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1 Effect of parental phenotype on dispersal, growth and maturation of offspring in wild
2 masu salmon (*Oncorhynchus masou*)

3

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13 Running head: Parental effects on offspring traits

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16

17 **Author contributions:** TY, SK and NBM conceived the ideas for the manuscript; TY
18 and SK led the project and designed methodology; TY and NBM led the writing of the
19 manuscript and SK provided data. All authors contributed critically to the drafts and
20 gave final approval for publication.

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22

23

24 **Abstract**

25 Offspring traits are influenced by complex interactions among parent genotypes and
26 phenotypes. However, ecological studies of these effects have tended to focus on one of
27 either maternal or paternal influences. In this study, we investigated the effects of both
28 parental phenotypes on offspring dispersal, growth and early sexual maturity in masu
29 salmon. We used wild-caught parental fish in a half-sib mating design that allowed
30 comparison of offspring from males of two different life-history types (precocious
31 males that had lived only in fresh water and anadromous males that had migrated to the
32 sea). These males were mated with anadromous females and the eggs planted in natural
33 streams in three different years. Natal dispersal distance depended on offspring sex,
34 body size and paternal life history: female offspring moved further downstream than
35 males, whilst daughters of precocious fathers tended to move further downstream than
36 those of anadromous sires. There was a maternal effect on offspring growth, with larger
37 eggs resulting in larger offspring at least until these became precociously mature at the
38 end of the first summer. However, while faster growing male offspring were more likely
39 to become precociously mature, there was no evidence that the probability of precocious
40 maturation was influenced by parental life history. We conclude that, although body size
41 of young salmon was significantly influenced by egg size and there were sex differences
42 in dispersal, their growth rate and divergence in life history types were mainly
43 environmentally driven.

44

45 **Keywords** Natal dispersal · Life history strategies · Egg size · Inheritance · Maternal
46 effects · Paternal effects

47 **Introduction**

48

49 The phenotype of an offspring is influenced by both the genotype of its parents and non-
50 genetic ‘parental’ effects that they pass on (Mousseau and Fox 1998; Badyaev and Uller
51 2009). These non-genetic parental effects are complex and can influence offspring traits
52 through many routes including mate choice, maternal and paternal care, parental
53 nutritional state and allocation of resources (Crean and Bonduriansky 2014). The
54 genetic and non-genetic components of the parental phenotype often interact: as an
55 example, an individual’s body size or age at maturity have been shown to be influenced
56 by both its genotype and the environment in which it has lived, and can in turn affect the
57 phenotype and fitness of its offspring (Evans et al. 2015; Monaghan et al. 2020). Thus,
58 identifying the links between parental phenotypes and the phenotypes of their offspring
59 is critical to understand ecological and evolutionary dynamics.

60 For organisms that provide no parental care, the extent of non-genetic parental effects
61 is mainly restricted to prenatal provisioning of the embryo. This has primarily been
62 assumed to be under maternal control – for example, across a wide range of taxa larger
63 females produce comparatively larger eggs/offspring, which in turn affects their growth,
64 age at maturity and fitness (Marshall et al. 2010; Krist 2011). However, the assumption
65 that non-genetic paternal effects are negligible in species that lack parental care has
66 been challenged by studies that show the transmission of non-genetic paternal factors
67 for offspring traits (Evans et al. 2004; Eilertsen et al. 2009; Aich et al. 2020).

68 Since Mousseau and Fox’s (1998) seminal review there have been many studies
69 evaluating the importance of parental influences on offspring performance. However,
70 the majority have focussed on either maternal or paternal effects, with few attempting to

71 compare the relative importance of the two parents in shaping offspring traits.
72 Understanding the interaction between the phenotypes of the two parents is important
73 because the literature suggests that maternal and paternal effects can have very different
74 evolutionary consequences (Crean and Bonduriansky 2014). Moreover, the importance
75 of parental influences may be dependent on the gender of the offspring. Sex-specific
76 maternal effects have been reported in several species. For instance, in seed beetles
77 *Callosobruchus maculatus*, maternal effects were observed on the lifespan of sons but
78 not daughters (Fox et al. 2004), whereas in mosquitofish *Gambusia holbrooki* the
79 phenotype of the mother affected the body size of her daughters but not that of her sons
80 (Kruuk et al. 2015). Paternal effects dependent on gender are perhaps most likely when
81 there are two contrasting male phenotypes, such as alternative mating strategies (e.g.
82 males that control reproductive resources *versus* those that exhibit opportunistic mating
83 such as sneaking) (Gross 1996; Taborsky 2001). Sex-specific paternal influences have
84 indeed been found in the cichlid fish *Lamprologus callipterus*, with different growth
85 patterns of sons sired by large nest-owning males compared to sons of dwarf sneaker
86 males, but no difference in the growth rates of daughters of the two kinds of male
87 (Wirtz-Ocaña et al. 2013). However, there are few such studies that have investigated
88 the extent to which the parental effects differ for sons and daughters (possibly because it
89 is often difficult to measure traits in both parents and in both sexes of offspring), even
90 though traits in addition to growth rate are likely to be under different selection
91 pressures in sons and daughters. One such trait is natal dispersal. The advantages of
92 dispersal are to avoid local competition for food and inbreeding, including with parents
93 (Perrin and Mazalov 1999), but in many species the patterns of natal dispersal differ
94 between sons and daughters due to sex-related costs and benefits of philopatry (Dobson

