sciences*, 1–7.
1821 <https://doi.org/10.1139/cjfas-2017-0076>
- 1822 Haraldstad, T., Kroglund, F., Kristensen, T., Jonsson, B., & Haugen, T. O. (2017). Diel
1823 migration pattern of Atlantic salmon (*Salmo salar*) and sea trout (*Salmo trutta*)
1824 smolts: an assessment of environmental cues. *Ecology of Freshwater Fish*, 26(4),
1825 541–551. <https://doi.org/10.1111/eff.12298>
- 1826 Harris, G. (2017). *Sea Trout: Science & Management: Proceedings of the 2nd International*
1827 *Sea Trout Symposium*. S.l.: Matador.
- 1828 Harris, G., & Milner, N. (2006). *Sea Trout: Biology, Conservation and Management*. John
1829 Wiley & Sons.
- 1830 Harrison, L. R., Legleiter, C. J., Wydzga, M. A., & Dunne, T. (2011). Channel dynamics and
1831 habitat development in a meandering, gravel bed river. *Water Resources Research*,
1832 47(4).
- 1833 Harwood, A. J., Metcalfe, N. B., Armstrong, J. D., & Griffiths, S. W. (2001). Spatial and
1834 temporal effects of interspecific competition between Atlantic salmon (*Salmo salar*)

- 1835 and brown trout (*Salmo trutta*) in winter. *Canadian Journal of Fisheries and Aquatic*
1836 *Sciences*, 58(6), 1133–1140.
- 1837 Haury, J., Ombredane, D., & Baglinière, J.-L. (1999). The habitat of the brown trout (*Salmo*
1838 *trutta* L.) in water courses. In *Biology and ecology of the brown and sea trout* (pp.
1839 37–89). Springer.
- 1840 Hearn, W. E. (1987). Interspecific competition and habitat segregation among stream-
1841 dwelling trout and salmon: a review. *Fisheries*, 12(5), 24–31.
- 1842 Heggberget, T. G. (1984). Habitat selection and segregation of parr of Arctic charr
1843 (*Salvelinus alpinus*), brown trout (*Salmo trutta*) and Atlantic salmon (*Salmo salar* L.)
1844 in two streams in North Norway. *Biology of the Arctic Charr*, 217–231.
- 1845 Heggenes, J., Baglinière, J.-L., & Cunjak, R. A. (1999). Spatial niche variability for young
1846 Atlantic salmon (*Salmo salar*) and brown trout (*S. trutta*) in heterogeneous streams.
1847 *Ecology of Freshwater Fish*, 8(1), 1–21.
- 1848 Hendry, A. P., & Day, T. (2003). Revisiting the positive correlation between female size and
1849 egg size. *Evolutionary Ecology Research*, 5(3), 421–429.
- 1850 Henrikson, L., & Brodin, Y.-W. (1995). Liming of surface waters in Sweden — a synthesis.
1851 In *Liming of Acidified Surface Waters* (pp. 1–44). [https://doi.org/10.1007/978-3-642-](https://doi.org/10.1007/978-3-642-79309-7_1)
1852 [79309-7_1](https://doi.org/10.1007/978-3-642-79309-7_1)
- 1853 Hesse, C. (1935). Gotlands Havlaxöring. *Kungl Lantbruksstyrelsen*, (7), 1–12.
- 1854 Hesthagen, T., & Heggenes, J. (2003). Competitive habitat displacement of brown trout by
1855 Siberian sculpin: the role of size and density. *Journal of Fish Biology*, 62(1), 222–
1856 236.
- 1857 Hesthagen, T., Larsen, B. M., Bolstad, G., Fiske, P., & Jonsson, B. (2017). Mitigation of
1858 acidified salmon rivers—effects of liming on young brown trout *Salmo trutta*. *Journal*
1859 *of Fish Biology*, 91(5), 1350–1364.

- 1860 Heywood, M. J. T., & Walling, D. E. (2007). The sedimentation of salmonid spawning
1861 gravels in the Hampshire Avon catchment, UK: implications for the dissolved oxygen
1862 content of intragravel water and embryo survival. *Hydrological Processes*, 21(6),
1863 770–788. <https://doi.org/10.1002/hyp.6266>
- 1864 Hindar, K., Jonsson, B., Ryman, N., & Ståhl, G. (1991). Genetic relationships among
1865 landlocked, resident, and anadromous Brown Trout, *Salmo trutta* L. *Heredity*, 66(1),
1866 83–91. <https://doi.org/10.1038/hdy.1991.11>
- 1867 Höjesjö, J., Stradmeyer, L., Griffiths, S., & Armstrong, J. (2010). Effects of Competing
1868 Brown Trout on Habitat Use by Atlantic Salmon Parr: Controlled Investigations in a
1869 Laboratory Stream. In *Salmonid Fisheries* (pp. 194–208).
1870 <https://doi.org/10.1002/9781444323337.ch9>
- 1871 Holmen, J., Olsen, E. M., & Vøllestad, L. A. (2003). Interspecific competition between
1872 stream-dwelling brown trout and Alpine bullhead. *Journal of Fish Biology*, 62(6),
1873 1312–1325.
- 1874 Houde, A. L. S., Wilson, C. C., & Neff, B. D. (2017). Performance of four salmonids species
1875 in competition with Atlantic salmon. *Journal of Great Lakes Research*, 43(1), 211–
1876 215.
- 1877 Hughes, M. R., Hooker, O. E., Leeuwen, T. E. V., Kettle-White, A., Thorne, A., Prodöhl, P.,
1878 & Adams, C. E. (2019). Alternative routes to piscivory: Contrasting growth
1879 trajectories in brown trout (*Salmo trutta*) ecotypes exhibiting contrasting life history
1880 strategies. *Ecology of Freshwater Fish*, 28(1), 4–10. <https://doi.org/10.1111/eff.12421>
- 1881 Hutchings, J. A., & Myers, R. A. (1985). Mating between anadromous and nonanadromous
1882 Atlantic salmon, *Salmo salar*. *Canadian Journal of Zoology*, 63(9), 2219–2221.
- 1883 Hutchings, J. A., & Myers, R. A. (1994). The evolution of alternative mating strategies in
1884 variable environments. *Evolutionary Ecology*, 8(3), 256–268.

- 1885 ICES. (1997). *Report of the Workshop on the Interactions between salmon lice and salmonids*
1886 (No. ICES CM 1997/M:4 Ref.:F). Edinburgh, United Kingdom, 11-15 November
1887 1996.
- 1888 ICES. (2018). *Report of the Baltic Salmon and Trout Assessment Working Group (WGBAST)*
1889 (p. 371p). Turku, Finland.
- 1890 IPCC. (2013). *Climate change 2013: the physical science basis. Contribution of Working*
1891 *Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate*
1892 *Change. K., Tignor, M., Allen, SK, Boschung, J., Nauels, A., Xia, Y., Bex, V., and*
1893 *Midgley, PM, Cambridge University Press Cambridge, United Kingdom and New*
1894 *York, NY, USA.*
- 1895 Jensen, A. J., Finstad, B., Fiske, P., Hvidsten, N. A., Rikardsen, A. H., & Saksgård, L.
1896 (2012). Timing of smolt migration in sympatric populations of Atlantic salmon
1897 (*Salmo salar*), brown trout (*Salmo trutta*), and Arctic char (*Salvelinus alpinus*).
1898 *Canadian Journal of Fisheries and Aquatic Sciences*, 69(4), 711–723.
- 1899 Jensen, J. L. A., & Rikardsen, A. H. (2012). Archival tags reveal that Arctic charr *Salvelinus*
1900 *alpinus* and brown trout *Salmo trutta* can use estuarine and marine waters during
1901 winter. *Journal of Fish Biology*, 81(2), 735–749.
- 1902 Jensen, K. W. (1968). *Seatrout (Salmo trutta, L.) of the River Istra, western Norway*. National
1903 Swedish Board of Fisheries.
- 1904 Jensen, L. F., Hansen, M. M., Pertoldi, G., Holdensgaard, G., Mensberg, K. D., & Loeschcke,
1905 V. (2008). Local adaptation in brown trout early life-history traits: implications for
1906 climate change adaptability. *Proceedings of the Royal Society B: Biological Sciences*,
1907 275(1653), 2859–2868. <https://doi.org/10.1098/rspb.2008.0870>

