

1 **Population specific smolt development, migration and maturity schedules in**
2 **Atlantic salmon in a natural river environment**

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12

13 **Abstract**

14

15 Identifying differences in quantitative life history traits between cultured and
16 native or non-native wild populations is important in assessing the impact of
17 accidental and deliberate introductions of hatchery-reared fish into the wild. As the
18 ability to exploit the marine environment is the defining life history characteristic of
19 anadromous salmonids, knowledge of variation in smoltification characteristics
20 among populations is crucial in determining how these introductions affect fitness in
21 recipient populations. Data are presented here describing the timing and extent of the
22 autumn migration; the propensity for male parr maturation; the timing of the spring
23 migration; and the size of autumn and spring migrants from Atlantic salmon (*Salmo*
24 *salar*) populations from various genetic backgrounds. These experiments were carried

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25 out under common garden conditions over a decade in the Srahrevagh River in the
26 west of Ireland. Population specific genetically determined differences in quantitative
27 life history traits associated with smoltification were apparent. These differences may
28 reflect smolt quality and therefore impact on marine survival and ultimately lifetime
29 fitness. Both hatchery domestication and geography (different selective environments)
30 were found to be important factors determining smolt phenotypes, although it was
31 difficult to measure the relative contribution of each. These results indicate that farm,
32 native hatchery, non-native wild salmon (even from a neighbouring catchment) and
33 their hybrids with native wild fish, are likely to produce less well adapted and thus
34 poorer quality smolts than native wild populations and, where wild populations are
35 extant, such stocks should not be used for enhancement purposes.

36

37 **Keywords:** common garden experiment; parr migration; *Salmo salar*; smoltification

38

39 **1. Introduction**

40

41 As the status of many wild salmon populations becomes more precarious,
42 concern has increased as to the potential detrimental genetic changes that may occur
43 in wild populations as a result of escaped farm Atlantic salmon (Ferguson et al., 2006)
44 and of the deliberate release of hatchery bred fish (both of local and non-local origin)
45 for stock enhancement (Cross et al., 2006). Most of the information available on the
46 genetic differences among Atlantic salmon stocks has come from the study of
47 molecular variation, either at single coding loci e.g. allozymes (Verspoor et al., 2005)
48 or the assessment of allele variation in non-coding markers such as DNA
49 microsatellites (King et al., 2001). These reviews suggest generally increasing

50 genetic differences with increasing geographic distance. However, it is the
51 quantitative genetic variation (i.e. phenotypes culminating from the effect of multiple
52 genes together with environmental influences) in important physiological and
53 behavioural traits, such as egg size and time of emergence (Einum and Fleming,
54 2000), dispersal strategy (Nislow et al., 2004), growth rate (Einum and Fleming,
55 2000), competitive ability (Fausch, 1998), disease resistance (Mills, 1989), predator
56 avoidance (Hansen et al., 2003), male parr maturation (Aubin-Horth and Dodson,
57 2004), time of smoltification and smolt migration (McCormick et al., 1998), that
58 ultimately determine the performance of individual fish within a given population.
59 Other traits, that are important in the marine environment or the return from the sea to
60 the river, such as smolt size (Saloniemi et al., 2004), age of maturation (McGinnity et
61 al., 2003), time of return to freshwater and spawning time (Mills, 1989), will also be
62 important for adult performance and lifetime success (fitness). These behavioural and
63 life history differences among populations are thought to reflect local adaptation
64 (Taylor, 1991). It is also considered that salmon populations separated by small
65 distances are locally adapted (Youngson et al., 2003). Adkison (1994) suggests,
66 however, that there are definite limits to local adaptation, that local adaptation
67 operates over large rather than small areas and that that the trait differences observed,
68 particularly at local or regional scales, result from differential gene expression in
69 different environments.

70 In many instances, particularly for sea ranching and wild population
71 enhancement, local stocks are used, with varying degrees of hatchery intervention
72 (Reisenbichler et al., 2003). The molecular or qualitative genetic effects of hatchery
73 rearing on Atlantic salmon (comparing hatchery populations to their wild source
74 populations), have been examined by a number of authors (e.g. McGinnity et al.,

75 2004). In contrast to wild populations, genetic composition of hatchery populations,
76 as measured by allele frequencies at molecular marker loci, is often observed to vary
77 significantly between year classes of the same strain. Levels of genetic variability,
78 measured as the number of alleles per locus are also seen to decline. Sometimes
79 lower levels of heterozygosity are also observed. Verspoor (1988) found that these
80 qualitative changes could occur within a single hatchery generation if broodstock
81 numbers were low.

82 The most direct method to examine quantitative genetic differences among
83 groups of fish in the wild, and to assess their adaptive significance, is to carry out
84 common garden experiments where fish are reared under communal conditions from
85 the egg stage onwards in a natural stream. As environmental variability is eliminated,
86 any difference found in performance will reflect genetic differences or maternal
87 effects. The development of microsatellite DNA profiling has enabled accurate
88 parentage identification and allowed direct comparison of groups from egg stage
89 onwards under natural conditions. Such common garden experiments undertaken,
90 over a 10 year period, in the Srahrevagh river in the west of Ireland have shown that
91 there are differential lifetime success and performance of native, native hatchery and
92 non-native Atlantic salmon from the same region (McGinnity et al., 2004) and among
93 native (Irish) and farm (Norwegian origin) salmon populations (McGinnity et al.,
94 1997; McGinnity et al., 2003). In these studies significant differences in quantitative
95 traits were reported e.g. differential survival, fry dispersal from spawning areas, parr
96 size at age, incidence of male parr maturity, age of adult maturation and thus adult
97 size and female fecundity.