95 2013). It is therefore possible that the phenotype of the mother or the father could
96 influence the direction or scale of natal dispersal, and that any such effect will depend
97 on the sex of the offspring. However, this has rarely been investigated (but see Tschirren
98 et al. 2007). It is also important to study parental influences in an appropriate setting,
99 but the great majority of previous studies of parental phenotype on offspring
100 performance have been performed in the laboratory rather than in the wild (e.g. Evans et
101 al. 2004; Aich et al. 2020). This means that such findings – in particular those related to
102 offspring traits such as movement patterns, growth and survival – may not be easily
103 generalized to natural settings and so their evolutionary importance is not clear.

104 Salmonid fishes are ideal species for teasing apart the maternal and paternal
105 influences on offspring performance, and to explore whether such influences are
106 dependent on offspring gender, for a number of reasons. They have no parental care and
107 fertilisation takes place externally (making it possible to conduct IVF half-sib mating
108 experiments that allow separation of maternal and paternal influences), offspring sex
109 can be genetically analysed (Yano et al. 2012), and they produce enough offspring per
110 family for it to be possible to quantify family-specific survival rates in the field. They
111 also exhibit distinct and measurable sex-specific reproductive traits, such as variation in
112 egg size that is negligible within females but substantial among them (Beacham and
113 Murray 1985; Fleming and Gross 1990), and diverse life history strategies within
114 species (Fleming and Reynolds 2004). In most salmonid species two basic life history
115 patterns can be observed: the anadromous life history (in which the fish migrate to sea
116 after a juvenile phase in fresh water, and later return to their natal site to breed), and the
117 resident life history in which the fish remain in fresh water throughout their life. The
118 prevalence of the two strategies is dependent on environmental conditions, but both can

119 coexist in the same population – most frequently when a fraction of the males grow fast
120 and mature precociously without going to sea, and then attempt to fertilise eggs by
121 sneaking whereas the (much larger) anadromous males gain fertilisations through
122 fighting for priority of access to spawning females; there is thus diversity in mating as
123 well as migratory strategies.

124 Here we explore sex-specific parental influences on offspring performance in the
125 wild, using masu salmon *Oncorhynchus masou*. In this species natal dispersal is sex-
126 biased, with males tending to remain in a river's upper reaches while females disperse
127 downstream to the mid and lower reaches (Mayama 1989; Nagata and Irvine 1997). The
128 reason is believed to be related to the fact that usually only males become precociously
129 mature, and so on average breed at a younger age than females; males that become
130 precociously mature will benefit from establishing feeding territories close to the
131 spawning areas. In contrast, females will all eventually migrate to sea and so have no
132 immediate reason to stay close to the spawning areas; instead juvenile females may
133 benefit from reduced competition for feeding areas if they move further downstream,
134 away from the males. This suggests that if the male offspring of precocious males are
135 themselves more likely to become precociously mature, the life history pattern of a
136 father may influence the dispersal pattern of his sons (but not his daughters). We can
137 also predict that the paternal life history strategy in salmonids (anadromous versus
138 precocious) may influence offspring performance through an effect on metabolic rate,
139 given that offspring of sneaker salmon have been found to have higher metabolic rates
140 than those of anadromous males (Van Leeuwen et al. 2016). The metabolic rate of
141 offspring could influence the rate at which they utilize their egg yolk reserves and hence
142 the date on which they emerge from the nest and try to establish a feeding territory. This

143 emergence date is known to have a strong influence on the chances of acquiring a
144 feeding territory and hence their early growth rate (Metcalf and Thorpe 1992; Einum
145 and Fleming 2000).