- 1908 Jepsen, N., Holthe, E., & Økland, F. (2006). Observations of predation on salmon and trout
1909 smolts in a river mouth. *Fisheries Management and Ecology*, *13*(5), 341–343.
1910 <https://doi.org/10.1111/j.1365-2400.2006.00509.x>
- 1911 Johnsson, J. I., Rydeborg, A., & Sundström, L. F. (2004). Predation risk and the territory
1912 value of cover: an experimental study. *Behavioral Ecology and Sociobiology*, *56*(4),
1913 388–392. <https://doi.org/10.1007/s00265-004-0791-8>
- 1914 Jones, D. A., Bergman, E., & Greenberg, L. (2015). Food availability in spring affects
1915 smolting in brown trout (*Salmo trutta*). *Canadian Journal of Fisheries and Aquatic*
1916 *Sciences*, *72*(11), 1694–1699. <https://doi.org/10.1139/cjfas-2015-0106>
- 1917 Jones, J. I., Murphy, J. F., Collins, A. L., Sear, D. A., Naden, P. S., & Armitage, P. D. (2012).
1918 The impact of fine sediment on macro-invertebrates. *River Research and*
1919 *Applications*, *28*(8), 1055–1071.
- 1920 Jonsson, B. (1981). *Life History Strategies of Trout (Salmo Trutta L)*. (PhD Thesis).
1921 University of Oslo Oslo, Norway.
- 1922 Jonsson, B. (1982). Diadromous and Resident Trout *Salmo trutta*: Is Their Difference Due to
1923 Genetics? *Oikos*, *38*(3), 297–300. <https://doi.org/10.2307/3544668>
- 1924 Jonsson, B. (1985). Life history patterns of freshwater resident and sea-run migrant brown
1925 trout in Norway. *Transactions of the American Fisheries Society*, *114*(2), 182–194.
- 1926 Jonsson, B. (1989). Life history and habitat use of Norwegian brown trout (*Salmo trutta*).
1927 *Freshwater Biology*, *21*(1), 71–86. <https://doi.org/10.1111/j.1365->
1928 [2427.1989.tb01349.x](https://doi.org/10.1111/j.1365-2427.1989.tb01349.x)
- 1929 Jonsson, B., Jonsson, M., & Jonsson, N. (2017). Influences of migration phenology on
1930 survival are size-dependent in juvenile Atlantic salmon (*Salmo salar*). *Canadian*
1931 *Journal of Zoology*, *95*(8), 581–587. <https://doi.org/10.1139/cjz-2016-0136>

- 1932 Jonsson, B., & Jonsson, N. (1993). Partial migration: niche shift versus sexual maturation in
1933 fishes. *Reviews in Fish Biology and Fisheries*, 3(4), 348–365.
1934 <https://doi.org/10.1007/BF00043384>
- 1935 Jonsson, B., & Jonsson, N. (2005). Lipid energy reserves influence life-history decision of
1936 Atlantic salmon (*Salmo salar*) and brown trout (*S. trutta*) in fresh water. *Ecology of*
1937 *Freshwater Fish*, 14(3), 296–301. <https://doi.org/10.1111/j.1600-0633.2005.00098.x>
- 1938 Jonsson, B., & Jonsson, N. (2006a). *Life history of the anadromous trout Salmo trutta* (Vol.
1939 14). Chapter.
- 1940 Jonsson, B., & Jonsson, N. (2006b). Life-history effects of migratory costs in anadromous
1941 brown trout. *Journal of Fish Biology*, 69(3), 860–869. [https://doi.org/10.1111/j.1095-](https://doi.org/10.1111/j.1095-8649.2006.01160.x)
1942 [8649.2006.01160.x](https://doi.org/10.1111/j.1095-8649.2006.01160.x)
- 1943 Jonsson, B., & Jonsson, N. (2009a). A review of the likely effects of climate change on
1944 anadromous Atlantic salmon *Salmo salar* and brown trout *Salmo trutta*, with
1945 particular reference to water temperature and flow. *Journal of Fish Biology*, 75(10),
1946 2381–2447. <https://doi.org/10.1111/j.1095-8649.2009.02380.x>
- 1947 Jonsson, B., & Jonsson, N. (2009b). Migratory timing, marine survival and growth of
1948 anadromous brown trout *Salmo trutta* in the River Imsa, Norway. *Journal of Fish*
1949 *Biology*, 74(3), 621–638. <https://doi.org/10.1111/j.1095-8649.2008.02152.x>
- 1950 Jonsson, B., & Jonsson, N. (2011). *Ecology of Atlantic Salmon and Brown Trout. Habitat as*
1951 *a template for life histories*. Dordrecht: Springer Netherlands.
- 1952 Jonsson, B., & Jonsson, N. (2014). Naturally and hatchery produced European trout *Salmo*
1953 *trutta*: do their marine survival and dispersal differ? *Journal of Coastal Conservation*,
1954 18(2), 79–87.
- 1955 Jonsson, B., & Jonsson, N. (2015). Sexual size dimorphism in anadromous brown trout
1956 *Salmo trutta*. *Journal of Fish Biology*, 87(1), 187–193.

- 1957 Jonsson, B., & Jonsson, N. (2016). Trans-generational maternal effect: temperature
1958 influences egg size of the offspring in Atlantic salmon *Salmo salar*. *Journal of Fish*
1959 *Biology*, 89(2), 1482–1487. <https://doi.org/10.1111/jfb.13040>
- 1960 Jonsson, B., & Jonsson, N. (2018). Egg incubation temperature affects the timing of the
1961 Atlantic salmon *Salmo salar* homing migration. *Journal of Fish Biology*, 93(5), 1016–
1962 1020. <https://doi.org/10.1111/jfb.13817>
- 1963 Jonsson, B., & Jonsson, N. (2019). Phenotypic plasticity and epigenetics of fish: embryo
1964 temperature affects later developing traits. *Aquatic Biology*, 28, 21–32.
- 1965 Jonsson, B., Jonsson, N., & Albrechtsen, J. (2016). Environmental change influences the life
1966 history of salmon *Salmo salar* in the North Atlantic Ocean: *salmo salar* at sea.
1967 *Journal of Fish Biology*, n/a-n/a. <https://doi.org/10.1111/jfb.12854>
- 1968 Jonsson, B., Jonsson, N., Brodtkorb, E., & Ingebrigtsen, P.-J. (2001). Life-history traits of
1969 Brown Trout vary with the size of small streams. *Functional Ecology*, 15(3), 310–
1970 317.
- 1971 Jonsson, B., Jonsson, N., & Finstad, A. G. (2013). Effects of temperature and food quality on
1972 age and size at maturity in ectotherms: an experimental test with Atlantic salmon.
1973 *Journal of Animal Ecology*, 82(1), 201–210. <https://doi.org/10.1111/j.1365->
1974 [2656.2012.02022.x](https://doi.org/10.1111/j.1365-2656.2012.02022.x)
- 1975 Jonsson, B., Jonsson, N., & Finstad, A. G. (2014). Linking embryonic temperature with adult
1976 reproductive investment in Atlantic salmon *Salmo salar*. *Marine Ecology Progress*
1977 *Series*, 515, 217–226.
- 1978 Jonsson, B., Jonsson, N., & Jonsson, M. (2018). Water level influences migratory patterns of
1979 anadromous brown trout in small streams. *Ecology of Freshwater Fish*.
1980 <https://doi.org/10.1111/eff.12415>

- 1981 Jonsson, B., Jonsson, N., & Ugedal, O. (2011). Production of juvenile salmonids in small
1982 Norwegian streams is affected by agricultural land use. *Freshwater Biology*, *56*(12),
1983 2529–2542. <https://doi.org/10.1111/j.1365-2427.2011.02678.x>
- 1984 Jonsson, B., & Ruud-Hansen, J. (1985). Water Temperature as the Primary Influence on
1985 Timing of Seaward Migrations of Atlantic Salmon (*Salmo salar*) Smolts. *Canadian*
1986 *Journal of Fisheries and Aquatic Sciences*, *42*(3), 593–595.
1987 <https://doi.org/10.1139/f85-076>
- 1988 Jonsson, B., & Sandlund, O. T. (1979). Environmental factors and life histories of isolated
1989 river stocks of brown trout (*Salmo trutta m. fario*) in Søre Osa river system, Norway.
1990 *Environmental Biology of Fishes*, *4*(1), 43–54. <https://doi.org/10.1007/BF00005927>
- 1991 Jonsson, N., & Jonsson, B. (1997a). Energy allocation in polymorphic Brown Trout.
1992 *Functional Ecology*, *11*(3), 310–317. <https://doi.org/10.1046/j.1365->
1993 [2435.1997.00083.x](https://doi.org/10.1046/j.1365-2435.1997.00083.x)
- 1994 Jonsson, N., & Jonsson, B. (1997b). Energy allocation in polymorphic Brown Trout.
1995 *Functional Ecology*, *11*(3), 310–317. <https://doi.org/10.1046/j.1365->
1996 [2435.1997.00083.x](https://doi.org/10.1046/j.1365-2435.1997.00083.x)
- 1997 Jonsson, N., & Jonsson, B. (1998). Body composition and energy allocation in life-history
1998 stages of brown trout. *Journal of Fish Biology*, *53*(6), 1306–1316.
1999 <https://doi.org/10.1111/j.1095-8649.1998.tb00250.x>
- 2000 Jonsson, N., & Jonsson, B. (1999). Trade-off between egg mass and egg number in brown
2001 trout. *Journal of Fish Biology*, *55*(4), 767–783.
- 2002 Jonsson, N., & Jonsson, B. (2002). Migration of anadromous brown trout *Salmo trutta* in a
2003 Norwegian river. *Freshwater Biology*, *47*(8), 1391–1401.