98 Intuitively smoltification would seem to be a critical life history event for
99 salmon and has accordingly been defined by McCormick et al. (1998) as an adaptive

100 specialisation for downstream migration, sea-water entry and marine residence.
101 Moreover these authors suggest that smolt survival is affected by the match / mis-
102 match of migrating fish during an optimum physiological smolt window and their
103 timing of seawater entry with environmental conditions such as temperature, food and
104 predators (an ecological smolt window). Stock specific differences in behaviour and
105 development associated with smoltification might therefore be expected to have a
106 significant affect on smolt fitness in a given environment. The progeny of fish of
107 non-native origin, or fish subject to artificial selection (farm fish), would therefore be
108 expected to do less well than native fish in their own environment.

109 To identify whether such differences exist in smolting among salmon
110 populations from different genetic and geographical backgrounds, comparative data
111 on the smolt migration from two sets of experiments are presented. McGinnity et al.
112 (1997; 2003; 2004) have previously reported the experimental design and the overall
113 lifetime fitness and performance of the Atlantic salmon in these experiments. The
114 first experiment compared the performance of progeny of Irish wild native salmon
115 and a farm population of Norwegian origin and was repeated for three different
116 cohorts (1993, 1994 and 1998). The data presented describe the autumn pre-smolt
117 migration, its magnitude and duration; and associated with the autumn migration, the
118 propensity for male parr maturation. The duration of the spring migration and the size
119 of autumn and spring migrants are also described. These performance parameters
120 were also examined for reciprocal F1 wild by farm hybrids to ascertain the degree of
121 additive genetic variation. The second experiment measured and compared the
122 performance of wild native, hatchery native and wild non-native salmon populations
123 for the 1998 cohort only. Performance among these groups was examined for the

124 same six parameters listed above. The results are discussed in the context of the
125 conservation of genetic resources.

126

127 **2. Methods**

128

129 *2.1 Field experiments*

130

131 Common garden experiments were undertaken in the Burrishoole system in
132 western Ireland between 1993 and 2001. This system consists of a freshwater lake
133 (Lough Feeagh), connected to Lough Furnace, a tidal brackish lough, by two outlet
134 channels with permanent smolt and adult trapping facilities ('sea entry traps'), and a
135 number of afferent rivers (Fig. 1). One of these rivers (Srahrevagh: ca. 7250m² of
136 juvenile salmonid habitat) was used for the freshwater stages of the experiments and
137 was equipped with a further trap capable of capturing all downstream juvenile
138 migrants and upstream adults (hereafter referred to as the 'experiment-river' and
139 'experiment-trap'). Natural spawners were excluded from the experiment-river in
140 1992, 1993 and 1997. Juvenile salmon from the 1991 natural spawning were present
141 in the river until May 1994, with salmon from the 1994 natural spawning being
142 present from April 1995 and those from the 1998 natural spawning being present from
143 April 1999.

144 Details of crosses, family numbers and mating design for all experimental
145 groups are outlined in Table 1. The first experiment compared the performance of
146 three cohorts (1993, 1994 and 1998) of Irish wild native salmon and Norwegian farm
147 salmon. In 1993 and 1994, reciprocal F₁ hybrids of the wild and farmed groups were
148 also included in the comparison. Wild native eggs were sourced from Burrishoole

149 wild adults returning to the main adult trapping facilities (Fig. 1) in 1992, 1993 and
150 1997. Farm eggs were derived the Norwegian Mowi stock, then the most commonly
151 used strain in the Irish aquaculture industry, acquired in December 1992, 1993 and
152 1997. Native wild Burrishoole salmon of one sea winter maturity (1SW) and 2SW
153 farm salmon were used in establishing the 1998 experimental cohorts, whereas 3SW
154 and 4SW farm fishes were used for the earlier cohorts.

155 The second experiment compared the relative performance of native wild,
156 native hatchery and non-native wild fish. The wild eggs were collected from wild
157 Burrishoole adult salmon (these brood fish were not the same individuals as those
158 used in the first experiment) returning to the adult traps in 1997. Since 1997,
159 effectively all returning ranched adults have been removed at the sea entry traps.
160 However prior to 1997 a varying a proportion (average 23%, 1960 – 1997) of the
161 natural spawning escapement in the Burrishoole system consisted of Burrishoole
162 hatchery-reared ranched fish. It is not known what impact these fish have had on the
163 genetic integrity of the wild stock, although a number of contemporary but
164 unpublished studies show, at least at the molecular level, that the genetic composition
165 of the wild population, as indicated by microsatellite loci markers, to be genetically
166 stable over time (J. Coughlan, pers. comm.). Thus any domestication effects on the
167 wild stock are likely to be small relative to those exhibited by the hatchery stock.
168 Native hatchery eggs were derived from the Burrishoole ocean ranch strain since
169 1965, approximately twelve generations, using returning ranched adult fish. The
170 ranched fish are reared in the hatchery on the Burrishoole system and released as
171 adipose fin clipped smolts into Lough Furnace (Fig. 1). Eggs for the native hatchery
172 groups used in this experiment were stripped from ranched adults captured in the
173 upstream traps in December 1997. Eggs for the non-native wild group were obtained

174 from the Owenmore River by electrofishing in December 1997. The mouth of the
175 Owenmore is c. 60 km north-west of the mouth of the Burrishoole system (Fig.1).

