

1 Plasticity in response to feed availability - does feeding regime influence the relative
2 growth performance of domesticated, wild and hybrid Atlantic salmon *Salmo salar*
3 parr?

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9 Interactions of farm and wild Atlantic salmon

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23 ABSTRACT

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26 Growth of farmed, wild and F1 hybrid Atlantic salmon parr, *Salmo salar*, was investigated
27 under three contrasting feeding regimes in order to understand how varying levels of food
28 availability affects relative growth. Treatments consisted of standard hatchery feeding (*ad*
29 *libitum*), access to feed for 4h every day, and access to feed for 24h on three alternate days
30 weekly. Mortality was low in all treatments, and food availability had no effect on survival of
31 all groups. The offspring of farmed *S. salar* significantly outgrew the wild *S. salar*, while
32 hybrids displayed intermediate growth. Furthermore, the relative growth differences between
33 the farmed and wild *S. salar* did not change across feeding treatments, indicating a similar
34 plasticity in response to feed availability. Although undertaken in a hatchery setting, these
35 results suggest that food availability may not be the sole driver behind the observed reduced
36 growth differences found between farmed and wild fishes under natural conditions.

37 **Key words:** Escapees, Farmed, Food availability, Genetic interaction, Hybridisation,
38 Reaction norms

39 INTRODUCTION

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42 Aquaculture is undergoing rapid expansion on a global scale. However, there is increasing
43 evidence of a diverse array of negative consequences on both the natural environment and
44 wild fish stocks (Naylor *et al.*, 2000; McGinnity *et al.*, 2003; Heuch *et al.*, 2005). To ensure

45 the sustainability of aquaculture, especially at a time when many natural populations continue
46 to decline, greater understanding of the threats to wild populations and potential mitigation
47 strategies is required. Specifically for Atlantic salmon *Salmo salar* (Linnaeus 1758)
48 aquaculture, one of the world's most socio-economically important farmed fishes, several
49 challenges to sustainability have been identified, including, parasitic sea lice *Lepeophtheirus*
50 *salmonis* (Krøyer 1837) and farm escapees (Taranger *et al.*, 2014).

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53 Each year, numerous farmed *S. salar* escape into the wild. While most escapees fail to recruit
54 (Skilbrei *et al.*, 2014), some enter rivers and attempt to spawn with wild *S. salar* (Lura and
55 Saegrov, 1991; Webb *et al.*, 1993; Saegrov *et al.*, 1997). Following successful spawning,
56 genetic changes in native salmonid populations have been demonstrated in Ireland (Crozier,
57 1993; Clifford *et al.*, 1997), Canada (Bourret *et al.*, 2011) and Norway (Skaala *et al.*, 2006;
58 Glover *et al.*, 2012; 2013). Wild salmonid populations may be locally adapted to their native
59 rivers (Taylor, 1991; Garcia de Leaniz *et al.*, 2007; Fraser *et al.*, 2011), and experimental
60 studies have demonstrated that offspring of farmed *S. salar* display significantly reduced
61 survival in the wild compared to wild *S. salar* offspring (McGinnity *et al.*, 1997; Fleming *et*
62 *al.*, 2000; McGinnity *et al.*, 2003; Skaala *et al.*, 2012). Such findings indicate that
63 interbreeding of farmed escapees with wild fishes is likely to inflict a negative fitness effect
64 upon the native population.

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67 In addition to domestication selection (Glover *et al.*, 2004), aquaculture species typically
68 undergo directional selection for a variety of commercially important traits, for example
69 increased growth and late maturation (Gjedrem, 2000; 2010; Thodesen and Gjedrem, 2006).
70 The hatchery environment is typically characterised by high densities, a lack of predation, and
71 continuous feed availability. Farmed *Salmo salar* have exhibited changes in behavioural traits
72 such as increased aggression, higher stress resistance and decreased predator awareness that
73 are attributed to inadvertent selection resulting from the artificial hatchery environment
74 (Einum and Fleming, 1997; Fleming and Einum, 1997; Houde *et al.*, 2010a; b; Solberg *et al.*,
75 2013a; Debes and Hutchings, 2014). Thus, direct and indirect selection has resulted in
76 domesticated fishes that are adapted to their captive environment and that typically display
77 traits which may be maladaptive in the wild relative to their wild counterparts.