- 2004 Jonsson, N., Jonsson, B., & Hansen, L. P. (1994). Sea-ranching of brown trout, *Salmo trutta*
2005 L. *Fisheries Management and Ecology*, 1(1), 67–76. <https://doi.org/10.1111/j.1365->
2006 2400.1970.tb00007.x
- 2007 Jonsson, N., Jonsson, B., & Hansen, L. P. (1998). Long-term study of the ecology of wild
2008 Atlantic salmon smolts in a small Norwegian river. *Journal of Fish Biology*, 52(3),
2009 638–650.
- 2010 Jonsson, N., Jonsson, B., Hansen, L. P., & Aass, P. (1994). Effects of seawater-
2011 acclimatization and release sites on survival of hatchery-reared brown trout *Salmo*
2012 *trutta*. *Journal of Fish Biology*, 44(6), 973–981. <https://doi.org/10.1111/j.1095->
2013 8649.1994.tb01269.x
- 2014 Kalleberg, H. (1958). Observations in a stream tank of territoriality and competition in
2015 juvenile salmon and trout. *Rep. Inst. Freshw. Res. Drottningholm*, 39, 55–98.
- 2016 Kano, Y., Shimizu, Y., & Kondou, K. (2006). Status-dependent female mimicry in
2017 landlocked red-spotted masu salmon. *Journal of Ethology*, 24(1), 1–7.
- 2018 Karlström, Ö. (1977). Habitat selection and population densities of salmon (*Salmo salar* L.)
2019 and trout (*Salmo trutta* L.) parr in Swedish rivers with some reference to human
2020 activities. *Abstracts of Uppsala Dissertations from the Faculty of Science (Sweden)*.
2021 No. 404.
- 2022 Keenleyside, M. H., & Dupuis, H. M. (1988). Courtship and spawning competition in pink
2023 salmon (*Oncorhynchus gorbuscha*). *Canadian Journal of Zoology*, 66(1), 262–265.
- 2024 Keller, I., Taverna, A., & Seehausen, O. (2011). A pyrosequencing assay for the rapid
2025 discrimination of mitochondrial lineages in the *Salmo trutta* species complex.
2026 *Molecular Ecology Resources*, 11(1), 196–199. <https://doi.org/10.1111/j.1755->
2027 0998.2010.02897.x

- 2028 Kendall, N. W., McMillan, J. R., Sloat, M. R., Buehrens, T. W., Quinn, T. P., Pess, G. R., ...
2029 Zabel, R. W. (2014). Anadromy and residency in steelhead and rainbow trout
2030 (*Oncorhynchus mykiss*): a review of the processes and patterns. *Canadian Journal of*
2031 *Fisheries and Aquatic Sciences*, 72(3), 319–342. [https://doi.org/10.1139/cjfas-2014-](https://doi.org/10.1139/cjfas-2014-0192)
2032 0192
- 2033 Kennedy, G. J. A., & Strange, C. D. (1986). The effects of intra-and inter-specific
2034 competition on the survival and growth of stocked juvenile Atlantic salmon, *Salmo*
2035 *solar* L., and resident trout, *Salmo trutta* L., in an upland stream. *Journal of Fish*
2036 *Biology*, 28(4), 479–489.
- 2037 Klemetsen, A., Amundsen, P.-A., Dempson, J. B., Jonsson, B., Jonsson, N., O'connell, M. F.,
2038 & Mortensen, E. (2003). Atlantic salmon *Salmo salar* L., brown trout *Salmo trutta* L.
2039 and Arctic charr *Salvelinus alpinus* (L.): a review of aspects of their life histories.
2040 *Ecology of Freshwater Fish*, 12(1), 1–59.
- 2041 Knudsen, C. M., Johnston, M. V., Schroder, S. L., Bosch, W. J., Fast, D. E., & Strom, C. R.
2042 (2009). Effects of Passive Integrated Transponder Tags on Smolt-to-Adult Recruit
2043 Survival, Growth, and Behavior of Hatchery Spring Chinook Salmon. *North*
2044 *American Journal of Fisheries Management*, 29(3), 658–669.
2045 <https://doi.org/10.1577/M07-020.1>
- 2046 Knutsen, J. A., Knutsen, H., Gjørseter, J., & Jonsson, B. (2001). Food of anadromous brown
2047 trout at sea. *Journal of Fish Biology*, 59(3), 533–543. [https://doi.org/10.1111/j.1095-](https://doi.org/10.1111/j.1095-8649.2001.tb02359.x)
2048 8649.2001.tb02359.x
- 2049 Kondolf, G. M., & Wolman, M. G. (1993). The sizes of salmonid spawning gravels. *Water*
2050 *Resources Research*, 29(7), 2275–2285. <https://doi.org/10.1029/93WR00402>

- 2051 Kristensen, M. L., Righton, D., del Villar-Guerra, D., Baktoft, H., & Aarestrup, K. (2018).
2052 Temperature and depth preferences of adult sea trout *Salmo trutta* during the marine
2053 migration phase. *Marine Ecology Progress Series*, 599, 209–224.
- 2054 Krkošek, M., Revie, C. W., Gargan, P. G., Skilbrei, O. T., Finstad, B., & Todd, C. D. (2013).
2055 Impact of parasites on salmon recruitment in the Northeast Atlantic Ocean. *Proc. R.*
2056 *Soc. B*, 280(1750), 20122359. <https://doi.org/10.1098/rspb.2012.2359>
- 2057 Kroglund, F., Finstad, B., Stefansson, S. O., Nilsen, T. O., Kristensen, T., Rosseland, B. O.,
2058 ... Salbu, B. (2007). Exposure to moderate acid water and aluminum reduces Atlantic
2059 salmon post-smolt survival. *Aquaculture*, 273(2), 360–373.
2060 <https://doi.org/10.1016/j.aquaculture.2007.10.018>
- 2061 L’Abee-Lund, J. H., Jonsson, B., Jensen, A. J., Sættem, L. M., Heggberget, T. G., Johnsen,
2062 B. O., & Naesje, T. F. (1989). Latitudinal Variation in Life-History Characteristics of
2063 Sea-Run Migrant Brown Trout *Salmo trutta*. *The Journal of Animal Ecology*, 58(2),
2064 525. <https://doi.org/10.2307/4846>
- 2065 Landergren, P. (2001). Survival and growth of sea trout parr in fresh and brackish water.
2066 *Journal of Fish Biology*, 58(2), 591–593.
- 2067 Landergren, P. (2004). Factors affecting early migration of sea trout *Salmo trutta* parr to
2068 brackish water. *Fisheries Research*, 67(3), 283–294.
2069 <https://doi.org/10.1016/j.fishres.2003.10.005>
- 2070 Landergren, P. (2005). Survival and growth of sea trout parr in fresh and brackish water.
2071 *Journal of Fish Biology*, 58(2), 591–593. [https://doi.org/10.1111/j.1095-](https://doi.org/10.1111/j.1095-8649.2001.tb02275.x)
2072 [8649.2001.tb02275.x](https://doi.org/10.1111/j.1095-8649.2001.tb02275.x)
- 2073 Landergren, P., & Vallin, L. (1998). Spawning of sea trout, *Salmo trutta* L., in brackish
2074 waters—lost effort or successful strategy? *Fisheries Research*, 35(3), 229–236.
2075 [https://doi.org/10.1016/S0165-7836\(98\)00073-3](https://doi.org/10.1016/S0165-7836(98)00073-3)

- 2076 Langeland, A., L'Abée-Lund, J. H., Jonsson, B., & Jonsson, N. (1991). Resource partitioning
2077 and niche shift in Arctic charr *Salvelinus alpinus* and brown trout *Salmo trutta*. *The*
2078 *Journal of Animal Ecology*, 895–912.
- 2079 Larinier, M. (2002). Fish passage through culverts, rock weirs and estuarine obstructions.
2080 *Bulletin Français de La Pêche et de La Pisciculture*, (364 supplément), 119–134.
2081 <https://doi.org/10.1051/kmae/2002097>
- 2082 Larios-López, J. E., de Figueroa, J. M. T., Galiana-García, M., Gortázar, J., & Alonso, C.
2083 (2015). Extended spawning in brown trout (*Salmo trutta*) populations from the
2084 Southern Iberian Peninsula: the role of climate variability. *Journal of Limnology*,
2085 74(2).
- 2086 Larsson, S., Serrano, I., & Eriksson, L.-O. (2011). ools. *Canadian Journal of Fisheries and*
2087 *Aquatic Sciences*, 69(1), 1–12. <https://doi.org/10.1139/f2011-128>
- 2088 Lassalle, G., & Rochard, E. (2009). Impact of twenty-first century climate change on
2089 diadromous fish spread over Europe, North Africa and the Middle East. *Global*
2090 *Change Biology*, 15(5), 1072–1089.
- 2091 Lauridsen, R. B., Moore, A., Gregory, S. D., Beaumont, W. R. C., Privitera, L., & Kavanagh,
2092 J. A. (2017). Migration behaviour and loss rate of trout smolts in the transitional zone
2093 between freshwater and saltwater. In *Sea Trout: Science & Management* (pp. 292–
2094 307).
- 2095 Lecomte, F., Beall, E., Chat, J., Davaine, P., & Gaudin, P. (2013). The complete history of
2096 salmonid introductions in the Kerguelen Islands, Southern Ocean. *Polar Biology*,
2097 36(4), 457–475. <https://doi.org/10.1007/s00300-012-1281-5>
- 2098 Lemopoulos, A., Uusi-Heikkilä, S., Huusko, A., Vasemägi, A., Vainikka, A., & Yi, S.
2099 (2018). Comparison of Migratory and Resident Populations of Brown Trout Reveals