176 In both experiments fertilized eggs were incubated in the hatchery on the
177 Burrishoole system, until the developmental stage when eyes were visible ('eyed
178 eggs'). At this stage, live eggs were counted accurately and families were mixed, eggs
179 were then planted out in the experiment river in artificial redds (Donaghy and
180 Verspoor, 2000). All downstream migrants (fry, parr, pre-smolts and smolts) caught
181 in the experiment trap on the Srahrevagh river were sampled. Sampled individuals
182 were identified to family and group by microsatellite profiling (1997; 2003; 2004).

183

184 *2.2 Data analysis*

185

186 The data analysed here comprised six components related to smoltification:
187 ratio of autumn migrants to total smolt migrants; ratio of precocious males to total
188 migrants; duration of autumn migration (days); duration of spring migration (days);
189 median length of autumn migrants (cm); median length of spring migrants (cm).
190 Presmolt migration was defined as any 1+ fish moving through the downstream trap
191 after the summer solstice (21st June), which was taken to be day 1. The migration was
192 divided into autumn and spring migrations (see Fig. 2, which shows a clear gap in
193 numbers migrating between day 235-240, and then a subsequent rise as the spring
194 migration started). The autumn migration therefore contains fish moving between 2nd
195 September (day 74) and 15th February (day 240), and the spring migration contains
196 fish moving between the 16th February (day 241) and the 24th May (day 339).

197 The ratio of autumn migrants to total migrants, and the ratio of precocious
198 male parr to total migrants, was examined by calculating the value relative to the wild

199 of that year. Observed values were then compared to the value for the wild population
200 using a g-test for goodness of fit, with Williams's correction for the two-cell case
201 (Sokal and Rohlf, 1995), with expected values calculated from the ratios of total
202 smolts for the relevant year. G-tests were conducted on actual numbers, but values are
203 presented in the results as percentages. The duration of the autumn and spring runs for
204 the three cohorts were compared using Mann-Whitney U tests, and the variance in the
205 runs between groups was tested using *F*-tests. Size variables (length) were analysed
206 using linear models (ANOVA) in the statistics package Brodgar v. 2.4.3
207 (www.brodgar.com). Where a significant Pearson correlation between ordinal day and
208 size was found within groups, ordinal day was included as a covariate in the analysis
209 (ANCOVA).

210

211 **3. Results**

212

213 *3.1 First experiment: Wild vs farm*

214

215 Over the three cohorts, the native wild salmon had higher proportions of
216 autumn migrants than the farm fish (46% and 18% on average respectively) (Fig 3a,
217 Table 2). The native wild fish had significantly more autumn migration when
218 compared to the farm fish in 1993 (64% and 35%, g-test, $p=0.036$) and in 1994 (52%
219 and 4%, g-test, $p=0.001$). The wild fish also had a higher level of autumn migration
220 than the farm fish (22% and 14% respectively) in 1998, consistent with 1993 and
221 1994, but this difference was not significant.

222 The pattern in mature male parr was very similar to that outlined for the

223 autumn migration, with the native wild fish having generally higher proportions of

224 mature male parr than the farm fish (40% and 10% on average respectively) (Fig. 3b,
225 Table 2). The native wild fish had significantly more mature male parr than the farm
226 fish in 1993 (47% and 12%, g test, $p=0.001$) and 1994 (55% and 4%, g test, $p<0.001$).
227 The difference was not significant in 1998, although there were still more mature
228 male parr in the native wild fish than the farm fish (18% and 14%, g test, $p=0.62$).

229 The duration of the autumn migration was quantified as the number of days
230 between the 5th and 95th percentile of fish moving through the trap (i.e. the middle
231 90%). This approach was used to account for the large amount of days either side of
232 the main migration when the occasional fish (outliers) pass through the trap. On
233 average, the autumn migration of the native wild fish was 60 days, while that of farm
234 fish was 38 days (Fig. 3c, Table 2) although this difference was not statistically
235 significant (Mann-Whitney test, $p=0.7$). However, the variance between years was
236 higher in the farm fish cohorts than the wild fish, and this difference approached
237 significance (F -test, $p=0.068$). The large variance between cohorts of farm fish is
238 owing to the fact that the autumn migration ranged from 1 day in 1994 to 101 days in
239 1993. It should be noted that only one farm fish migrated in 1994, and that generally,
240 the proportion of autumn migrants and mature male parr was low in farm fish.

241 On average, the spring migration of the native wild fish was 45 days, while
242 that of farm fish was 32 days (Fig. 3d, Table 2) with again this difference not being
243 statistically significant (Mann-Whitney test, $p=0.7$). However, in contrast to the
244 autumn migration, variance between years was significantly lower in the farm fish
245 groups than in the wild fish (F -test, $p=0.012$), with the number of days ranging from
246 only 30 to 34 over the three years studied.

247 On average, native wild autumn migrants were 10.98 cm in length, while farm
248 autumn migrants measured 11.68 cm (Fig. 3e, Table 2). Size of autumn migrants was

249 not correlated with ordinal day (Pearson correlation, $p=0.83$), indicating that the fish
250 were not growing significantly over the autumn migration period. Ordinal day was
251 not, therefore, included as a covariate in the ANOVA. Although the number of farm
252 autumn migrants was small, there were significant differences in the length of fish
253 between the native wild and farm groups (ANOVA, $p=0.034$), with farm fish being
254 generally bigger (LSD post-hoc test, $p=0.003$).