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79 Since *S. salar* farming began in the late 1960s, domestication selection has been primarily
80 directed at growth, with gains of up to 15% per generation seen in farmed *S. salar* (Gjedrem
81 *et al.*, 1991; Thodesen and Gjedrem, 2006). Increased growth has been linked to an increased
82 appetite and food conversion efficiency in farmed *S. salar* (Thodesen *et al.*, 1999; Gjedrem,
83 2000). Growth is mediated by the growth hormone (GH) in most vertebrates, including fish
84 (Björnsson, 1997). Studies have documented higher levels of GH (Fleming *et al.*, 2002) and
85 IGF-I (insulin-like growth factor I) (Solberg *et al.*, 2012; although no changes were detected
86 in Bicskei *et al.*, 2014) in farmed *S. salar* compared to wild conspecifics, suggesting that
87 selection for growth in farmed fishes stimulates shifts in endocrine control. Growth hormone
88 influences appetite, feed conversion efficiency, foraging behaviour (through increased
89 movement and risk taking), and may influence aggression (Neregård *et al.*, 2008a; b). Farmed
90 *S. salar* exhibit differences relative to wild *S. salar* in all of the above behavioural traits
91 (Fleming and Einum, 1997; Thodesen *et al.*, 1999; Houde *et al.*, 2010a), supporting the

92 endocrine findings of Fleming *et al.* (2002) and Solberg *et al.* (2012). Increased GH levels
93 are also linked to a higher metabolism (Björnsson, 1997). It has been suggested that higher
94 levels of growth may incur a metabolic cost when resources are low or predation levels are
95 high, such as in the wild (Sundt-Hansen *et al.*, 2009). For example Sundt-Hansen *et al.* (2012)
96 found that while GH-treated *S. salar* grew optimally under standard hatchery conditions (*ad*
97 *libitum* feeding) their growth was negatively affected by the GH treatment under natural
98 stream conditions.

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101 When studied under hatchery conditions, growth differences of up to 2-3 fold exist between
102 offspring of farmed and wild *S. salar* (Fleming and Einum, 1997; Glover *et al.*, 2009; Solberg
103 *et al.*, 2013a; b). In contrast, studies in the wild have shown that growth differences between
104 farmed and wild *S. salar* are lower than in hatchery-reared *S. salar* (Fleming *et al.*, 2000;
105 Skaala *et al.*, 2012). Thus, the question arises: what causes such differences in the relative
106 growth rates of wild and farmed *S. salar*? Several potential explanations exist, including
107 behavioural changes associated with higher growth in farmed *S. salar*, such as less efficient
108 foraging behaviour, increased aggression and higher risk behaviour. Such behaviours will
109 incur a higher metabolic cost, thus, while faster growth is often linked to higher fitness, such
110 behavioural-mediated trade-offs may limit growth and survival of individuals with higher
111 growth rates in the wild through reduced starvation tolerance and increased predation risk
112 (Martin-Smith *et al.*, 2004; Biro *et al.*, 2006). An especially pertinent factor influencing
113 growth differences between farmed and wild fishes is variation in resource availability,
114 specifically levels of food availability between the hatchery and the wild. Under standard
115 hatchery conditions feed is readily available, and thus not limiting growth, while the

116 frequency and nature of food in the wild is often more heterogeneous in time and space
117 (Jonsson and Jonsson, 2011). It is possible that generations of direct and inadvertent
118 domestication selection in farmed fishes will have resulted in a decreased ability to cope with
119 the typically variable feed availability in the wild environment. Elucidating the factors
120 influencing the ability of escaped farmed fishes in the wild to forage effectively crucially
121 represents a key component of risk assessment.

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124 In order to elucidate the potential mechanisms underlying the observed larger growth rate of
125 farmed vs. wild fishes in the hatchery, contrary to trends detected in the wild, here the
126 influence of varying levels of food availability on relative growth performance was examined.
127 Growth of farmed, wild and F1 hybrid *S. salar* under three feeding regimes differing in
128 availability and frequency of feed were examined under hatchery conditions. A gradient of
129 feed availability were selected, ranging from the farmed environment (*ad libitum*) towards the
130 wild environment (patchy and restricted).

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133 MATERIALS & METHODS

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136 FAMILY PRODUCTION

137 The farmed, hybrid and wild *S. salar* families used in this study were produced in November
138 2013 (week 46) at Matre Research station, Institute of Marine Research (IMR), Norway.
139 *Salmo salar* originating from the commercial farmed Mowi strain, and wild *S. salar* caught in
140 the River Etne (59°40'N, 5°56'E), were used to produce seven pure farmed, seven pure wild,
141 and seven F1 hybrid families (SI Table I). Mowi represents one of the oldest Norwegian
142 domestic *S. salar* strains (Gjedrem *et al.*, 1991) and has been selected for, among other traits,
143 increased growth rate, and is known to display significantly higher growth rates under
144 standard hatchery conditions in comparison with the offspring of wild *S. salar* (Glover *et al.*,
145 2009; Solberg *et al.*, 2013a; b). However, in the wild, this farmed strain only displays slightly
146 higher growth rates than the offspring of wild *S. salar* (Skaala *et al.*, 2012). The three strains
147 are from here on referred to as farmed, wild and hybrid groups.