- 2100 Candidate Genes for Migration Tendency. *Genome Biology and Evolution*, 10(6),
2101 1493–1503. <https://doi.org/10.1093/gbe/evy102>
- 2102 Lemopoulos, A., Uusi-Heikkilä, S., Vasemägi, A., Huusko, A., Kokko, H., & Vainikka, A.
2103 (2017). Genome-wide divergence patterns support fine-scaled genetic structuring
2104 associated with migration tendency in brown trout. *Canadian Journal of Fisheries
2105 and Aquatic Sciences*, 75(10), 1680–1692. <https://doi.org/10.1139/cjfas-2017-0014>
- 2106 Limburg, K. E., Landergren, P., Westin, L., Elfman, M., & Kristiansson, P. (2001). Flexible
2107 modes of anadromy in Baltic sea trout: making the most of marginal spawning
2108 streams. *Journal of Fish Biology*, 59(3), 682–695. [https://doi.org/10.1111/j.1095-
2109 8649.2001.tb02372.x](https://doi.org/10.1111/j.1095-8649.2001.tb02372.x)
- 2110 Linnaeus, C. (1758). *Systema naturae*, Vol. 1. *Systema naturae, Vol. 1.*
- 2111 Lobón-Cerviá, J. (2007). Numerical changes in stream-resident brown trout (*Salmo trutta*):
2112 uncovering the roles of density-dependent and density-independent factors across
2113 space and time. *Canadian Journal of Fisheries and Aquatic Sciences*, 64(10), 1429–
2114 1447. <https://doi.org/10.1139/f07-111>
- 2115 Lobón-Cerviá, J., Rasmussen, G. H., & Mortensen, E. (2017). Discharge-Dependent
2116 Recruitment in Stream-Spawning Brown Trout. In J. Lobón-Cerviá & N. Sanz (Eds.),
2117 *Brown Trout* (pp. 297–318). <https://doi.org/10.1002/9781119268352.ch13>
- 2118 Lobón-Cerviá, J., & Sanz, N. (2017). *Brown Trout: Biology, Ecology and Management*. John
2119 Wiley & Sons.
- 2120 Maise, G., & Baglinière, J.-L. (1990). The biology of brown trout, *Salmo trutta* L., in the
2121 River Scorff, Brittany: a synthesis of studies from 1973 to 1984. *Aquaculture
2122 Research*, 21(1), 95–106. <https://doi.org/10.1111/j.1365-2109.1990.tb00385.x>

- 2123 Maise, G., & Baglinière, J.-L. (1999). Biology of the brown trout (*Salmo trutta* L.) in French
2124 rivers. In J.-L. Baglinière & G. Maise (Eds.), *Biology and Ecology of the Brown and*
2125 *Sea Trout* (pp. 15–35). https://doi.org/10.1007/978-1-4471-0775-0_2
- 2126 Maise, G., Mourot, B., Breton, B., Fostier, A., Marcuzzi, O., Le Bail, P. Y., ... Richard, A.
2127 (1991). Sexual maturity in sea trout, *Salmo trutta* L., running up the River Calonne
2128 (Normandy, France) at the ‘finnock’ stage. *Journal of Fish Biology*, 39(5), 705–715.
- 2129 Mäki-Petäys, A., Vehanen, T., & Muotka, T. (2000). Microhabitat use by age-0 brown trout
2130 and grayling: seasonal responses to streambed restoration under different flows.
2131 *Transactions of the American Fisheries Society*, 129(3), 771–781.
- 2132 Marco-Rius, F., Caballero, P., Moran, P., & Leaniz, C. G. de. (2012). And the Last Shall Be
2133 First: Heterochrony and Compensatory Marine Growth in Sea Trout (*Salmo trutta*).
2134 *PLOS ONE*, 7(10), e45528. <https://doi.org/10.1371/journal.pone.0045528>
- 2135 Marco-Rius, F., Caballero, P., Moran, P., & Leaniz, C. G. de. (2013). Can migrants escape
2136 from density dependence? *Ecology and Evolution*, 3(8), 2524–2534.
2137 <https://doi.org/10.1002/ece3.652>
- 2138 Massa, F., Baglinière, J.-L., Prunet, P., & Grimaldi, C. (2000). Survie embryo-larvaire de la
2139 truite (*Salmo trutta*) et conditions chimiques dans la frayère | French Ichthyological
2140 Society - Cybium. *Cybium*, 24(3), 129–140.
- 2141 McCormick, S. D., Hansen, L. P., Quinn, T. P., & Saunders, R. L. (1998). Movement,
2142 migration, and smolting of Atlantic salmon (*Salmo salar*). *Canadian Journal of*
2143 *Fisheries and Aquatic Sciences*, 55(S1), 77–92. <https://doi.org/10.1139/d98-011>
- 2144 McCormick, S. D., Shrimpton, J. M., & Zydlewski, J. D. (1996). *Temperature effects on*
2145 *osmoregulatory physiology of juvenile anadromous fish*.
- 2146 McKeown, N. J., Hynes, R. A., Duguid, R. A., Ferguson, A., & Prodöhl, P. A. (2010).
2147 Phylogeographic structure of brown trout *Salmo trutta* in Britain and Ireland: glacial

- 2148 refugia, postglacial colonization and origins of sympatric populations. *Journal of Fish*
2149 *Biology*, 76(2), 319–347. <https://doi.org/10.1111/j.1095-8649.2009.02490.x>
- 2150 McLean, J. E., Bentzen, P., & Quinn, T. P. (2004). Does Size Matter? Fitness-Related Factors
2151 in Steelhead Trout Determined by Genetic Parentage Assignment. *Ecology*, 85(11),
2152 2979–2985. <https://doi.org/10.1890/03-0488>
- 2153 McMillan, J. R., Katz, S. L., & Pess, G. R. (2007). Observational evidence of spatial and
2154 temporal structure in a sympatric anadromous (winter steelhead) and resident rainbow
2155 trout mating system on the Olympic Peninsula, Washington. *Transactions of the*
2156 *American Fisheries Society*, 136(3), 736–748.
- 2157 McNeil, W. J. (1964). Redd superimposition and egg capacity of pink salmon spawning beds.
2158 *Journal of the Fisheries Board of Canada*, 21(6), 1385–1396.
- 2159 Meier, K., Hansen, M. M., Bekkevold, D., Skaala, Ø., & Mensberg, K. D. (2011). An
2160 assessment of the spatial scale of local adaptation in brown trout (*Salmo trutta* L.):
2161 footprints of selection at microsatellite DNA loci. *Heredity*, 106(3), 488.
- 2162 Meland, S., Borgstrøm, R., Heier, L. S., Rosseland, B. O., Lindholm, O., & Salbu, B. (2010).
2163 Chemical and ecological effects of contaminated tunnel wash water runoff to a small
2164 Norwegian stream. *Science of The Total Environment*, 408(19), 4107–4117.
2165 <https://doi.org/10.1016/j.scitotenv.2010.05.034>
- 2166 Mills, C. P. R., Mahon, G. A. T., & Piggins, D. J. (1986). Influence of stock levels, fishing
2167 effort and environmental factors on anglers' catches of Atlantic salmon, *Salmo salar*
2168 L., and sea trout, *Salmo trutta* L. *Aquaculture Research*, 17(4), 289–297.
- 2169 Mills, C. P. R., Piggins, D. J., & Cross, T. F. (1990). Burrishoole sea trout—a twenty year
2170 study. *20th Annual Study Course Proceedings*, 61–78.
- 2171 Milner, N. J., Harris, G., Gargan, P., Beveridge, M., Pawson, M. G., Walker, A., & Whelan,
2172 K. F. (2007). Perspectives on Sea Trout Science and Management. In *Sea Trout:*

- 2173 *Biology, Conservation and Management* (pp. 480–490).
2174 <https://doi.org/10.1002/9780470996027.ch34>
- 2175 Montgomery, D. R., Buffington, J. M., Peterson, N. P., Schuett-Hames, D., & Quinn, T. P.
2176 (1996). *Stream-bed scour, egg burial depths, and the influence of salmonid spawning*
2177 *on bed surface mobility and embryo survival*. 53, 10.
- 2178 Montorio, L., Evanno, G., & Nevoux, M. (2018). Intra- and interspecific densities shape life-
2179 history traits in a salmonid population. *Oecologia*, 188(2), 451–464.
2180 <https://doi.org/10.1007/s00442-018-4213-4>
- 2181 Moore, A., Lower, N., Mayer, I., & Greenwood, L. (2007). The impact of a pesticide on
2182 migratory activity and olfactory function in Atlantic salmon (*Salmo salar* L.) smolts.
2183 *Aquaculture*, 273(2), 350–359. <https://doi.org/10.1016/j.aquaculture.2007.10.017>
- 2184 Moore, I., Dodd, J. A., Newton, M., Bean, C. W., Lindsay, I., Jarosz, P., & Adams, C. E.
2185 (2018). The influence of aquaculture unit proximity on the pattern of *Lepeophtheirus*
2186 *salmonis* infection of anadromous *Salmo trutta* populations on the isle of Skye,
2187 Scotland. *Journal of Fish Biology*, 92(6), 1849–1865.
2188 <https://doi.org/10.1111/jfb.13625>
- 2189 Moran, P., Marco-Rius, F., Megías, M., Covelo-Soto, L., & Pérez-Figueroa, A. (2013).
2190 Environmental induced methylation changes associated with seawater adaptation in
2191 brown trout. *Aquaculture*, 392–395(Supplement C), 77–83.
2192 <https://doi.org/10.1016/j.aquaculture.2013.02.006>
- 2193 Moran, P., & Pérez-Figueroa, A. (2011). Methylation changes associated with early
2194 maturation stages in the Atlantic salmon. *BMC Genetics*, 12(1), 86.
2195 <https://doi.org/10.1186/1471-2156-12-86>
- 2196 Morinville, G. R., & Rasmussen, J. B. (2003). Early juvenile bioenergetic differences
2197 between anadromous and resident brook trout (*Salvelinus fontinalis*). *Canadian*