255 On average, native wild spring migrants were 12.71 cm in length, while farm
256 spring migrants measured 13.23 cm (Fig. 3f). In contrast to the autumn migrants,
257 length did increase significantly with ordinal day (Pearson correlation, $p<0.001$), so
258 ordinal day was included here as a covariate in the analysis. Farm spring migrants
259 were significantly bigger than native wild spring migrants (ANCOVA, $p=0.04$, Table
260 2).

261 There is strong evidence that the differences in some of the traits between
262 native wild and farm fish are attributable to additive genetic variation. In 1993 and
263 1994, F1 hybrids of farm and native wild had intermediate proportions of autumn
264 migrants and mature male parr when compared to the native wild and farmed groups
265 (Fig. 4). The lengths of the autumn and spring migrant hybrids were also intermediate
266 between the two parental groups in 1994 (Fig. 5), although there was no obvious
267 pattern in the 1993 cohort.

268

269 *3.2 Second experiment: 1998 Wild native vs Wild non- native vs native hatchery*

270

271 Native hatchery fish had a significantly higher level of autumn migration than the
272 native wild fish (33% versus 22%, g-test, $p=0.02$), while the native wild and non-
273 native wild groups had the same proportions of autumn migrants (22 %) (Fig. 6a,

274 Table 3). Native wild fish had a slightly lower proportion of mature male parr when
275 compared to the native hatchery fish, although the difference was not significant (18%
276 and 27%, g -test, $p=0.069$). The native wild fish had similar proportions of mature
277 male parr as the non-native wild fish (18% and 17%, $p=0.8$) (Fig. 6b, Table 3).

278 In 1998, both the native hatchery and non-native wild fish had longer autumn
279 migrations than the native wild group (24 and 41% longer respectively) (Fig. 6c).
280 Similarly, both the native hatchery and non-native wild fish had longer spring
281 migrations than the native wild fish (60% longer in each case) (Fig. 6d, Table 3).

282 There was a significant correlation between ordinal day and length of fish
283 migrating in the autumn (Pearson correlation, $p=0.044$) and in the spring (Pearson
284 correlation, $p=0.0015$), so ordinal day was included in both analyses as a covariate.
285 Group was a significant source of variation in length in autumn migrants (ANCOVA,
286 $p=0.012$), with the non-native wild fish being significantly smaller than the native
287 wild fish ($p=0.03$). Native hatchery fish were of similar size as native wild fish
288 ($p=0.79$) (Fig. 6e). Group was also a significant source of variation in length of spring
289 migrants (ANCOVA, $p<0.001$), with the non-native wild and native hatchery fish
290 being significantly smaller than the native wild fish ($p<0.01$) (Fig. 6f, Table 3).

291

292 **4. Discussion**

293

294 There was considerable inter year variation within farm and wild native
295 cohorts for all characteristics measured in the study, and in many instances the
296 variation was greater within cohorts than between groups, suggesting that
297 environment is an important determinant of observed variability. However, even
298 though there was large temporal variation within cohorts of fish, the pattern of trait

299 expression in wild and farm fish was consistent across years – e.g. the proportion of
300 wild native fish migrating in the autumn was always greater than the proportion of
301 farm fish in the same year, suggesting that genetic variation is also important in
302 determining smolt characteristics. Furthermore, an examination of the performance of
303 F₁ hybrids between wild and farm for traits associated with smoltification showed
304 consistent intermediate values for several of the traits of interest, indicating additive
305 genetic variation. This confirms the importance of genetics in producing the
306 phenotypes observed and subsequently determining their fitness.

307 McGinnity et al., (2003) found that farm fish produce fewer smolts than native
308 wild fish, with a relative success in the freshwater phase of 41% relative to the native
309 wild fish (Table 2). The results presented in this paper show that these two groups of
310 fish also produce smolts that have different phenotypes with regard to propensity for
311 autumn migration, early maturation, duration of migration and size. An important
312 question is whether these life history differences observed during smoltification
313 contribute substantially to performance in the sea and subsequently to lifetime success
314 of future generations, i.e. are the factors that affect smolt quality more important than
315 the actual number of smolts produced? If smolt quality were not a factor in
316 determining survival it might be expected that smolt-to -adult survival rates would be
317 the same for both native wild and farm fish in the marine environment. In fact, the
318 relative smolt –to-adult survival of farm fish in terms of adult numbers was found to
319 be only 7% relative to the native wild fish (McGinnity et al., 2003) (Table 2),
320 indicating that smoltification, and the traits which we describe in this paper, may have
321 a considerable impact on fitness. Unfortunately, because of experimental constraints,
322 it was not possible to monitor the performance of the actual smolts emanating from
323 the freshwater experiment as these were sacrificed on collection. Instead, as a

324 surrogate, representative samples from the same groups and families were reared
325 under a common hatchery conditions and released as smolts (McGinnity et al., 2003)
326 in order to provide sufficient numbers to ensure adequate returns for statistical
327 analysis. However release subsequent to hatchery rearing is likely to underestimate
328 the degree of differentiation between the two populations, as there is some equalising
329 of the advantages or disadvantages carried over from the freshwater phase. It should
330 also be noted that farm fish remain twice as long at sea relative to native wild fish
331 (McGinnity et al., 2003) raising the possibility that the maturity schedule, which also
332 could be considered as an important smolt quality parameter under strong genetic
333 control, is an important factor determining survival in the marine environment.