146 The purpose of this study was therefore to investigate the influence of maternal
147 egg size and paternal life history form on the dispersal pattern, growth, and early
148 maturation of offspring of each sex in a natural stream. We predicted the following:
149 First, that more male offspring remain in a river's upper reaches (i.e. near the spawning
150 grounds) than females. Second, that among males, the offspring of precocious males
151 and/or those hatched from larger eggs (presumed to be better competitors) remain
152 further upstream than would those from anadromous males and/or smaller eggs. Third,
153 offspring of precocious males and/or those hatched from larger eggs grow faster than
154 those from anadromous males and/or smaller eggs. Fourth, male offspring of precocious
155 males and/or those hatched from larger eggs would be more likely to themselves
156 become precociously mature.

157

158 **Methods and materials**

159

160 **Study sites**

161

162 This study was conducted by planting out eggs in sections of two rivers that provided
163 suitable habitats for young masu salmon but in which no wild masu salmon reside or
164 reproduce due to barriers to upstream migration. One study site (used for experiments
165 starting in 2009 and 2014) is a tributary of the Atsuta River (43°27'N, 141°29'E) located
166 in the central west part of Hokkaido, Japan (Fig. S1). The main stem of the Atsuta river

167 is 34 km long, and the survey was conducted in a secondary tributary (width: 2-3 m)
168 approximately 400 m upstream from the confluence with the Hidari tributary. The study
169 area was approximately 1300 m upstream from a culvert that prevented the upstream
170 migration of fish (see Fig. S1). The only other fish in this part of the stream were low
171 densities of white spotted char *Salvelinus leucomaenis* (0.01 fish/m²) and sculpin *Cottus*
172 *hangiongensis* (0.03 fish/m²).

173 The other study site (used for an experiment starting in 2015) was on the Bishabetsu
174 River (43°33'N, 141°25'E), the main stem of which is 8.4 km long. There is an erosion
175 control dam with a difference in elevation of approximately 6 m located approximately
176 3.5 km upstream from the river mouth, which forms a barrier to the upstream migration
177 of masu salmon (see Fig. S1). In this study, the length of the survey site was set as
178 approximately 2000 m, with the lower point approximately 400 m upstream from this
179 dam (stream width: 3-4 m). Within the study area white spotted char and rainbow trout
180 *Oncorhynchus mykiss* were found at a density of 0.04 fish/m² and sculpin at 0.005/m².
181 The results of water temperature measurements taken every 2 hours with a data logger
182 (Onset Computer Corporation, USA) for the entire period of the study revealed that the
183 mean water temperature was $7.01 \pm 5.92^{\circ}\text{C}$ in the first experiment (from 1 October
184 2009 until 30 September 2010 in Atsuta R.), $7.19 \pm 6.28^{\circ}\text{C}$ in the second (from October
185 2014 to September 2015 in Atsuta R.) and $7.05 \pm 5.55^{\circ}\text{C}$ in the third (from Oct 2015 to
186 Sep 2016 in Bishabetsu R.).

187

188 **Experimental design**

189

190 Masu salmon have two alternative life histories: either growing in the river for 1 or 2

191 years and migrating to sea for one year and then returning to their natal river to spawn
192 (the anadromous life history), or maturing precociously in the river without ever going
193 to sea (the precocious life history) (Kato 1991). In this region of Japan all females are
194 anadromous whereas males can be either precocious or anadromous. The size and age at
195 sexual maturity differ significantly between these two life histories, with anadromous
196 individuals maturing at 3-4 years of age and a size of 40-60 cm, whereas precocious
197 males mature aged 1-2 at a size of 8-25 cm. On the masu salmon spawning grounds in
198 Hokkaido, anadromous males generally fight with other males to become dominant,
199 while precocious males attempt to sneak (Yamamoto and Edo 2002).

200 This study used as parents wild anadromous fish of both sexes plus precocious males,
201 all caught by backpack electrofishing in September in the lower reaches of the same
202 river for each site (the Atsuta River in September 2009 and 2014 and the Bishabetsu
203 River in 2015). The captured individuals were anesthetized with 2-phenoxyethanol
204 (0.2ml/L), and their fork length measured to 0.1 cm. The eggs were then stripped from
205 females and divided into equal parts to make clumps of approximately 150 to 200 eggs;
206 each egg clump was then fertilized with the sperm extracted from a single male. In
207 2009, we created a total of 40 half-sib families using 5 anadromous and 5 precocious
208 males, with each male paired with each of 4 females. In 2014 we created 12 half-sib
209 families from 5 anadromous and 5 precocious males paired with 2 females (note that not
210 all males were used with each female), and in 2015 we created 36 half-sib families
211 using 3 anadromous males, 7 precocious males and 4 females (full details in Table S1).
212 The adult fish were then culled so that otoliths could be collected to determine their age.
213 The artificially fertilized eggs were immediately buried in an artificial nest covering an
214 area 1 m wide x 2 m long, 830 m upstream from the culvert in the Atsuta River (2009