- 2198 *Journal of Fisheries and Aquatic Sciences*, 60(4), 401–410.
- 2199 <https://doi.org/10.1139/f03-036>
- 2200 Morita, K., Fukuwaka, M., Tanimata, N., & Yamamura, O. (2010). Size-dependent thermal
2201 preferences in a pelagic fish. *Oikos*, 119(8), 1265–1272.
- 2202 <https://doi.org/10.1111/j.1600-0706.2009.18125.x>
- 2203 Morita, K., Tamate, T., Kuroki, M., & Nagasawa, T. (2014). Temperature-dependent
2204 variation in alternative migratory tactics and its implications for fitness and
2205 population dynamics in a salmonid fish. *Journal of Animal Ecology*, 83(6), 1268–
2206 1278. <https://doi.org/10.1111/1365-2656.12240>
- 2207 Myksvoll, M. S., Sandvik, A. D., Albretsen, J., Asplin, L., Johnsen, I. A., Karlsen, Ø., ...
2208 Ådlandsvik, B. (2018). Evaluation of a national operational salmon lice monitoring
2209 system—From physics to fish. *PLOS ONE*, 13(7), e0201338.
- 2210 <https://doi.org/10.1371/journal.pone.0201338>
- 2211 Näslund, J., Sundström, L. F., & Johnsson, J. I. (2015). Autumn food restriction reduces
2212 smoltification rate, but not over-winter survival, in juvenile brown trout *Salmo trutta*.
2213 *Ecology of Freshwater Fish*, 26(2), 205–216. <https://doi.org/10.1111/eff.12268>
- 2214 Nielsen, C., Aarestrup, K., & Madsen, S. S. (2006). Comparison of physiological smolt status
2215 in descending and nondescending wild brown trout (*Salmo trutta*) in a Danish stream.
2216 *Ecology of Freshwater Fish*, 15(2), 229–236. [https://doi.org/10.1111/j.1600-
2217 0633.2006.00143.x](https://doi.org/10.1111/j.1600-0633.2006.00143.x)
- 2218 Nielsen, J. (1994). *Vandløbsfiskenes verden – med biologen på arbejde*. Copenhagen,
2219 Denmark: Gad.
- 2220 Nika, N., Virbickas, T., & Kontautas, A. (2011). Spawning site selection and redd gravel
2221 characteristics of sea trout *Salmo trutta* in the lowland streams of Lithuania.

- 2222 *Oceanological and Hydrobiological Studies*, 40(1), 46–56.
- 2223 <https://doi.org/10.2478/s13545-011-0006-7>
- 2224 Nomoto, K., Omiya, H., Sugimoto, T., Akiba, K., Edo, K., & Higashi, S. (2010). Potential
2225 negative impacts of introduced rainbow trout on endangered Sakhalin taimen through
2226 redd disturbance in an agricultural stream, eastern Hokkaido. *Ecology of Freshwater*
2227 *Fish*, 19(1), 116–126.
- 2228 Nordeng, H. (1983). Solution to the " char problem" based on Arctic char (*Salvelinus alpinus*)
2229 in Norway. *Canadian Journal of Fisheries and Aquatic Sciences*, 40(9), 1372–1387.
- 2230 Northcote, T. G. (1992). Migration and residency in stream salmonids- some ecological
2231 considerations and evolutionary consequences. *Nordic Journal of Freshwater*
2232 *Research. Drottningholm*, 67, 5–17.
- 2233 Økland, F., Jonsson, B., Jensen, A. J., & Hansen, L. P. (1993). Is there a threshold size
2234 regulating seaward migration of brown trout and Atlantic salmon? *Journal of Fish*
2235 *Biology*, 42(4), 541–550. <https://doi.org/10.1111/j.1095-8649.1993.tb00358.x>
- 2236 Okumuş, I., Kurtoglu, I. Z., & Atasaral, Ş. (2006). General Overview of Turkish Sea Trout
2237 (*Salmo trutta* L.) Populations. *Sea Trout: Biology, Conservation and Management*,
2238 115–127.
- 2239 Olsen, E. M., Knutsen, H., Simonsen, J. H., Jonsson, B., & Knutsen, J. A. (2006). Seasonal
2240 variation in marine growth of sea trout, *Salmo trutta*, in coastal Skagerrak. *Ecology of*
2241 *Freshwater Fish*, 15(4), 446–452.
- 2242 Olsén, K. H., Järvi, J. T., Mayer, I., Petersson, E., & Kroon, F. (1998). Spawning behaviour
2243 and sex hormone levels in adult and precocious brown trout (*Salmo trutta* L.) males
2244 and the effect of anosmia. *Chemoecology*, 8(1), 9–17.
- 2245 <https://doi.org/10.1007/PL00001803>

- 2246 Olsson, I. C., Greenberg, L. A., Bergman, E., & Wysujack, K. (2006). Environmentally
2247 induced migration: the importance of food. *Ecology Letters*, 9(6), 645–651.
2248 <https://doi.org/10.1111/j.1461-0248.2006.00909.x>
- 2249 Ombredane, D., Siegler, L., Baglinière, J.-L., & Prunet, P. (1996). Migration et smoltification
2250 des juvéniles de truite (*Salmo trutta*) dans deux cours d'eau de Basse-Normandie.
2251 *Cybiurn*, 20(3), 27–42.
- 2252 Otero, J., L'Abée-Lund, J. H., Castro-Santos, T., Leonardsson, K., Storvik, G. O., Jonsson,
2253 B., ... Vøllestad, L. A. (2014). Basin-scale phenology and effects of climate
2254 variability on global timing of initial seaward migration of Atlantic salmon (*Salmo*
2255 *salar*). *Global Change Biology*, 20(1), 61–75. <https://doi.org/10.1111/gcb.12363>
- 2256 Patarnello, T., Bargelloni, L., Caldara, F., & Colombo, L. (1994). Cytochrome b and 16S
2257 rRNA Sequence Variation in the *Salmo trutta* (Salmonidae, Teleostei) Species
2258 Complex. *Molecular Phylogenetics and Evolution*, 3(1), 69–74.
2259 <https://doi.org/10.1006/mpev.1994.1008>
- 2260 Peiman, K. S., Birnie Gauvin, K., Midwood, J. D., Larsen, M. H., Wilson, A. D. M.,
2261 Aarestrup, K., & Cooke, S. J. (2017). If and when: intrinsic differences and
2262 environmental stressors influence migration in brown trout (*Salmo trutta*). *Oecologia*,
2263 184(2), 375–384. <https://doi.org/10.1007/s00442-017-3873-9>
- 2264 Peterson, D. P., Rieman, B. E., Young, M. K., & Brammer, J. A. (2010). Modeling predicts
2265 that redd trampling by cattle may contribute to population declines of native trout.
2266 *Ecological Applications*, 20(4), 954–966. <https://doi.org/10.1890/09-0679.1>
- 2267 Pettersson, J. C. E., Hansen, M. M., & Bohlin, T. (2001). Does dispersal from landlocked
2268 trout explain the coexistence of resident and migratory trout females in a small
2269 stream? *Journal of Fish Biology*, 58(2), 487–495. [https://doi.org/10.1111/j.1095-](https://doi.org/10.1111/j.1095-8649.2001.tb02267.x)
2270 [8649.2001.tb02267.x](https://doi.org/10.1111/j.1095-8649.2001.tb02267.x)

- 2271 Poole, W. R., Byrne, C. J., Dillane, M. G., Whelan, K. F., & Gargan, P. G. (2002). The Irish
2272 sea trout enhancement programme: a review of the broodstock and ova production
2273 programmes. *Fisheries Management and Ecology*, 9(6), 315–328.
- 2274 Poole, W. R., Dillane, M., DeEyto, E., Rogan, G., McGinnity, P., & Whelan, K. F. (2006).
2275 Characteristics of the Burrishoole Sea Trout Population: Census, Marine Survival,
2276 Enhancement and Stock-Recruitment Relationship, 1971-2003. In *Sea Trout: Biology,
2277 Conservation and Management* (pp. 279–306).
2278 <https://doi.org/10.1002/9780470996027.ch19>
- 2279 Poole, W. R., & Dillane, M. G. (1998). Estimation of sperm concentration of wild and
2280 reconditioned brown trout, *Salmo trutta* L. *Aquaculture Research*, 29(6), 439–445.
2281 <https://doi.org/10.1046/j.1365-2109.1998.00223.x>
- 2282 Poole, W. R., Nolan, D., & Tully, O. (2000). Extrapolating baseline blood cortisol levels in
2283 trout: modelling capture effects in wild sea trout *Salmo trutta* (L.) infested with
2284 *Lepeophtheirus salmonis* (Krøyer). *Aquaculture Research*, 31(11), 835–841.
- 2285 Poole, W. R., Whelan, K. F., Dillane, M. G., Cooke, D. J., & Matthews, M. (1996). The
2286 performance of sea trout, *Salmo trutta* L., stocks from the Burrishoole system western
2287 Ireland, 1970–1994. *Fisheries Management and Ecology*, 3(1), 73–92.
- 2288 Potter, E., Campbell, R. N., Sumner, K., & Marshall, S. (2017). *Marine migrations and
2289 distribution of sea trout from rivers in Great Britain*.
- 2290 Prodöhl, P., Antoniacomi, A., Bradley, C., Carlson, J., Carvalho, G. R., Coughlan, J., ...
2291 Cross, T. F. (2017). Population genetics and Genetic Stock Identification of
2292 anadromous *Salmo trutta* from the Irish Sea and adjacent areas, using microsatellite
2293 DNA loci. In *Sea Trout: Science and Management : Proceedings of the 2nd
2294 International Sea Trout Symposium* (pp. 69–95). Retrieved from
2295 <https://pure.qub.ac.uk/portal/en/publications/population-genetics-and-genetic-stock->