334 The downward movement of fish in the autumn is closely related to the
335 phenomenon of male parr maturation. Given the significant correlation between
336 autumn migrants and mature male parr, it can be assumed confidently that the main
337 motivation for migrating at this time of the year is reproduction, although, it should be
338 noted that a significant proportion of the autumn migrating fish are either female or
339 non-mature male parr. It has been shown by Youngson et al., (1994) that these parr
340 will ultimately smoltify and return in subsequent years as adult salmon, but the
341 probability of smolting is much less for maturing than for immature fish (Myers,
342 1984; Whalen and Parrish, 1999). The native wild population in the Burrishoole
343 catchment demonstrates a high propensity for male parr maturation compared to the
344 farm fish. This early maturation of parr in the Burrishoole wild population is likely to
345 be adaptive, and should confer a reproductive advantage (Gross, 1996). Therefore it
346 can be assumed that a lower occurrence of parr maturity would reduce the potential of
347 the farm fish to contribute to reproduction, particularly as subsequent adult marine
348 survival is lower in this group (McGinnity et al., 2003). Therefore the contribution to

349 subsequent generations from both life history phases would be much less relative to
350 the native wild populations. However, Garant et al., (2003) found that farm origin
351 male parr have higher breeding and fertilization success than wild and hybrid male
352 parr. Specifically, hybrid parr had 57% and wild parr 25% of the success of farm parr
353 and they suggest that, on the basis of these results, early maturing males would speed
354 introgression of farm salmon into wild populations. This high breeding success of
355 farm origin parr therefore implies that although numbers may be small, their relative
356 impact may be much higher. From a conservation point of view, this is contrary to the
357 expectation that in wholly natural populations, the genetic contribution of mature
358 male parr is important in maintaining genetic variability or reducing its rate of decline
359 as the size of anadromous populations decline and, as observed by Parrish et al.,
360 (1998), goes some way to addressing the demographic imbalance now common
361 throughout much of the species' range.

362 There are two plausible explanations for low level of occurrence of early
363 maturation of parr in the farm strain: the first is that the broodstock used to establish
364 the farm populations did not have an inherent propensity for early maturation. This
365 may be related to their geographical origin (Dalley et al., 1983). In this regard, it
366 should be noted that the farm population in this experiment originated from a
367 Norwegian wild stock. Secondly, and more likely, low rate of early male maturation
368 may be a consequence of intense selection against the trait in the commercial breeding
369 program (Gjerde, 1984; Fleming and Einum, 1997). Regardless of the reason behind
370 the lack of early maturation, it is reasonable to speculate that the high propensity of
371 mature male parr in the native wild population is an adaptation to the natural
372 environment in Irish rivers, thus increasing fitness compared to farmed strains which
373 have been domesticated, and therefore are not under the same selective pressures.

374 While specific information is not available on the fate of the smolts in this
375 experiment (as for experimental reasons they were not given the opportunity to go to
376 sea), it is reasonable to assume that the duration of the spring migration would have a
377 significant influence on smolt quality. The timing of the spring migration has been
378 found by a number of authors to have an important role in determining smolt survival
379 in the marine environment (McCormick et al., 1998). Typically natural wild
380 populations would have variable and extended smolt migrations, and this is possibly
381 an adaptive strategy to spread the risk of fatality (“spread betting”) in an
382 unpredictable environment. This variability is evident in the results for the native wild
383 fish in this experiment. In contrast, the farm fish displayed a lack of variation in the
384 duration of the spring migration. This may be a product of inadvertent selection in the
385 hatchery environment, where smolts are systematically released into the marine
386 environment over time periods that correspond to narrow production cycle targets. It
387 may also reflect a much narrower genetic base owing to founder and or domestication
388 effects, which restrict the phenotypic plasticity of this population and therefore would
389 detrimentally affect fitness in unpredictable environmental conditions, which are the
390 norm in the wild.

391 In the first experiment, farm smolts were found to be significantly longer than
392 native wild smolts. Previous studies would suggest that large size at smoltification
393 confers an advantage in the marine phase of the lifecycle, and improves the prospects
394 for individual survival (Saloniemi et al., 2004). It might be assumed therefore, that the
395 farm fish in this experiment would have higher marine survival. As previously
396 mentioned, this was not found to be the case (McGinnity et al., 2003) suggesting that
397 performance in the marine environment is controlled by a wide variety of traits and

398 characters, some of which may override the advantages conferred by one particular
399 phenotype.

400 It has been found, as described, above that the progeny of wild and farm
401 salmon vary significantly in important quantitative traits and that these may
402 subsequently affect survival. It is not clear whether these differences occur as a
403 consequence of the geographical origin (local adaptation) of those stocks or because
404 of domestication selection and adaptation to the hatchery environment. However,
405 some insight into the relative importance of these two factors can be gained from the
406 results of the second experiment; firstly by comparing a hatchery population that has
407 been domesticated from its local wild progenitor; and secondly by comparing two
408 wild populations from different rivers in the same geographical region. It must be
409 noted that this second experiment was only carried out once, and thus caution must be
410 exercised in drawing conclusions.