215 and 2014) and an area 2 m wide x 4 m long 1430 m upstream from the dam in
216 Bishabetsu River (2015). The mean egg weight was 135.4 ± 27.9 mg (based on
217 measuring 10 eggs from each of 10 females); using these values and the total mass of
218 the eggs, we estimated the number of buried eggs to be 3190 in 2009, 1420 in 2014 and
219 5840 in 2015.

220 In both early June and September of the following summer (2010, 2015 and 2016) the
221 surviving offspring (by this time approximately 1-2 and 4-5 months since first feeding,
222 respectively) were captured by fishing a 1-2km length of the relevant study area using a
223 backpack electrofisher (see Fig. S1). On each occasion the study section was fished
224 twice to maximise the number of recaptures. The 50m length of stream in which each
225 fish was captured was recorded, and the fish were then anesthetized with 2-
226 phenoxyethanol (0.2ml/L) and their size (fork length) measured to 1 mm. A piece of the
227 adipose fin was removed and stored in 100% ethanol for later genetic analysis. During
228 the September sampling, the abdomen of the fish was pressed to confirm if sperm could
229 be discharged, as a test for male fish reaching sexual maturity. All fish were then
230 released back into the study section in which they had been caught.

231 Field sampling was conducted in accordance with a permit issued by the Governor of
232 Hokkaido Prefecture (Permission number 2009-96, 2010-28, 2015-17, 2016-31); no
233 ethical permits were required by the university.

234

235 **DNA analysis**

236 DNA was extracted from the adipose fin sample of each individual and used to
237 determine its parentage (based on microsatellites (Table S2), with the results analysed
238 using CERVUS 3.0 (Kalinowski et al. 2007) and its sex (using the sex determination

239 gene sdY, which is a gene marker specific to the Y chromosome (Yano et al. 2012)).

240 Further details of both protocols are given in the online supplement.

241

242

243 **Statistical Analysis**

244 To examine the causes of variation in body size and distance dispersed from the
245 nest at each sampling time (June and September), we conducted Bayesian analyses
246 using a Markov Chain Monte Carlo (MCMC) approach. The distance estimated from
247 the location of the nest (0 m) to downstream or upstream capture locations was
248 expressed as minus or plus values, respectively. The explanatory variables were the sex
249 of the offspring, the mean egg size, and the life history form (anadromous or
250 precocious) of the father. When we examined the causes of variation in growth rate and
251 distance moved between June and September using recaptured individuals (identified
252 through the genetic analysis), the fish's body size and location at time of first capture
253 were included in analyses. Specific growth rates of each individual (percent per day)
254 over the summer were calculated as $100 \times (\ln(\text{body size in September}) - \ln(\text{body size in June})) / (\text{time elapsed in days})$ (Ricker 1975). The distance moved between June and
255 September was defined as the shortest distance along the spine of the stream between
256 the midpoint of the stream section in which an individual was captured in June and the
257 section in which it was captured in September. We also incorporated three random
258 effects in each model: the individual IDs of the male and female parent, and the year
259 (i.e. which of the three experimental runs). The response variables were assumed to
260 show a normal distribution. Our models can be expressed as:

262

263 $OV_{jk} \sim \text{Normal}(O_{jk}, \text{Variance}),$
 264 $Ov_{jk} = \text{Intercept} + Os_{jk} + ML_j + Fek + ML_j * Fek + Os_{jk} * ML_j + Os_{jk} * Fek + Os_{jk}$
 265 $* ML_j * Fek + BS_{\text{June}} + DJ + R_j + R_k + R_y$

266

267 where Ov_{jk} is the variable of interest of offspring with father j and mother k . Os_{jk} is
 268 the sex of the offspring, ML_j is the life history form of the father j and Fek is the mean
 269 egg size of the mother k . R_j and R_k are the random effects of the identity of male
 270 parent j and female parent k , respectively, while R_y is the random effect of the year of
 271 the study. The models with growth rate and distance moved between June and
 272 September of recaptured individuals as the response variable also included offspring
 273 body size (BS) and distance along the stream from the nest to the point where fish were
 274 captured in June (DJ) as an explanatory variable. Covariates were standardized to have
 275 a mean of 0 and a standard deviation of 1.