- 2296 identification-of-anadromous-salmo-trutta-from-the-irish-sea-and-adjacent-areas-
2297 using-microsatellite-dna-loci(86dedf32-1d65-4de0-80e6-4d0583fb8c85)/export.html
- 2298 Prouzet, P., Le Bail, P. Y., & Heydorff, M. (1984). Sex Ratio and Potential Fecundity of
2299 Atlantic Salmon (*Salmo salar* L.) Caught by Anglers on the Elorn River (Northern
2300 Brittany, France) during 1979 and 1980. *Aquaculture Research*, 15(3), 123–130.
2301 <https://doi.org/10.1111/j.1365-2109.1984.tb00843.x>
- 2302 Pulg, U., Barlaup, B. T., Sternecker, K., Trepl, L., & Unfer, G. (2013). Restoration of
2303 spawning habitats of brown trout (*Salmo trutta*) in a regulated chalk stream. *River*
2304 *Research and Applications*, 29(2), 172–182.
- 2305 Quéméré, E., Baglinière, J.-L., Roussel, J.-M., Evanno, G., McGinnity, P., & Launey, S.
2306 (2016). Seascape and its effect on migratory life-history strategy influences gene flow
2307 among coastal brown trout (*Salmo trutta*) populations in the English Channel. *Journal*
2308 *of Biogeography*, 43(3), 498–509. <https://doi.org/10.1111/jbi.12632>
- 2309 Quéméré, E., le Gentil, J., & Launey, S. (2011). *Analyse spatiale et temporelle des*
2310 *caractéristiques génétiques de la population de truite de mer de la Bresle* (Fiche
2311 Action Onema No. Rapport final; p. 124p).
- 2312 Regan, C. T. (1911). *The freshwater fishes of the British Isles*. London, Methuen & Co. Ltd.
- 2313 Richardson, J. L., Urban, M. C., Bolnick, D. I., & Skelly, D. K. (2014). Microgeographic
2314 adaptation and the spatial scale of evolution. *Trends in Ecology & Evolution*, 29(3),
2315 165–176. <https://doi.org/10.1016/j.tree.2014.01.002>
- 2316 Riley, W. D., Bendall, B., Ives, M. J., Edmonds, N. J., & Maxwell, D. L. (2012). Street
2317 lighting disrupts the diel migratory pattern of wild Atlantic salmon, *Salmo salar* L.,
2318 smolts leaving their natal stream. *Aquaculture*, 330–333, 74–81.
2319 <https://doi.org/10.1016/j.aquaculture.2011.12.009>

- 2320 Rivot, E., Perrier, C., Jouanin, C., Roussel, J.-M., Riera, P., Porcher, J. P., & Baglinière, J.-L.
2321 (2009). Climate change may have affected growth and life history in Atlantic Salmon
2322 Juveniles over the past 30 years. *American Fisheries Society Symposium*, 69, 855–
2323 857.
- 2324 Roberts, R. J. (1993). Ulcerative dermal necrosis (UDN) in wild salmonids. *Fisheries*
2325 *Research*, 17(1), 3–14. [https://doi.org/10.1016/0165-7836\(93\)90003-P](https://doi.org/10.1016/0165-7836(93)90003-P)
- 2326 Rohtla, M., Matetski, L., Svirgsden, R., Kesler, M., Taal, I., Saura, A., ... Vetemaa, M.
2327 (2017). Do sea trout *Salmo trutta* parr surveys monitor the densities of anadromous or
2328 resident maternal origin parr, or both? *Fisheries Management and Ecology*, 24(2),
2329 156–162. <https://doi.org/10.1111/fme.12214>
- 2330 Rosseland, B. O., & Kroglund, F. (2010). Lessons from Acidification and Pesticides. In
2331 *Atlantic Salmon Ecology* (pp. 387–407). <https://doi.org/10.1002/9781444327755.ch15>
- 2332 Rounsefell, G. A. (1958). Anadromy in North American Salmonidae. *US Fish and Wildlife*
2333 *Service Fisheries Bulletin*, 58, 171–185.
- 2334 Roussel, J.-M. (2007). Carry-over effects in brown trout (*Salmo trutta*): hypoxia on embryos
2335 impairs predator avoidance by alevins in experimental channels. *Canadian Journal of*
2336 *Fisheries and Aquatic Sciences*, 64(5), 786–792. <https://doi.org/10.1139/f07-055>
- 2337 Roussel, J.-M., Perrier, C., Erkinaro, J., Niemelä, E., Cunjak, R. A., Huteau, D., & Riera, P.
2338 (2013). Stable isotope analyses on archived fish scales reveal the long-term effect of
2339 nitrogen loads on carbon cycling in rivers. *Global Change Biology*, 20(2), 523–530.
2340 <https://doi.org/10.1111/gcb.12293>
- 2341 Rubin, J.-F., Glimsäter, C., & Jarvi, T. (2005). Spawning characteristics of the anadromous
2342 brown trout in a small Swedish stream. *Journal of Fish Biology*, 66(1), 107–121.

- 2343 Rundio, D. E., Williams, T. H., Pearse, D. E., & Lindley, S. T. (2012). Male-biased sex ratio
2344 of nonanadromous *Oncorhynchus mykiss* in a partially migratory population in
2345 California. *Ecology of Freshwater Fish*, 21(2), 293–299.
- 2346 Saltveit, S. J., Halleraker, J. H., Arnekleiv, J. V., & Harby, A. (2001). Field experiments on
2347 stranding in juvenile Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*)
2348 during rapid flow decreases caused by hydropeaking. *Regulated Rivers: Research &*
2349 *Management: An International Journal Devoted to River Research and Management*,
2350 17(4–5), 609–622.
- 2351 Sánchez-Hernández, J., Eloranta, A. P., Finstad, A. G., & Amundsen, P.-A. (2017).
2352 Community structure affects trophic ontogeny in a predatory fish. *Ecology and*
2353 *Evolution*, 7(1), 358–367. <https://doi.org/10.1002/ece3.2600>
- 2354 Sandlund, O. T., & Jonsson, B. (2016). Life history plasticity: migration ceased in response
2355 to environmental change? *Ecology of Freshwater Fish*, 25(2), 225–233.
- 2356 Sanz, N. (2017). Phylogeographic History of Brown Trout. In *Brown Trout* (pp. 15–63).
2357 <https://doi.org/10.1002/9781119268352.ch2>
- 2358 Scheurer, K., Alewell, C., Bänninger, D., & Burkhardt-Holm, P. (2009). Climate and land-
2359 use changes affecting river sediment and brown trout in alpine countries—a review.
2360 *Environmental Science and Pollution Research*, 16(2), 232–242.
2361 <https://doi.org/10.1007/s11356-008-0075-3>
- 2362 Schram, T. A., Knutsen, J. A., Heuch, P. A., & Mo, T. A. (1998). Seasonal occurrence of
2363 *Lepeophtheirus salmonis* and *Caligus elongatus* (Copepoda: Caligidae) on sea trout
2364 (*Salmo trutta*), off southern Norway. *ICES Journal of Marine Science*, 55(2), 163–
2365 175. <https://doi.org/10.1006/jmsc.1997.0357>
- 2366 Scott, G. R., & Johnston, I. A. (2012). Temperature during embryonic development has
2367 persistent effects on thermal acclimation capacity in zebrafish. *Proceedings of the*

- 2368 *National Academy of Sciences*, 109(35), 14247–14252.
2369 <https://doi.org/10.1073/pnas.1205012109>
- 2370 Segers, F. H., & Taborsky, B. (2011). Egg size and food abundance interactively affect
2371 juvenile growth and behaviour. *Functional Ecology*, 25(1), 166–176.
- 2372 Serbezov, D., Jorde, P. E., Bernatchez, L., Olsen, E. M., & Vøllestad, L. A. (2012). Life
2373 history and demographic determinants of effective/census size ratios as exemplified
2374 by brown trout (*Salmo trutta*). *Evolutionary Applications*, 5(6), 607–618.
2375 <https://doi.org/10.1111/j.1752-4571.2012.00239.x>
- 2376 Serra-Llinares, R. M., Bjørn, P. A., Finstad, B., Nilsen, R., & Asplin, L. (2016). Nearby
2377 farms are a source of lice for wild salmonids: a reply to Jansen et al.(2016).
2378 *Aquaculture Environment Interactions*, 8, 351–356.
- 2379 Serra-Llinares, R. M., Bjørn, P. A., Finstad, B., Nilsen, R., Harbitz, A., Berg, M., & Asplin,
2380 L. (2014). *Salmon lice infection on wild salmonids in marine protected areas: an*
2381 *evaluation of the Norwegian 'National Salmon Fjords*.
- 2382 Shephard, S, MacIntyre, C., & Gargan, P. (2016). Aquaculture and environmental drivers of
2383 salmon lice infestation and body condition in sea trout. *Aquaculture Environment*
2384 *Interactions*, 8, 597–610. <https://doi.org/10.3354/aei00201>
- 2385 Shephard, Samuel, Davidson, I. C., Walker, A. M., & Gargan, P. G. (2018). Length-based
2386 indicators and reference points for assessing data-poor stocks of diadromous trout
2387 *Salmo trutta*. *Fisheries Research*, 199, 36–43.
2388 <https://doi.org/10.1016/j.fishres.2017.11.024>
- 2389 Sigurjónsdóttir, H., & Gunnarsson, K. (1989). Alternative mating tactics of arctic charr,
2390 *Salvelinus alpinus*, in Thingvallavatn, Iceland. *Environmental Biology of Fishes*,
2391 26(3), 159–176.