411 Previous work has shown that there were no significant differences in the
412 numbers of smolts produced by native wild and native hatchery populations
413 (McGinnity et al., 2004). However, the same experiment found significant
414 differences in smolt quality variables (quantitative genetic differences) between the
415 native wild and native hatchery populations, in terms of male parr maturity, duration
416 of spring and autumn migrations, size of spring migrants (this study) and also greater
417 proportion of 1+ year smolts (McGinnity et al., 2004). However the effect of this
418 variability in smolt quality on overall lifetime success has not been tested to date.
419 Thus, smoltification needs to be targeted specifically in future common garden
420 experiments in order to quantify the specific contribution of smolt quality to marine
421 survival and overall fitness.

422 Some indication of the relative importance of geographical origin in
423 determining the fitness of individuals from a specific population is apparent in the
424 differences in juvenile freshwater performance, which were observed between native
425 wild and non-native wild salmon from a neighbouring river. Differences were found
426 in smolt size, and duration of the smolt migration and in the overall lifetime success,
427 which was only 18% of the native wild population. Contrary to the suggestion of
428 Adkison (1994) that local adaptation would only theoretically operate at large
429 regional scale, the findings of these common garden experiments indicate that local
430 adaptation, with substantial fitness consequences, can occur between rivers separated
431 by no more than 60 km. The fact that this was a common garden experiment, and thus
432 the same environment, excludes the possibility that the observed differences are the
433 result of differential trait expression of similar genotypes.

434

435 **5. Conclusion**

436

437 In conclusion, it would seem that that there are population specific genetically
438 determined differences in quantitative life history traits associated with smoltification.
439 These differences may impact on smolt quality and hence marine survival and
440 ultimately on lifetime fitness. Furthermore, it would appear both domestication and
441 geographical origin impact on the smolt phenotypes although it is difficult to separate
442 the relative contribution of each. While McGinnity et al. (2004) showed that the
443 relative lifetime success of native hatchery fish are comparable to their native
444 progenitors and thus opened the possibility of using these fish for enhancement
445 purposes in their river of origin, the variation in smolt quality observed here between
446 the two groups would indicate that such an action may be to the detriment of the

447 recipient wild population. The arguments for supplemental stocking using the nearest
448 local wild stocks based on the assumption that geographically close rivers would be
449 genetically similar, reviewed by McGinnity et al. (2004), are similarly flawed because
450 they are based on the assumption that important adaptive differences do not exist
451 between neighbouring populations. This is clearly not the case.

452

453 **Acknowledgements**

454

455 This work was funded by the Marine Institute, Ireland, the European Commission [EU
456 AIR1-CT92-0719] and the UK Natural Environment Research Council. We thank E.
457 Verspoor for providing microsatellite primers and for assistance with experimental
458 design, and the staff of the Marine Institute, Newport for logistical support.

459

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566 Table 1. Details of the groups and cohorts of Atlantic salmon used in the two experiments.

	Cohort	No. of males	No. of females	Mating design	No. of families	No. of eggs
1 st experiment	Wild 1993	6	6	Full-sib	6	5273
	Farm 1993	15	15	Full-sib	15	14997
	F ₁ Hybrid Wild 1993	6	6	Full-sib	6	5886
	F ₁ Hybrid Farm 1993	8	8	Full-sib	8	8659
	Wild 1994	11	11	Full-sib	11	10537
	Farm 1994	11	11	Full-sib	11	10537
	F ₁ Hybrid Wild 1994	11	11	Full-sib	11	10537
	F ₁ Hybrid Farm 1994	11	11	Full-sib	11	10537
	Wild 1998	8	5	Family tie*	12	8787
	Farm 1998	6	9	Family tie*	33	9832
2 nd experiment	Native wild 1998	8	5	Family tie*	12	7228
	Native hatchery 1998	10	5	Family tie*	24	7714
	Non-native wild 1998	10	5	Family tie*	27	10912

567 *(Winkelman and Peterson, 1994)

568 Table 2. Survival variables (average of all cohorts) of Atlantic salmon introduced into a common environment in 1993, 1994 and 1998 (1st
 569 experiment). Survival variables of the wild group are taken as 1.0, and the other groups are calculated relative to this. Smoltification variables
 570 are presented as ranges over all cohorts.

		Native wild	Farm	F ₁ Hybrid Wild Female	F ₁ Hybrid Farm Female
Survival variables	Eyed egg-smolt survival*†	1	0.41	0.73	0.50
	Smolt to adult survival†	1	0.07	0.58	0.61
	Lifetime success*†	1	0.02	0.42	0.27
Smoltification variables	Ratio of autumn migrants to total migrants	0.22-0.64	0.04-0.35	0.35-0.43	0.21
	Ratio of precocious males to total migrants	0.18-0.55	0.04-0.14	0.28-0.35	0.10-0.17
	90% duration of autumn migration (days)	51-71	0-101	20-118	1-140
	90% duration of spring migration (days)	27-65	36-58	16-28	22-40
	Median length of autumn migrants (cm)	10.8-11.5	10.7-12.6	11-11.4	11.2-11.5
	Median length of spring migrants (cm)	11.9-13.4	12.9-14.0	12.5-13.1	12.7-12.9

571
 572 *This assumes that displaced parr have the same survival as parr of the same group remaining in the experiment river, i.e. that the river is not at
 573 its parr carrying capacity. †Data are taken from McGinnity et al. (1997, 2003, 2004).
 574

575 Table 3. Survival and smoltification variables (one cohort) of Atlantic salmon introduced into a common environment in 1998 (2nd experiment).
 576 Survival variables of the wild group are taken as 1.0, and the other groups are calculated relative to this.