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150 The *S. salar* stock in the River Etne is the largest in Hordaland, Norway. Wild adult
151 broodstock were collected in this river in the autumn of 2013 by angling, and transferred to
152 the local hatchery and held until stripping of gametes. Fish scales were read on individuals to
153 validate that they were indeed born in the wild and were not farmed escapees (Lund and
154 Hansen, 1991). The F1 hybrid *S. salar* were produced by crossing farmed females and wild
155 males (Mowi ♀ x Etne ♂). Five of the seven hybrid families were maternal and paternal half-
156 siblings with the farmed and wild families, respectively. One hybrid family was paternal half-
157 siblings to one wild family and one hybrid family was maternal half-siblings to one farmed
158 family.

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161 Eyed eggs from families were sorted into hatchery trays representing the single-strain
162 replicate treatments in week 5 of 2014. Each replicate treatment consisted of 20 eggs per
163 family of each group, yielding 140 eggs in each of 18 tanks. Each replicate was start-fed and
164 thereafter reared in 1.5 m³ tanks at ambient water temperature (varying from 12.5 to 13°C
165 during the experimental period). The treatments began when start feeding commenced in
166 week 18, with fish fed on Skretting Nutra pellets (www.Skretting.com), which were size
167 adjusted according to manufacturer's tables. The *S. salar* were kept on a 24 h photoperiod
168 from transfer to tanks until experiment termination as per standard hatchery conditions, also
169 known to reduce the development of precocious males (Good *et al.*, 2015).

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172 EXPERIMENTAL DESIGN

173 *Salmo salar* were reared in single-strain treatment tanks (two replicates/ treatment) with three
174 contrasting feeding regimes (Table I). The first treatment was regarded as the standard
175 hatchery control, and involved feeding *S. salar* continually with automatic feeders 24 h a day,
176 every day, with an excess ration. The second treatment consisted of providing *S. salar* with an
177 excess ration for 4 h every day (thus 20 h without any feeding each day), referred to as the
178 daily restricted treatment. The third treatment involved feeding an excess ration for 24 h on
179 three alternative days in a week (Monday, Wednesday, and Friday), referred to as the
180 triweekly treatment. The selected gradient of feed availability, ranging from the farmed
181 environment (*ad libitum*) towards the wild environment [patchy and restricted (Jonsson and
182 Jonsson, 2011)] was designed in order to elucidate how growth differences between strains
183 change with variable levels of food availability. Thus, treatments were chosen to represent a
184 gradient in feeding opportunity from standard excess hatchery ration (treatment 1) to a more

185 limited feed supply (treatment 3). Treatments are referred to as the control, daily restricted
186 and triweekly treatments respectively.

187 The experiment was continued for 20 weeks, and terminated in week 37, 2014 *i.e.* *S. salar*
188 were reared from egg to the parr stage. Upon termination, all *S. salar* in each tank replicate
189 were euthanised with an overdose of Finquel® Vet anaesthetic (<http://www.aqui-s.com>,
190 Årnes, Norway), and recordings of individual wet mass and fork length (L_F) were measured.
191 A total of 2329 individuals were sampled.

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194 STATISTICAL ANALYSIS

195 Statistical analysis was carried out using R version 3.2.2, and all critical P-values were set to
196 0.05 unless otherwise stated (R Core Team, 2014).

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199 Mortality from week 5 (sorting into hatchery trays) to week 18 (commencement of
200 experimental treatments) was low overall (<0.02%). Mortality for each tank was recorded
201 during the experimental period. To investigate whether different feeding regimes or group
202 origin had any effect on survival, a generalized linear mixed effect model (GLMM) was fitted
203 using the *glmer* function in the *lme4* package (Bates *et al.*, 2014). The full model included the
204 fixed covariates of group (G = representing the three groups; farmed, hybrid, and wild),
205 treatment (T = representing the three feed treatments; control, daily restricted, and triweekly),

206 and their interaction term (T_G). Tank was included in the model as a random intercept
 207 covariate (b_t):

$$208 \quad \text{logit}(Y) = \beta_0 + \beta_1 T + \beta_2 G + \beta_3 T_G + b_t + \varepsilon \quad (1)$$

209 where β_0 is the model intercept and ε is a random error term. The response variable, survival,
 210 was binary, and thus a binomial distribution was used, with the default logit link function. The
 211 random effect structure was investigated by plotting the 95% prediction intervals of the
 212 random effect using the *dotplot* function of the *lattice* package. If any of the tanks did not
 213 overlap zero, the effect was retained in the model. The *mixed* function from the *afex* package
 214 was used to investigate the significance of the fixed covariates (Singmann and Bolker, 2014).
 215 The function calculates type 3-like P -values for each fixed covariate based on parametric
 216 bootstrapping (Singmann and Bolker, 2014).