276 To fit the Bayesian hierarchical models, we used WinBUGS and R version 3.2.3
 277 software with the R2WinBUGS package to conduct an MCMC analysis using Gibbs
 278 sampling. A necessary initial consideration in a Bayesian analysis is that the prior
 279 distributions for each variable are known. Because we had little empirical support for
 280 choosing one distribution over another, we used a standard normal distribution with a
 281 mean of 0 and precision of 0.001 on all fixed effects and random intercepts. We used
 282 random starting values for all parameters. To use the MCMC results, the Markov chain
 283 must change from the initial values to a stationary distribution. We conducted MCMC
 284 sampling for 20,000 counts and discarded the initial 5,000 as burn-ins. In addition, to
 285 minimize the influence of initial values on the results, we conducted an analysis of three
 286 sets of initial values during MCMC sampling. We used R to generate these initial values

287 based on random number generation and evaluated the contribution of fixed effects
288 using a posterior predictive check based on a 95% credible interval.

289 Next, we conducted a logistic regression analysis to investigate predictors of whether
290 males would become precociously mature. The response variable was a binary value
291 for the precocious maturation of males, with mature males coded as 1 and immature
292 males coded as 0, and the explanatory variables were the egg size of the mother, life
293 history of the father (i.e. whether he was precocious or anadromous) and body size of
294 offspring in September. When the predictors of male maturation were examined using
295 recaptured individuals, body size in June and captured location in June and growth rate
296 between June and September were included in the model. We incorporated the same
297 three random effects in the model as in earlier analyses. Our models can be expressed
298 as:

299

$$300 \quad Om_{jk} \sim \text{Bin}(G_{jk}),$$

$$301 \quad \text{Logit}(G_{jk}) = \text{Intercept} + ML_j + Fe_k + ML_j * Fe_k + BS_{\text{Sep.}} + BS_{\text{June}} + CL + GR + R_j + R_k$$
$$302 \quad + R_y$$

303

304 where OM is the mature state (immature or mature) of male offspring with father j
305 and mother k , $BS_{\text{Sep.}}$ is body size in September, GR is growth rate of recaptured
306 individuals between June and September. Other terms are as described above.

307 Finally, the incidence of precocious males was measured as a binary response, so the
308 relationship between size and probability of precocious males among each male was
309 determined using the logistic regression model:

310

311 $\text{Logit}(P_m) = \beta_0 + \beta_1 S$

312

313 where P_m is the probability of a male being precociously mature, β_0 is the coefficient
314 estimate for the constant and β_1 is the coefficient estimate for body size S . Next, the
315 body size at which the probability of becoming precociously mature = 0.5 (defined as
316 the threshold for precocious maturation) was determined from the parameter estimates
317 from the logistic regression model and was run separately for offspring of each male life
318 history and female parent. These threshold body sizes for precocious maturation were
319 compared between life history forms and females using two-way ANOVA.

320 A p -value of less than 0.05 was considered to indicate significant difference in all
321 analyses, which were performed with R.3.2.3 (R core Team, 2015).

322

323 **Results**

324

325 **Data on recaptured fish**

326

327 In the first experiment a total of 1043 individual offspring were caught in June and 323
328 in September 2010. In the second experiment, 246 individuals were caught in June and
329 178 in September 2015, whilst in the last experiment 517 individuals were caught in
330 June and 792 in September 2016 (Table 1). Parentage identification with known parent
331 and filial information could be determined based on 8 or 9 microsatellite loci for 1675
332 individuals (92.7%) in June and 1286 individuals (99.4%) in September; full details of
333 the parentage assignment are given in the Supplementary information. 1745 (96.6%) of
334 the individuals captured in June and 1288 individuals (99.6%) captured in September

335 were sexed based on DNA, respectively.

336

337 **Variation in offspring dispersal patterns and body size**

338

339 By June the fish had dispersed 349.4 ± 212.54 m (mean \pm SD) downstream from the
340 nest site in 2010, 229.68 ± 160.78 m in 2015 and 385.01 ± 257.88 m in 2016 (Fig. 1).

341 There were no individuals that had moved by June more than 50 m upstream from the
342 location where the eggs were buried in any survey year. The dispersal distance
343 depended on the sex: by June females had dispersed more downstream than had males
344 (Fig. 2, Table S3). In both sexes the distance that they had dispersed from the nest was
345 related to their body size (Fig. 2, Table S3): individuals that had dispersed downstream
346 were larger than those staying closer to the nest. There was some evidence of a paternal
347 life history effect dependent on sex on the dispersal of offspring, since the credible
348 interval of the interaction between sex and sire only just overlapped with zero (Fig. 2,
349 Table S3); thus while the dispersal of sons was unaffected by paternal life history,
350 daughters of precocious fathers had a greater tendency to move downstream than did
351 daughters of anadromous fathers.