- 2392 Skilbrei, O. T., Finstad, B., Urdal, K., Bakke, G., Kroglund, F., & Strand, R. (2013). Impact
2393 of early salmon louse, *Lepeophtheirus salmonis*, infestation and differences in
2394 survival and marine growth of sea-ranched Atlantic salmon, *Salmo salar* L., smolts
2395 1997–2009. *Journal of Fish Diseases*, 36(3), 249–260.
2396 <https://doi.org/10.1111/jfd.12052>
- 2397 Skrochowska, S. (1969). Migration of sea trout (*Salmo trutta* L.), brown trout (*Salmo trutta*
2398 *m. fario* L.) and their crosses. *Polish Archiv Hydrobiologie*, 16, 125–192.
- 2399 Solomon, D. J. (1997). *Review of sea trout fecundity* (p. 22pp) [Technical report for the
2400 Welsh Environment Agency]. Environment Agency.
- 2401 Solomon, D. J., & Czerwinski, M. (2007). Catch and Release, Net Fishing and Sea Trout
2402 Fisheries Management. In *Sea Trout: Biology, Conservation and Management* (pp.
2403 434–440). <https://doi.org/10.1002/9780470996027.ch30>
- 2404 Stradmeyer, L., Höjesjö, J., Griffiths, S. W., Gilvear, D. J., & Armstrong, J. D. (2008).
2405 Competition between brown trout and Atlantic salmon parr over pool refuges during
2406 rapid dewatering. *Journal of Fish Biology*, 72(4), 848–860.
- 2407 Summers, D. W., Giles, N., & Stubbing, D. N. (2008). Rehabilitation of brown trout, *Salmo*
2408 *trutta*, habitat damaged by riparian grazing in an English chalkstream. *Fisheries*
2409 *Management and Ecology*, 15(3), 231–240. <https://doi.org/10.1111/j.1365->
2410 [2400.2008.00604.x](https://doi.org/10.1111/j.1365-2400.2008.00604.x)
- 2411 Summers, D. W., Giles, N., & Willis, D. J. (1996). *Restoration of Riverine Trout Habitats –*
2412 *A Guidance Manual* (R&D Technical Report W18 No. Fisheries Technical Manual 1;
2413 p. 230p). Bristol: Environmental Agency.
- 2414 Svärdson, G. (1966). Öringen. *Fiske*, (66), 1–31.
- 2415 Taal, I., Kesler, M., Saks, L., Rohtla, M., Verliin, A., Svirgsden, R., ... Saat, T. (2014).
2416 Evidence for an autumn downstream migration of Atlantic salmon *Salmo salar*

- 2417 (Linnaeus) and brown trout *Salmo trutta* (Linnaeus) parr to the Baltic Sea. *Helgoland*
2418 *Marine Research*, 68(2), 373–377. <https://doi.org/10.1007/s10152-014-0395-2>
- 2419 Taal, I., Rohtla, M., Saks, L., Kesler, M., Jürgens, K., Svirgsden, R., ... Vetemaa, M. (2018).
2420 Parr dispersal between streams via a marine environment: A novel mechanism behind
2421 straying for anadromous brown trout? *Ecology of Freshwater Fish*, 27(1), 209–215.
2422 <https://doi.org/10.1111/eff.12338>
- 2423 Tamate, T., & Maekawa, K. (2004). Female-biased mortality rate and sexual size dimorphism
2424 of migratory masu salmon, *Oncorhynchus masou*. *Ecology of Freshwater Fish*, 13(2),
2425 96–103.
- 2426 Tanguy, J. M., Ombredane, D., Baglinière, J.-L., & Prunet, P. (1994). Aspects of parr-smolt
2427 transformation in anadromous and resident forms of brown trout (*Salmo trutta*) in
2428 comparison with Atlantic salmon (*Salmo salar*). *Aquaculture*, 121(1), 51–63.
2429 [https://doi.org/10.1016/0044-8486\(94\)90007-8](https://doi.org/10.1016/0044-8486(94)90007-8)
- 2430 Tappel, P. D., & Bjornn, T. C. (1983). A New Method of Relating Size of Spawning Gravel
2431 to Salmonid Embryo Survival. *North American Journal of Fisheries Management*,
2432 3(2), 123–135. [https://doi.org/10.1577/1548-8659\(1983\)3<123:ANMORS>2.0.CO;2](https://doi.org/10.1577/1548-8659(1983)3<123:ANMORS>2.0.CO;2)
- 2433 Taranger, G. L., Karlsen, Ø., Bannister, R. J., Glover, K. A., Husa, V., Karlsbakk, E., ...
2434 Svåsand, T. (2015). Risk assessment of the environmental impact of Norwegian
2435 Atlantic salmon farming. *ICES Journal of Marine Science*, 72(3), 997–1021.
2436 <https://doi.org/10.1093/icesjms/fsu132>
- 2437 Thomsen, D. S., Koed, A., Nielsen, C., & Madsen, S. S. (2007). Overwintering of sea trout
2438 (*Salmo trutta*) in freshwater: escaping salt and low temperature or an alternate life
2439 strategy? *Canadian Journal of Fisheries and Aquatic Sciences*, 64(5), 793–802.
2440 <https://doi.org/10.1139/f07-059>

- 2441 Thorpe, J. E., Talbot, C., & Villarreal, C. (1982). Bimodality of growth and smolting in
2442 Atlantic salmon, *Salmo salar* L. *Aquaculture*, 28(1–2), 123–132.
2443 [https://doi.org/10.1016/0044-8486\(82\)90015-1](https://doi.org/10.1016/0044-8486(82)90015-1)
- 2444 Thorstad, E. B., & Finstad, B. (2018). *Impacts of salmon lice emanating from salmon farms*
2445 *on wild Atlantic salmon and sea trout* (NINA Report No. 1449; p. 22p). NINA.
- 2446 Thorstad, E. B., Todd, C. D., Bjørn, P. A., Gargan, P. G., Vollset, K. W., Halttunen, E., ...
2447 Finstad, B. (2014). *Effects of salmon lice on sea trout. A literature review* (NINA
2448 Report No. 1044; p. 162p).
- 2449 Thorstad, E. B., Todd, C. D., Uglem, I., Bjørn, P. A., Gargan, P. G., Vollset, K. W., ...
2450 Finstad, B. (2016). Marine life of the sea trout. *Marine Biology*, 163(3), 47.
- 2451 Thorstad, E. B., Todd, C., Uglem, I., Bjørn, P., Gargan, P., Vollset, K., ... Finstad, B. (2015).
2452 Effects of salmon lice *Lepeophtheirus salmonis* on wild sea trout *Salmo trutta*—a
2453 literature review. *Aquaculture Environment Interactions*, 7(2), 91–113.
2454 <https://doi.org/10.3354/aei00142>
- 2455 Titus, R. G., & Mosegaard, H. (1992). Fluctuating recruitment and variable life history of
2456 migratory brown trout, *Salmo trutta* L., in a small, unstable stream. *Journal of Fish*
2457 *Biology*, 41(2), 239–255. <https://doi.org/10.1111/j.1095-8649.1992.tb02654.x>
- 2458 Tomkins, J. L., & Hazel, W. (2007). The status of the conditional evolutionarily stable
2459 strategy. *Trends in Ecology & Evolution*, 22(10), 522–528.
- 2460 Tully, O. (1992). Predicting infestation parameters and impacts of caligid copepods in wild
2461 and cultured fish populations. *Invertebrate Reproduction & Development*, 22(1–3),
2462 91–102.
- 2463 Tully, O., Gargan, P., Poole, W. R., & Whelan, K. F. (1999). Spatial and temporal variation
2464 in the infestation of sea trout (*Salmo trutta* L.) by the caligid copepod *Lepeophtheirus*

- 2465 *salmonis* (Krøyer) in relation to sources of infection in Ireland. *Parasitology*, 119(1),
2466 41–51.
- 2467 Tully, O., Poole, W. R., & Whelan, K. F. (1993). Infestation parameters for *Lepeophtheirus*
2468 *salmonis* (Kroyer)(Copepoda: Caligidae) parasitic on sea trout, *Salmo trutta* L., off
2469 the west coast of Ireland during 1990 and 1991. *Aquaculture Research*, 24(4), 545–
2470 555.
- 2471 Tully, O., Poole, W. R., Whelan, K. F., & Merigoux, S. (1993). Parameters and possible
2472 causes of epizootics of *Lepeophtheirus salmonis* (Krøyer) infesting sea trout (*Salmo*
2473 *trutta* L.) off the west coast of Ireland. *Pathogens of Wild and Farmed Fish: Sea Lice*,
2474 202–213.
- 2475 Tully, O., & Whelan, K. F. (1993). Production of nauplii of *Lepeophtheirus salmonis*
2476 (Krøyer)(Copepoda: Caligidae) from farmed and wild salmon and its relation to the
2477 infestation of wild sea trout (*Salmo trutta* L.) off the west coast of Ireland in 1991.
2478 *Fisheries Research*, 17(1–2), 187–200.
- 2479 Van Doornik, D. M., Berejikian, B. A., & Campbell, L. A. (2013). Gene flow between
2480 sympatric life history forms of *Oncorhynchus mykiss* located above and below
2481 migratory barriers. *PloS One*, 8(11), e79931.
- 2482 Vøllestad, L. A. (2017). Understanding Brown Trout Population Genetic Structure. In J.
2483 Lobón-Cervía & N. Sanz (Eds.), *Brown Trout* (pp. G1–G72).
2484 <https://doi.org/10.1002/9781119268352.app>
- 2485 Vollset, K. W., Dohoo, I., Karlsen, Ø., Halttunen, E., Kvamme, B. O., Finstad, B., ...
2486 Barlaup, B. T. (2018). Disentangling the role of sea lice on the marine survival of
2487 Atlantic salmon. *ICES Journal of Marine Science*, 75(1), 50–60.
2488 <https://doi.org/10.1093/icesjms/fsx104>