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219 A linear mixed model (LME) was used to investigate the effect of group origin and feeding
 220 regime treatment on *mass* at termination. The response variable was logged *mass* at
 221 termination. The full model covariates were identical to the mortality model described above:

$$222 \quad Y = \beta_0 + \beta_1 T + \beta_2 G + \beta_3 T_G + b_t + \varepsilon \text{ where } \varepsilon \sim N(0, \sigma^2) \quad (2)$$

223 where β_0 is the model intercept and ε is the normally distributed error term. The LME model
 224 was fitted using *lmer* from the *lme4* package in R (Bates *et al.*, 2014). The random effects
 225 structure was investigated as described above; similarly the P -values for the fixed effects
 226 were calculated as above while using the Kenward-Roger approximation for degrees of
 227 freedom.

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230 **Post-hoc** multiple comparisons were carried out using the function *pairs* in the *lsmeans*
231 package with a Tukey adjustment for multiple comparisons, which calculates the differences
232 of least squares means for the factor covariates of the fixed part of the final model (Lenth,
233 2015). The test computes all pair-wise comparisons of the interaction terms (Group x
234 Treatment), and reports **P**-values and **95%** confidence intervals for all comparisons (Lenth,
235 2015).

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238 **ETHICAL STATEMENT**

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241 The experimental protocol (permit number 6447) was approved **23** March 2014, by the
242 Norwegian Animal Research Authority (NARA). All welfare and use of experimental animals
243 was performed in strict accordance with the Norwegian Animal Welfare Act. In addition all
244 personnel involved in this experiment had undergone training approved by the Norwegian
245 Food Safety Authority, which is mandatory for all personnel running experiments involving
246 animals included in the Animal Welfare Act.

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249 RESULTS

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252 SAMPLING & DATA

253 The experiment was terminated in week 37 of 2014, when 2329 *S. salar* were sampled from
254 the 18 tanks. Five individuals were identified as outliers due to extreme condition factors
255 caused by recording errors and removed from the dataset prior to statistical analysis, thus the
256 final dataset consisted of 2324 *S. salar*.

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259 MORTALITY

260 Overall, mortality within each treatment was low, ranging from 3.2 to 10.4 % (Table I),
261 typically within the range observed from start-feeding to first autumn stage. None of the fixed
262 effects were found to be significant (Table II), thus mortality did not differ between
263 treatments or between strains. The random effect of tank replicate was found to be significant
264 and thus controlled for by being retained in the final model.

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266

267 GROWTH

268 All *Salmo salar* (*i.e.*, farmed, hybrid and wild) grew better in the control treatment than in the
269 two more restricted treatments, and growth within all groups was observed to be lowest in the
270 daily restricted treatment (Table III; Fig. 1). Farmed *S. salar* were larger than both hybrid and

271 wild *S. salar* at each treatment, and the hybrids displayed intermediate growth (Fig. 1). There
272 was a marginally significant treatment-by-group interaction effect detected ($P=0.05$); however
273 the relative growth differences between the groups across treatments were very similar (SI
274 Table II, Fig. 2). The relative growth differences between the wild and farmed *S. salar* were
275 almost identical across treatments (1:1.5-1.6), as were the relative growth differences between
276 hybrid and farmed *S. salar* (1:1.2-1.3) (SI Table II, Fig. 2). Relative growth differences
277 between the wild and hybrid *S. salar* increase incrementally from the daily restricted
278 treatment (1:1.2) through the control treatment (1:1.3) to the triweekly treatment (1:1.4) (Fig
279 2), which is probably driving the marginally significant interaction of group and treatment in
280 the LME model ($P=0.05$). Possible variation between tank replicates was taken into account
281 in the initial model by including replicate as a random effect which was retained in the final
282 model despite the model output suggesting it be dropped due to lack of effect.

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285 DISCUSSION

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288 The present study investigated the effect of feed variability on growth and survival of farmed,
289 wild and F1 hybrid *S. salar* reared in single strain tanks. Understanding how farmed escapees
290 interact with wild conspecifics is an important part of developing management and mitigation
291 efforts for both conservationists and the aquaculture industry. In the hatchery, farmed *S. salar*
292 typically outgrow wild *S. salar* markedly (Fleming and Einum, 1997; Glover *et al.*, 2009;
293 Solberg *et al.*, 2013a; b), while in the wild, corresponding growth differences are much lower

294 (Fleming *et al.*, 2002; Skaala *et al.*, 2012). A striking difference between the farm and wild
295 environments is the levels of food availability; constant *versus* varying in time and space
296 (Jonsson and Jonsson, 2011). It is possible that plasticity in response to variable feed supply
297 differs between farmed and wild *fishes*, which may potentially contribute to the contrast in
298 growth differences observed between farmed and wild *fishes* in each environment. Here,
299 although a marginally significant interaction *was found* between group and treatment, similar
300 growth differences were observed between the farmed and wild *S. salar* across the feed
301 availability gradient ranging from the farmed environment (*ad libitum*) to conditions more
302 resembling the wild environment (patchy and restricted). Thus *S. salar* of both origins
303 responded in a comparable manner relative to the varying levels of food availability,
304 indicating a similar plasticity in response to feed availability. Mortality was low both within
305 and among the treatments, indicating no effect of treatment or group origin on survival.