352 By September, the dispersal distance was 308.20 ± 368.06 m (mean \pm SD) downstream
353 in 2010, 211.24 ± 275.33 m in 2015 and 475.95 ± 388.74 m in 2016. By this time point
354 there was also evidence of upstream movements: in September 2010, there were 79
355 (24.5%) individuals that had migrated further upstream than the location at which the
356 eggs had been buried; this figure was 38 (21.3%) in 2015 and 66 (8.4%) in 2016 (Fig.
357 1). The maximum distance moved upstream was 700 m; 14.2% of these fish that had
358 moved upstream by their first September were precociously mature males. The effect of

359 sex on dispersal that was present in June had disappeared by September, and there was
360 no effect on dispersal of the life-history form of the father, nor the egg size of the
361 mother. However, larger fish tended to be distributed further upstream than smaller fish,
362 which was the opposite pattern to that seen in June (Fig. 2, Table S3).

363 The body size of offspring in June and September is summarized according to year and
364 father's life history in Table 1; there were no sex differences in body size, nor any
365 differences between offspring of anadromous and precocious fathers (Fig. 2, Table S3).
366 Only the size of egg was important according to the Bayesian hierarchical model
367 predicting offspring body size, with larger eggs producing larger offspring (Fig. 2, Table
368 S3).

369

370 **Precocious maturation of male offspring**

371

372 In September 2010 we recaptured 77 male offspring (40.1% of males) that had matured
373 as precocious sneakers; the corresponding figures were 40 (46.5%) in 2015 and 105
374 (24.8%) in 2016 (Table 1). A Bayesian hierarchical model conducted to investigate the
375 effect of the parent on the probability of precocious maturation in male offspring found
376 a significant positive effect of offspring body size at the time of recapturing, but no
377 significant effect of either egg size or paternal life history (Fig. 2, Table S3).

378 Logistic regression analyses confirmed a significant positive effect of body size on
379 the probability of a male becoming precociously sexually mature (Table S4). The
380 threshold body size at which 50% of males were mature precociously averaged $9.14 \pm$
381 $SD 0.68$ cm in offspring from anadromous sires ($n = 6$ anadromous sires) and $9.08 \pm SD$
382 0.68 cm in offspring from precocious sires ($n = 7$ precocious sires), a difference that was

383 not significant ($F_{1,5} = 0.02$, $P = 0.88$). While the threshold body size differed between
384 the offspring from individual females ($F_{6,5} = 5.37$, $p < 0.05$), there was no evidence that
385 this was driven by differences in egg size since there was no correlation between a
386 female's egg size and the threshold body size for precocious maturation in her sons ($r =$
387 0.05 , $n = 13$, $P > 0.05$).

388

389 **Variation in offspring growth rate and movement over the summer and** 390 **maturation in recaptured fish**

391

392 There were 116 individuals that were captured in both June and September in 2010, 91
393 in 2015 and 145 in 2016. Body size in September was predicted by body size in June
394 (Fig. S2). However, a Bayesian hierarchical model showed that growth rate over this
395 period was not influenced by paternal life history form (precocious versus anadromous
396 father) or dam (Fig. 3, Table S5). Many individuals were captured in September very
397 close to where they had been captured in June (Fig. S2). A Bayesian hierarchical model
398 of the linear distance between these two capture locations found a significant interaction
399 between sex of offspring and egg size, meaning that male offspring from larger eggs had
400 a greater tendency to move more upstream between June and September than did those
401 from smaller eggs (Fig. 3, Table S5).

402 In total, 72 of the 193 recaptured males matured as precocious sneakers. A Bayesian
403 hierarchical model showed that precocious maturation showed a tendency to be
404 positively related to body size in June and growth rate (although the 95% credible
405 interval just overlapped 0), but not location in June nor body size in September, nor
406 were there any significant parental effects (Fig. 3; Table S5).

407

408 **Discussion**

409

410 This study is one of the first to have successfully teased apart the effect of egg size and
411 paternal life history on offspring dispersal patterns, growth, and maturation in the
412 natural environment. Dispersal distances differed according to the sex and body size of
413 offspring. Moreover, the father's life history also influenced the dispersal patterns of
414 their daughters but not those of their sons. On the other hand, juvenile body size was
415 strongly influenced by egg size. The likelihood of early maturation in males differed
416 between families but was not directly related to egg size or paternal life history,
417 suggesting that environmental factors contributed more to maturation than genetic
418 factors.