- 2489 Vollset, K. W., Krøntveit, R. I., Jansen, P. A., Finstad, B., Barlaup, B. T., Skilbrei, O. T., ...
2490 Dohoo, I. (2016). Impacts of parasites on marine survival of Atlantic salmon: a meta-
2491 analysis. *Fish and Fisheries*, *17*(3), 714–730. <https://doi.org/10.1111/faf.12141>
- 2492 Walker, A. M., & Bayliss, B. D. (2007). The Spawning Habitat Requirements of Sea Trout:
2493 A Multi-Scale Approach. In *Sea Trout: Biology, Conservation and Management* (pp.
2494 325–341). <https://doi.org/10.1002/9780470996027.ch21>
- 2495 Watz, J., Bergman, E., Calles, O., Enefalk, Å., Gustafsson, S., Hagelin, A., ... Jonsson, B.
2496 (2015). Ice cover alters the behavior and stress level of brown trout *Salmo trutta*.
2497 *Behavioral Ecology*, *26*(3), 820–827. <https://doi.org/10.1093/beheco/arv019>
- 2498 Wells, A., Grierson, C. E., MacKenzie, M., Russon, I. J., Reinardy, H., Middlemiss, C., ...
2499 Hazon, N. (2006). Physiological effects of simultaneous, abrupt seawater entry and
2500 sea lice (*Lepeophtheirus salmonis*) infestation of wild, sea-run brown trout (*Salmo*
2501 *trutta*) smolts. *Canadian Journal of Fisheries and Aquatic Sciences*, *63*(12), 2809–
2502 2821. <https://doi.org/10.1139/f06-160>
- 2503 Wells, A., Grierson, C. E., Marshall, L., MacKenzie, M., Russon, I. J., Reinardy, H., ...
2504 Hazon, N. (2007). Physiological consequences of “premature freshwater return” for
2505 wild sea-run brown trout (*Salmo trutta*) postsmolts infested with sea lice
2506 (*Lepeophtheirus salmonis*). *Canadian Journal of Fisheries and Aquatic Sciences*,
2507 *64*(10), 1360–1369. <https://doi.org/10.1139/f07-107>
- 2508 Werner, E. E., & Gilliam, J. F. (1984). The Ontogenetic Niche and Species Interactions in
2509 Size-Structured Populations. *Annual Review of Ecology and Systematics*, *15*, 393–
2510 425.
- 2511 Whelan, K. F. (1989). *The angler in Ireland: game, coarse & sea*. Country House.
- 2512 Whelan, K. F., & Poole, W. R. (1993). The sea trout stock collapse, 1989-1992. *The*
2513 *Conservation of Aquatic Systems: Proceedings of a Seminar Held On*, 18–19.

- 2514 Winter, E. R., Tummers, J. S., Aarestrup, K., Baktoft, H., & Lucas, M. C. (2016).
2515 Investigating the phenology of seaward migration of juvenile brown trout (*Salmo*
2516 *trutta*) in two European populations. *Hydrobiologia*, 775(1), 139–151.
2517 <https://doi.org/10.1007/s10750-016-2720-z>
- 2518 Wysujack, K., Greenberg, L. A., Bergman, E., & Olsson, I. C. (2009). The role of the
2519 environment in partial migration: food availability affects the adoption of a migratory
2520 tactic in brown trout *Salmo trutta*. *Ecology of Freshwater Fish*, 18(1), 52–59.
2521 <https://doi.org/10.1111/j.1600-0633.2008.00322.x>
- 2522 Young, K. A. (2005). Life–history variation and allometry for sexual size dimorphism in
2523 Pacific salmon and trout. *Proceedings of the Royal Society of London B: Biological*
2524 *Sciences*, 272(1559), 167–172.
- 2525 Závorka, L., Koeck, B., Cucherousset, J., Brijs, J., Näslund, J., Aldvén, D., ... Johnsson, J. I.
2526 (2017). Co-existence with non-native brook trout breaks down the integration of
2527 phenotypic traits in brown trout parr. *Functional Ecology*, 31(8), 1582–1591.
- 2528 Zimmerman, C. E., & Reeves, G. H. (2000). Population structure of sympatric anadromous
2529 and nonanadromous *Oncorhynchus mykiss*: evidence from spawning surveys and
2530 otolith microchemistry. *Canadian Journal of Fisheries and Aquatic Sciences*, 57(10),
2531 2152–2162.
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- 2533

2534 **Table**

2535 Table 1. Sex ratio of smolts and sexually mature sea trout as reported from various rivers
 2536 across Europe.

2537

River	Life stage	Percent females	Reference
Voss, Norway	Smolts	58	(B. Jonsson, 1985)
Tweed, Scotland	Smolts	59	(J. S. Campbell, 1977)
Nybroån, Sweden	Smolts	61	(Dellefors, 1996)
Istra, Norway	Smolts	61	(K. W. Jensen, 1968)
Bresle, France	Smolts	62	(Quéméré et al., 2011)
Jutland (several streams), Denmark	Smolts	75	(J. Nielsen, 1994)
Verkeån, Sweden	Smolts	75	(Svärdson, 1966)
Vindelälven, Sweden	Smolts	73	Palm, D., personal communication
Mean \pm 1 SD	Smolts	65.5 \pm 7.4	
Mørfjær, Sweden	Adult	44	(B. Jonsson et al., 2018)
Själsoån, Sweden	Adult	48	(Rubin et al., 2005)
Urvold lake, Norway	Adult	52	Dauidsen, J.G., personal communication
Bresle, France	Adult	55	(Quéméré et al., 2011)
Bottenvassdraget, Norway	Adult	56	Dauidsen, J.G., personal communication

Saltdalselva, Norway	Adult	58	Dauidsen, J.G., personal communication
Vindelälven, Sweden	Adult	61	Norrfors fishladder, Vattenfall Vattenkraft AB
Åvaån, Sweden	Adult	63	(Alm, 1950)
Ihra, Sweden	Adult	64	(Hessle, 1935)
Voss, Norway	Adult	66	(B. Jonsson, 1985)
Verkeån, Sweden	Adult	73	(Svärdson, 1966)
Vistula, Poland	Adult	76	(Svärdson, 1966)
Oir, France	Adult	79	Marchand, F., personal communication
Mean \pm 1 SD	Adult	61.2 \pm 10.6	

2538

2539

2540 **Figure legends**

2541

2542 Figure 1. Endemic distribution of brown trout (*Salmo trutta*): dashed lines give distribution
2543 area of anadromous populations and shaded areas give those of freshwater resident
2544 populations. After Jonsson and Jonsson (2011). Localisation of six brown trout populations,
2545 from north to south: River Hals 70°N (Norway), River Vosso 60°N (Norway), River
2546 Burrishoole 54°N (Ireland), River Tamar 51°N (England), River Bresle 50°N (France) and
2547 River Oir 48°N (France).

2548

2549 Figure 2. Schematic representation of brown trout (*Salmo trutta*) life history, and some of the
2550 major threats affecting its abundance (© Bengt Finstad and Kari Sivertsen, NINA).

2551

2552 Figure 3. Mean length at age for resident (filled square) and anadromous (open dot) brown
2553 trout (*Salmo trutta*) combined for the River Hals, River Vosso, River Tamar, River Bresle
2554 and River Oir. The total age represents the freshwater age for resident trout and the sum of
2555 the freshwater age and the sea age for anadromous. See Table S1 for details.

2556

2557 Figure 4. Mean length at age for brown trout (*Salmo trutta*) smolts at River Hals (green),
2558 River Vosso (yellow), River Burrishoole (red), River Bresle (black) and River Oir (blue).
2559 Values are presented ± 1 SD, except for River Burrishoole. See Table S1 for details.

2560

2561 Figure 5. Correlation between mean length at age for resident and anadromous brown trout
2562 (*Salmo trutta*) at the River Hals (green), River Vosso (yellow), River Burrishoole (red), River
2563 Tamar (pink), River Bresle (black) and River Oir (blue). The solid line represents the 1:1 line.
2564 The dotted line represents the relative growth gain attributable to sea migration, with a slope

2565 estimated at 1.377 (SD: 0.138) and significantly different from 1 ($\text{Chi}^2 = 318.2$, $\text{df} = 1$, $P =$
2566 0.006). Values are presented ± 1 SD, except for River Burrishoole. See Table S1 for details.

2567

2568 Figure 6. Characterisation of the migration strategy in brown trout (*Salmo trutta*) along a
2569 latitudinal gradient of populations: River Hals 70°N (Norway), River Vosso 60°N (Norway),
2570 River Burrishoole 54°N (Ireland), River Tamar 51°N (England), River Bresle 50°N (France)
2571 and River Oir 48°N (France). Left panel: relative additional growth for anadromous trout
2572 related to sea age and smolt age, expressed as a growth difference with resident trout of
2573 similar age. Some values are missing when no resident trout of a similar total age were
2574 caught Right panel: age structure of returning anadromous trout, in terms of sea age and
2575 smolt age. The darker the cell, the higher the value.