306 River environmental conditions, such as fluctuating natural food availability, can adversely
307 affect the growth of fast growing *fishes* due to metabolic costs (Sundt-Hansen *et al.*, 2012). In
308 the present study growth of the farmed, hybrid and wild *S. salar* decreased along a food
309 availability gradient ranging from the farmed environment to conditions more resembling the
310 fluctuating levels in the wild. Lowest growth was observed in the daily restricted feeding
311 regime -the most variable food availability. Growth was significantly different between the
312 groups at all treatments, indicating an effect of feed availability on growth in all groups.

313 Farmed *S. salar* were significantly larger than the wild *S. salar* in all treatments, and hybrid
314 growth was intermediate between the farmed and wild *S. salar*. Despite differing growth
315 rates, farmed and wild *S. salar* responded identically to the increasingly variable food supply,
316 as shown by the similar relative growth differences and low mortality observed across the
317 treatments. This indicates that more than 10 generations of directional selection with
318 contentious access to feed has not resulted in farmed *S. salar* displaying reduced abilities to

319 cope with fluctuating and/or restricted levels of feed by not being able to maintain their
320 elevated growth rate as compared to wild *S. salar*. Morris *et al.* (2011) found that the response
321 to compensatory growth (CG) in farmed, wild and hybrid (including backcrossed) *S. salar*
322 was similar between the groups, although the mean control and CG growth rates were highest
323 in the farmed group. This indicates that although selection has acted on growth, farmed *S.*
324 *salar* have not lost their plastic ability to respond to a lack of food through compensation by
325 increasing their growth rates when food becomes available (Morris *et al.*, 2011).

326 The growth differences between farmed and wild *S. salar* observed in all treatments were, on
327 average, less than previously documented in hatchery studies (Glover *et al.*, 2009; Solberg *et*
328 *al.*, 2013a; b). It is still evident however that multiple generations of selection for growth in
329 farmed *S. salar* have resulted in significant elevated growth relative to wild *S. salar*. Under
330 typical hatchery conditions, where food supply is constant, generally uniform and plentiful,
331 growth differences between farmed and wild *S. salar*, as much as 3- to 5-fold, have been
332 observed (Solberg *et al.*, 2013a; b). Glover *et al.* (2009) investigated various trait differences
333 between farmed, wild and F1 hybrid *S. salar* throughout the farming production cycle,
334 including growth. For two experimental cohorts they found that at the freshwater stage the
335 wild *S. salar* had mean weights of 1:1.6 and 1:2.4 relative to the farmed *S. salar*. However in
336 nature, farmed and wild *S. salar* grow more similarly. For example, Skaala *et al.* (2012) found
337 growth differences within three year classes of wild and farmed *S. salar* in the wild to be just
338 1:1.07, 1:1.25 and 1:1.06 respectively. In an attempt to understand these growth differences,
339 Solberg *et al.* (2013b) investigated the competitive balance between farmed, wild and hybrid
340 *S. salar* by comparing growth in standard hatchery conditions, and restricted feed conditions
341 in the hatchery and semi-natural environments. They found that the growth of farmed, hybrid
342 and wild *S. salar* became more similar as their environmental conditions approached natural
343 conditions. They hypothesised that the reduced growth differences observed in their study and

344 in the wild (Skaala *et al.*, 2012) could be due to size-selective mortality. The wild
345 environment favours the survival of faster growing individuals which can out-compete
346 smaller individuals for resources (negative size-selective mortality), while also selecting
347 against larger risky individuals through mortality by predation (positive size-selective
348 mortality). Positive size-selective mortality was, however, not tested directly in their study
349 (Solberg *et al.*, 2013b). Biro *et al.* (2006) demonstrated under natural conditions that domestic
350 rainbow trout, *Oncorhynchus mykiss* (Walbaum 1792), were able to grow faster than their
351 wild conspecifics due to increased foraging behaviour, and that these larger *O. mykiss* were
352 more susceptible to predation due to higher risk behaviour linked to foraging (Biro *et al.*,
353 2006). Although studies indicate reduced predator awareness (Houde *et al.*, 2010b) and
354 potentially increased tolerance to predation stress (Fleming and Einum, 1997; Debes and
355 Hutchings, 2014) in farmed relative to wild salmonids, no explicit evidence has been found
356 for increased predator susceptibility in farmed *S. salar* (Skaala *et al.*, 2014; Solberg *et al.*,
357 2015). In the wild, faster growing farmed *S. salar* may also incur a metabolic cost through
358 behavioural changes such as increased appetite (Thodesen *et al.*, 1999) and foraging (Biro *et*
359 *al.*, 2006) which result in their expending more energy searching for food under low food
360 availability conditions, leading to lower growth (Sundt-Hansen *et al.*, 2009). The
361 juxtaposition of these potential positive and negative size-selective forces may partly explain
362 why growth differences seen in the wild are not as pronounced as in the hatchery environment
363 (Solberg *et al.*, 2013b).