	Native wild 1998	Native hatchery 1998	Non-native wild 1998
Survival variables			
Eyed egg-smolt survival*†	1	0.99	0.81
Smolt to adult survival†	1	1.10	0.08
Lifetime success*†	1	1.10	0.06
Smoltification variables			
Ratio of autumn migrants to total migrants	0.22	0.33	0.22
Ratio of precocious males to total migrants	0.18	0.27	0.17
90% duration of autumn migration (days)	51	63	72
90% duration of spring migration (days)	42	67	67
Median length of autumn migrants (cm)	11.5	11.6	11.2
Median length of spring migrants (cm)	13.4	13.2	12.9

577 *This assumes that displaced parr have the same survival as parr of the same group remaining in the experiment river, i.e. that the river is not at
 578 its parr carrying capacity. †Data are taken from McGinnity et al., (1997, 2003, 2004).

579

580

581 **Figure captions**

582 Fig. 1. Map showing the location of the Burrishoole and Owenmore River systems.

583 The locations of the experiment river (Srahrevagh River), experiment trap and
584 sea-entry traps are also indicated.

585 Fig. 2. Number of salmon moving downstream through the Srahrevagh River trap
586 between 1993 and 2005. The cut off point between the autumn and spring
587 migration is designated as the 16th February.

588 Fig. 3. Comparison of life history traits connected with smoltification between three
589 cohorts of native wild (white bars) and farm (grey bars) salmon. The right
590 hand bars in each panel represents means of three years, and error bars
591 indicate standard deviations: a - number of autumn migrants:total migrants; b -
592 number of mature male parr:total migrants; c - 90% duration of autumn
593 migrations in days; d - 90% duration of spring migrations in days; e - length of
594 autumn migrants (cm); f - length of spring migrants (cm)

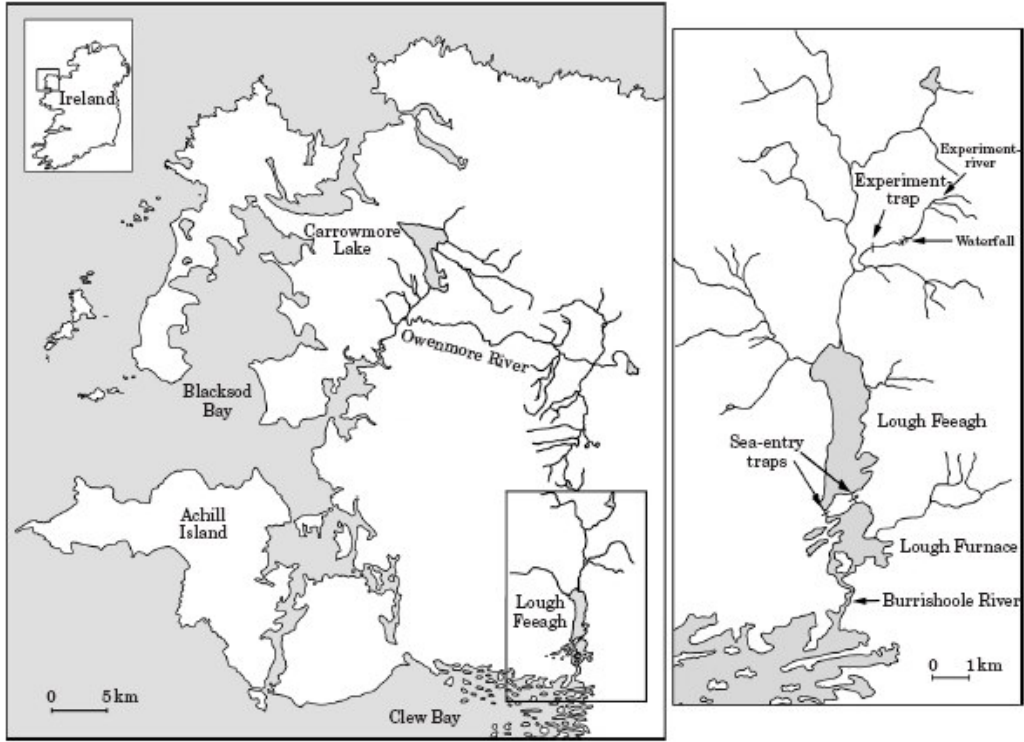
595 Fig. 4. The ratio of autumn migrants (a) and mature male parr (b) to total migrants in
596 four groups of fish comprising two cohorts (1993 - grey; 1994 - white). Values
597 for the hybrids and farm fish are calculated relative to a wild value of 1. F_1
598 Hybrid Wild – (wild female, farm male); F_1 Hybrid Farm – (Farm female, wild
599 male).

600 Fig. 5. The length of autumn migrants (a) and spring migrants (b) in four groups of
601 fish comprising two cohorts (1993 - grey; 1994 - white). (F_1 HW – wild dam,
602 farm sire); (F_1 HF – farm dam, wild sire).