419

420 **Dispersal pattern of juveniles**

421

422 There was an effect of an individual's sex and the life history strategy of its father on
423 early dispersal patterns. Females dispersed further from the nest in their first summer
424 than did males. Sex-biased dispersal patterns could be related to life history differences
425 between the sexes (Mayama 1989; Nagata and Irvine 1997). Although all female masu
426 salmon inhabiting the rivers in Hokkaido become anadromous, some of the males
427 become resident and never migrate to sea, instead maturing precociously at a small size
428 and spawning as sneakers (Kato 1991). Therefore, it is likely that dispersal patterns in
429 early life differ between males and females because it may be more beneficial for males
430 to remain in the upper reaches of rivers near the spawning grounds, and for females to

431 disperse downstream to the mid and lower reaches where feeding competition from
432 males is reduced and food sources are likely to be more abundant. There was also a
433 tendency for dispersal distance in females (but not males) to be influenced by the life
434 history strategy of the father, with daughters of anadromous sire remaining nearer to the
435 nest than those of precocious males. A genetic influence on natal dispersal has been
436 demonstrated in other contexts, notably a reduced tendency to move downstream in
437 populations of salmonids living above barriers such as dams or waterfalls (Morita and
438 Yamamoto 2001), but we are not aware of any previous evidence that it can be
439 influenced by the mating strategy of the father.

440 This study also found that the initial dispersal distance of juvenile fish correlated
441 positively with their body size attained by June. This pattern of larger fish apparently
442 dispersing further matches the results of Bradford and Taylor (1997), but is in contrast
443 to a number of other studies that found smaller juveniles to be more likely to move
444 away from nest sites than larger ones (Johnston 1997). Einum et al. (2012) showed that
445 this apparent contradiction can be resolved if smaller fish are forced to disperse further
446 (as a result of their poorer competitive ability), but then grow faster as a result of
447 reduced competition for food at greater distances from the nest. The negative correlation
448 between body size and dispersal distance that existed soon after emergence therefore
449 became a positive correlation later in the season (Einum et al. 2012). If small fish are
450 indeed poor competitors for feeding positions and are displaced downstream on first
451 emerging from the nest, we should expect offspring hatching from smaller eggs to be
452 found further downstream in June. However, this study found no effect of egg size on
453 the distribution of offspring within the river. Perhaps some individuals could have
454 moved downstream actively and grow faster while avoiding the competition. Kahler et

455 al. (2001) observed that fish that moved from the nest grew at a faster rate than did
456 sedentary individuals. Anderson et al. (2013) similarly found that the distance moved by
457 juvenile coho salmon was positively correlated with body size, indicating that these
458 were not subordinate individuals displaced by competition.

459 Those fish that were caught in both June and September had barely moved location,
460 although in 2010 there was a stronger tendency for mature males to move further
461 upstream. This may be related to the greater amount of rain in August in that year,
462 which may have triggered more mature males to move to the upper reaches of rivers just
463 prior to the spawning season. In contrast, females in all years were more likely to move
464 downstream between June and September than to move upstream. The movements
465 recorded in the present study are likely to be underestimates of the total scale of
466 dispersal since it was not possible to conduct surveys over the entire river. However,
467 genetic analyses have shown that few precocious masu salmon in the Atsuta River move
468 between different tributaries (Kitanishi et al. 2017). Moreover, while some juveniles are
469 likely to have dispersed outside the surveyed area, the significant differences in
470 dispersal distance and direction between the sexes are still valid, and are potentially
471 related to differences in life histories between males and females.

472

473 **Juvenile body size**

474

475 Maternal egg size was found to have a strong positive effect on the body size of the
476 resulting offspring. This finding is supported by previous studies in which body size in
477 young salmonids is affected by differences in the size of egg from which they hatched
478 (Einum and Fleming 1999, Thorn and Morbey 2017). However, it is notable that in the

479 present study this maternal effect on body size of offspring was maintained until at least
480 September, by which time the young fish had been feeding independently for 4-5
481 months and precocious males were already sexually mature. Some previous studies
482 have found that the effect of egg size on body size of offspring is strong at the time the
483 offspring emerge from the nest, but diminishes thereafter (Heath et al. 1999; Falica et al.
484 2017). This may be because of differences in growth rate: Segers et al. (2012)
485 demonstrated that fish originating from small eggs had higher growth hormone receptor
486 expression levels, causing juveniles from small eggs to grow faster than those from
487 larger eggs, a growth pattern also seen by Berejikian et al. (2011) in Chinook salmon.
488 Another reason for a negative relationship between egg size and growth rate is that fast-
489 growing female salmonids have a tendency to produce smaller eggs (Lobon-Cervia et
490 al. 1997), but may have relatively fast-growing offspring (Burton et al. 2013). These
491 complex interactions can influence the effect of egg size on body size, with
492 relationships shifting through ontogeny.