364 Growth in the wild may also be influenced by other environmental factors, such as density
365 and competition (Einum and Fleming, 1997; Bohlin *et al.*, 2002), and even natural stream
366 conditions like substrate composition and flow rate (Jonsson and Jonsson, 2011). In
367 comparative studies inter-strain competition between farmed, wild and hybrid groups could
368 potentially influence the levels of relative growth differences observed. Thus, as the groups

369 were reared in separate tanks, the lack of inter-strain competition in the present study may
370 potentially explain the lower relative growth differences observed. A study examining the
371 relative growth differences of the same groups of farmed, hybrid and wild *S. salar* in both
372 single strain and common garden experiments however found no difference in the relative
373 growth differences across experimental designs (Solberg *et al.*, 2013b). Therefore, it is
374 concluded that the present experimental design is unlikely to drive the lower relative growth
375 differences, and any potential tank effects were controlled for in the statistical model.

376 Based upon population genetic analyses, genetic changes in the population inhabiting the
377 River Etne have been observed (Glover *et al.*, 2012; 2013), and some level of admixture with
378 farmed escapees has been demonstrated. It is therefore not possible to exclude the possibility
379 that although the wild *S. salar* used in this study were indeed born in the wild (based upon
380 scale reading), some individuals used as broodstock may represent some admixture with
381 farmed escapees. This might explain why smaller growth differences were detected between
382 the farmed and wild *S. salar* in this study, as compared to other studies of the same strains
383 (Solberg *et al.*, 2013a).

384 In the present study the hybrids displayed intermediate growth relative to both their farmed
385 and wild conspecifics. There were slight differences in the slopes between each treatment for
386 the hybrids, versus the farmed and the wild *S. salar*, that likely resulted in the marginally
387 significant ($P=0.05$) group by treatment interaction. Intermediate hybrid growth relative to
388 their parental strains has been observed in similar studies under hatchery (Glover *et al.*, 2009;
389 Morris *et al.*, 2011; Solberg *et al.*, 2013a), semi-natural (Solberg *et al.*, 2013b), and wild
390 conditions (McGinnity *et al.*, 1997). There was no evidence for hybrid vigour or outbreeding
391 depression, whereby hybrids either perform better relative to their parents or display reduced
392 fitness due to under-dominance, respectively. The hybrids in the present study were maternal
393 half siblings to the farmed *S. salar*; therefore it is possible that maternal effects were

394 influencing growth, although maternal effects are considered to be low at this life stage
395 (Gilbey *et al.*, 2005). Bicskei *et al.* (2014) examined gene transcription in farmed, F1 hybrid
396 and wild *S. salar* at two early life stages, and found fewer significantly differentially
397 expressed transcripts between farmed and hybrid individuals than between hybrid and wild
398 individuals. Their hybrid crosses were generated from the farmed females, suggesting that
399 maternal effects might account for this bias (Bicskei *et al.*, 2014), highlighting the need for
400 reciprocal hybrid crosses in comparative studies.

401 In summary, the results of the present study have demonstrated that the three feeding regimes
402 implemented here did not influence the relative growth rate of farmed, hybrid and wild *S.*
403 *salar* in the hatchery. Thus, while restricted to the hatchery, the present study provides
404 evidence that variable food availability may not be the primary source governing the similar
405 growth between farmed and wild *S. salar* in natural environments. Similarly, no evidence was
406 found to indicate that more than 10 generations of adaption to the farmed environment, with
407 continuous access to feed, has resulted in farmed *S. salar* exhibiting a reduced tolerance to
408 limited or fluctuating levels of feed. Additional observations are required however that better
409 simulate natural variation in food supply, which is typically not only variable in composition,
410 but also varies markedly in time and space (Jonsson and Jonsson, 2011). It therefore remains
411 a priority to elucidate further the nature of hybridisation and farm-wild interactions. Further
412 studies in particular, exploring the key environmental differences between hatchery and wild
413 environments (*e.g.*, predation, density) are evidently required, in conjunction with direct
414 comparison of performance in respective conditions.

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416

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418

419

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593 northern Scottish rivers: egg deposition by females. *Aquaculture and Fisheries Management*
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1 TABLES

2 Table I: Experiment design. Each treatment consisted of two replicate tanks for each single
 3 group = 18 tanks in total. **Twenty** eggs from each family **of *Salmo salar*** within a group were
 4 sorted into each replicate tank = 2250 eggs in total. Average **mass (M)**, standard deviations
 5 (**S.D.**) and mortality are presented for each group within each tank replicate and pooled
 6 treatment. The pooled **mass** and mortality were calculated as averages of the total **mass** and
 7 mortality in the replicates of each treatment.