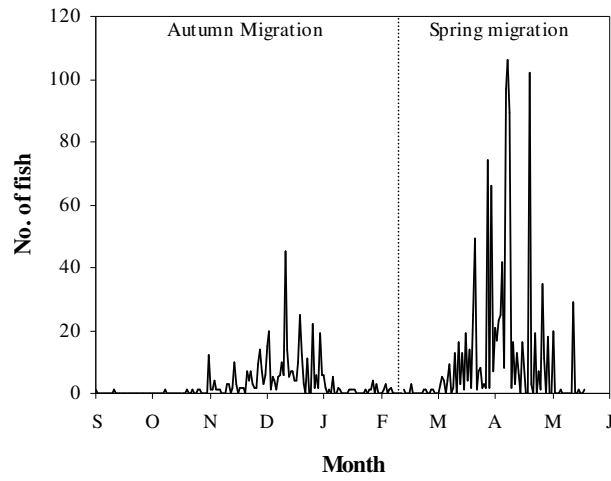
603 Fig. 6. Comparison of life history traits connected with smoltification, between native
604 wild, native hatchery and non-native wild salmon: a - number of autumn
605 migrants:total migrants; b - number of mature male parr:total migrants; c -

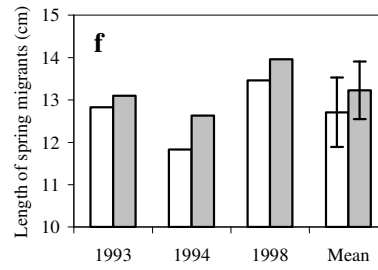
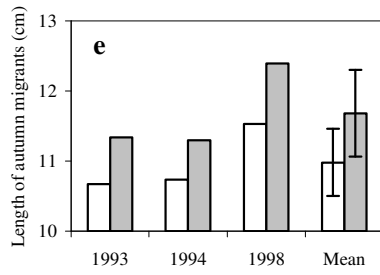
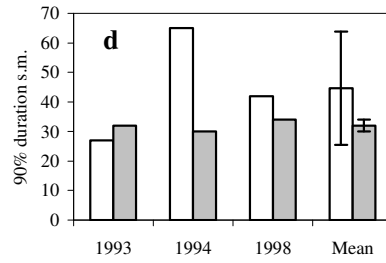
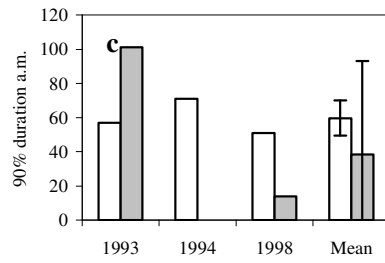
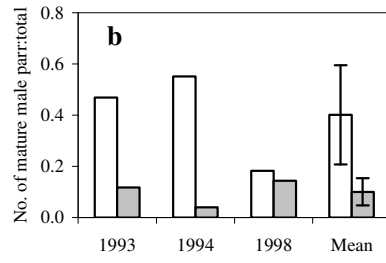
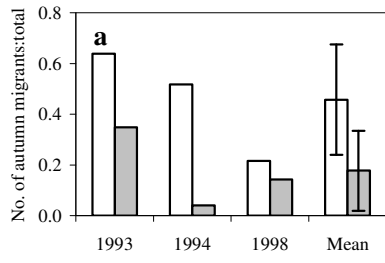
606 90% duration of autumn migrations in days; d - 90% duration of spring
607 migrations in days; e – average length of autumn migrants (cm) \pm s.d.; f –
608 average length of spring migrants (cm) \pm s.d..

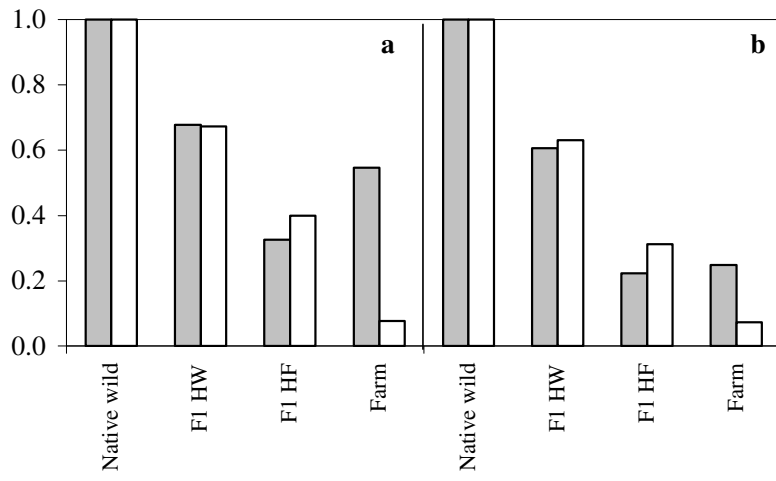
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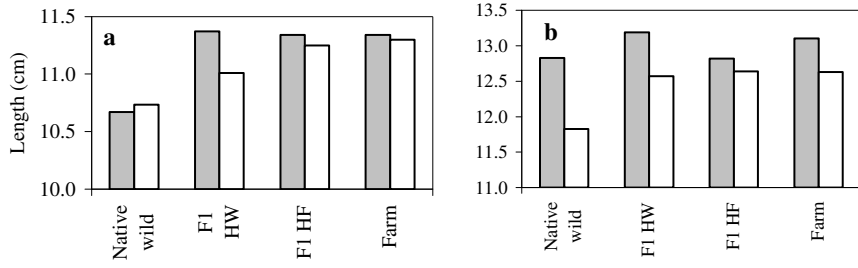
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