Treatment	Group	Tank	Initial <i>n</i>	Sampled <i>n</i>	Mean M (g)	S.D. (±)	Pooled W	Mortality <i>n</i>	Pooled mortality (%)
Daily Restricted	Farm	1	20 eggs	125	24.5	4.9	24.5	15	9.3
		2	per	129	24.5	4.9		11	
	Hybrid	3	family	117	19.4	5.7	19.4	23	10.4
		4	- 140	134	19.3	5.4		6	
	Wild	5	fish per	136	15.8	6.2	16.1	4	3.2
		6	tank	135	16.5	5.4		5	
Control	Farm	7	20 eggs	127	43.7	12.0	43.1	13	9.6
		8	per	126	42.5	10.6		14	
	Hybrid	9	family	131	34.4	8.8	36.4	9	8.6
		10	- 140	125	38.3	9.2		15	
	Wild	11	fish per	125	28.7	9.3	28.9	15	9.3
		12	tank	129	29.0	9.0		11	
Triweekly	Farm	13	20 eggs	127	36.4	8.7	36.1	13	6.4
		14	per	135	35.8	7.9		5	
	Hybrid	15	family	130	31.9	8.0	30.9	10	7.1
		16	- 140	130	29.9	7.1		10	
	Wild	17	fish per	134	22.4	8.5	22.6	6	4.3
		18	tank	134	22.9	9.1		6	

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10 Table II: P values of the fixed effects of the GLMM model investigating survival. The
11 Statistic represents a Chi-square value calculated as two- times the difference in likelihood
12 between full and restricted model as specified by the *afex* package.

Effect	Statistic	P value
Treatment	1.47	0.57
Group	0.08	0.97
T x G	4.45	0.57

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15 Table III: P values of the fixed effects of the LME model investigating growth. The F denotes
16 the F statistic, Num Df denotes the numerator degrees of freedom and Den Df denotes the
17 denominator degrees of freedom.

Effect	F	Num Df	Den Df	P value
Treatment	129.39	2	9.12	<0.0001
Group	74.32	2	9.25	<0.0001
T x G	3.67	4	8.99	0.05

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1 **FIGURE CAPTIONS**

2 Figure 1: Average (a) mass and (b) \log_{10} mass \pm S. E of each group (farm, hybrid and wild
3 Atlantic *Salmo salar*) across each feeding treatment (triweekly, daily restricted, control/*ad*
4 *libitum*). Log mass was examined in the statistical analysis.

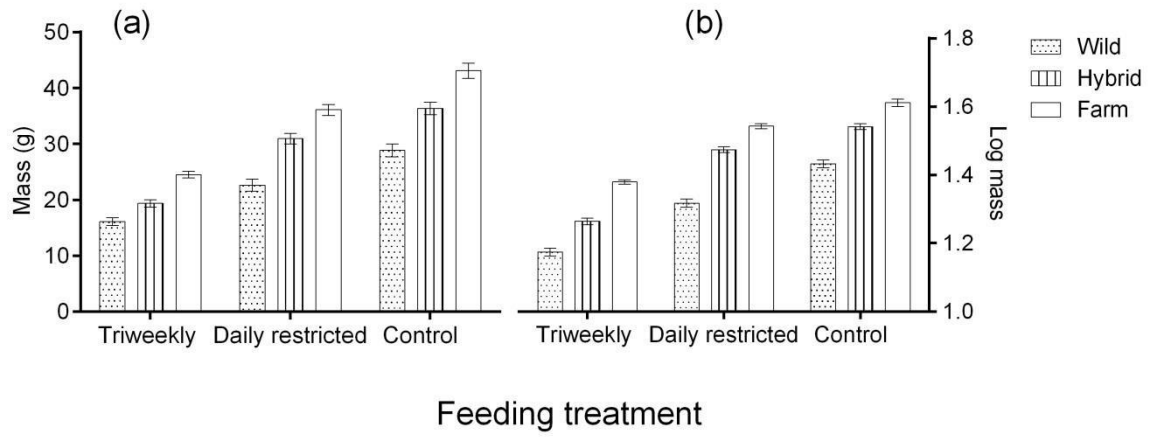
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6 Figure 2: (a) Relative growth reaction norms for each group (farm, hybrid and wild Atlantic
7 *Salmo salar*) and (b) their average log mass across the feeding treatments. In (a) the hybrid
8 and farmed groups are compared to the wild group within each treatment (based upon their
9 untransformed mass). The x-axis shows the feeding treatments (triweekly, daily restricted,
10 control/*ad libitum*).

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1 **FIGURES**

2 Figure 1



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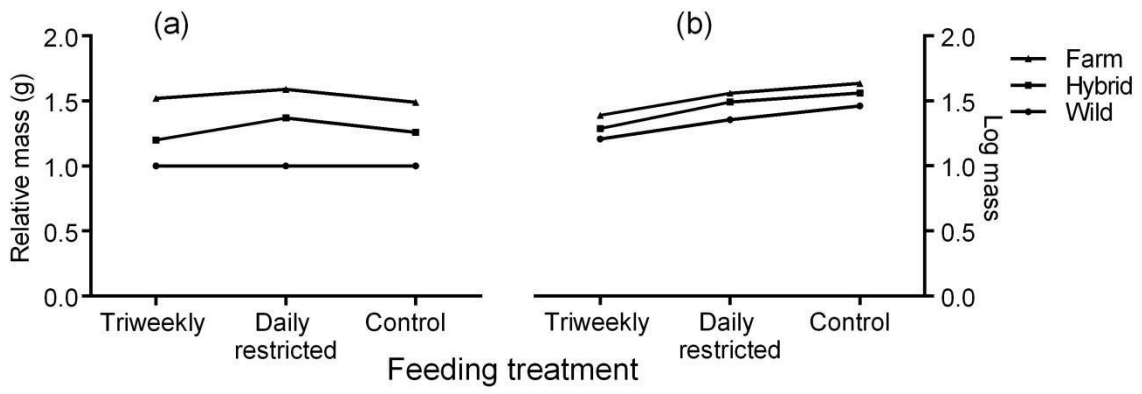
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15 Figure 2



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1 **SUPPLEMENTARY TABLES**

2 Table SI: Family crosses for the experiment. The commercial farmed strain Mowi and the
 3 wild strain Etne were used to make seven pure wild, seven pure farmed and seven hybrid F1
 4 groups. The hybrid families were made by crossing a female farmed *S. salar* with a wild
 5 male. Five of the seven hybrid families are half-siblings to five wild and five farmed families,
 6 and one family is maternal half siblings to one farmed family and one family is paternal half
 7 siblings to one wild family.

Family	Dam	Sire	Group
1	M1	M9	Farm
2	M1	E11	Hybrid
3	M2	M10	Farm
4	M2	E12	Hybrid
5	M3	M11	Farm
6	M3	E13	Hybrid
7	M4	M12	Farm
8	M4	E14	Hybrid
9	M5	M13	Farm
11	M6	M14	Farm
12	M6	E16	Hybrid
14	M7	E17	Hybrid
15	M8	M16	Farm
16	M8	E18	Hybrid
17	E1	E11	Wild
18	E2	E12	Wild
20	E4	E14	Wild
21	E5	E15	Wild
22	E6	E16	Wild
23	E7	E17	Wild
24	E8	E18	Wild

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13 Table II: Relative growth differences between each group within each treatment and Tukey adjusted P -values for the multiple pair-wise
 14 comparisons of groups within each treatment. The P -values are shown in the bottom left diagonal, and the significance level was set to 0.05,
 15 with non-significant P -values indicated in bold. Each group within a treatment was significantly different to each other group within that
 16 treatment. The relative growth differences between each group within each treatment are shown in bold in the top right section. The average
 17 mass of each group was compared to the average mass of the other groups by dividing the larger mass by the smaller mass (*i.e.* farm to wild),
 18 creating a relative growth difference ratio. Relative growth differences were not compared across treatments. Daily R corresponds to the daily
 19 restricted treatment and triweek corresponds to the triweekly treatment.

	DAILY R Farm	DAILY R Hybrid	DAILY R Wild	CONTROL Farm	CONTROL Hybrid	CONTROL Wild	TRIWEEK Farm	TRIWEEK Hybrid	TRIWEEK Wild
Mass (g)	24.51	19.345	16.125	43.09	36.355	28.845	36.09	30.91	22.64
DAILY R Farm	/	1: 1.3	1: 1.5						
DAILY R Hybrid	0.0005	/	1: 1.2						
DAILY R Wild	<0.001	0.0033	/						
CONTROL Farm	<0.001	<0.001	<0.001	/	1: 1.2	1: 1.5			
CONTROL Hybrid	<0.001	<0.001	<0.001	0.0181	/	1: 1.3			
CONTROL Wild	0.0825	<0.001	<0.001	<0.001	0.0007	/			
TRIWEEK Farm	<0.001	<0.001	<0.001	0.0189	1	0.0007	/	1: 1.2	1: 1.6
TRIWEEK Hybrid	0.0022	<0.001	<0.001	<0.001	0.0203	0.2231	0.0199	/	1: 1.4
TRIWEEK Wild	0.0366	0.0786	0.001	<0.001	<0.001	0.0006	<0.001	0.001	/