493 In contrast, we found no effect of paternal life history on the body size of offspring.
494 Previous studies have demonstrated a heritability for growth and body size in salmonids
495 (Thorpe et al. 1983; Berejikian et al. 2011). The lack of a paternal effect in the present
496 study may be related to the tendency for males to both show less dispersal and to
497 become precociously mature, both of which will influence their growth rates and make
498 it more difficult to detect a paternal effect in sons than in daughters.

499

500 **Maturation of male offspring**

501

502 No significant difference in the probability of precocious sexual maturation was found

503 between the male offspring of anadromous and precocious fathers, nor was the
504 probability influenced by the egg size of the mother. Previous studies of salmonids have
505 reported a high heritability for age at maturation (Gjerde et al. 1994; Lillehammer et al.
506 2013), which would suggest that it is more likely for the offspring of precocious males
507 to themselves become precocious. However, Páez et al. (2010) found no evidence for a
508 relationship between paternal life history form in salmon (i.e. precocious versus
509 anadromous) and early life traits, including likelihood of precocious maturation.
510 Moreover, even though they found a significant effect of egg size on offspring body size
511 in early life, this did not translate into an effect of egg size on precocious maturation.
512 Their results were thus similar to those found in the present study, and fit the pattern
513 suggested by Dodson et al. (2013) for traits that exist in alternative states (here
514 precocious maturation versus anadromous migration): the triggering of maturation
515 rather than migration may depend on a ‘liability’ trait such as growth rate or body size
516 during a key ontogenetic window, with individuals differing in the threshold required to
517 trigger one life history strategy over the other. This relationship between body size or
518 growth rate and the probability of maturation at a given age is also referred to as the
519 probabilistic maturation reaction norm (Heino et al. 2002). In this scenario threshold
520 values may be genetically determined: we found evidence for this, since the threshold
521 body size for maturation differed significantly among females. A similar result was
522 obtained by Piché et al. (2008). However, we found no evidence that the threshold body
523 size was related to either the life history of the father (i.e. sons of precocious males were
524 not more likely to mature at a given size than were those of anadromous males) or the
525 egg size of the mother, although statistical power for these tests was limited.

526 While the threshold value may be genetically determined, the liability trait may be

527 more under environmental control. Growth rate has been reported as the major factor
528 determining whether individual salmonids mature or not as precocious males (Friedland
529 and Haas 1996), and the threshold size-at-age for precocious maturation depends on the
530 local growth opportunity (with fish triggered to mature at smaller sizes in higher
531 elevation streams) (Baum et al. 2004). It is notable that Morita et al. (2009)
532 demonstrated plasticity in the threshold size for precocious maturation in white spotted
533 charr based on the environmental variation in river width and temperature.

534 As a result of these complex interactions, the apparent importance of parental life
535 history in determining offspring precocious maturation will likely depend on the extent
536 to which environmental variation in growth rates swamps genetic variation in the value
537 for the maturation threshold: the importance of the genetic contribution is likely to be
538 much less in populations living in natural streams than in laboratory populations, due to
539 the greater spatial variation in growth opportunity. This is worthy of further
540 investigation, although in experiments conducted in the wild there are logistical
541 challenges to achieving sufficient statistical power to separate the effects of parental and
542 environmental influences on offspring life history strategy.

543

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552

553 **Ethics declarations**

554 Conflict of interest

555 The authors declare no conflicts of interest.

556

557 **References**

558

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711

712 **Fig. 1** Natal dispersal in masu salmon, illustrated by the number of male and female
713 offspring that were captured in each section of surveyed stream in June and September,
714 in 2010, 2015 and 2016. The triangles indicate the location where fertilized eggs were
715 buried (0 m), negative values indicate downstream and positive values upstream
716 dispersal respectively. Black, gray, white and striped gray bars indicate immature and
717 (precociously) mature males, females and unknown sex respectively. The stippled band
718 at the top of the figure indicates the area that was searched by electrofishing in each
719 year.

720 **Fig. 2** Mean and 95% credible intervals of standardized covariates associated with
721 offspring traits, with analyses based on all captured offspring: linear dispersal distance
722 from the nest and body size in both June and September, and probability of precocious
723 maturation of male offspring. Parameters of each model estimate the influence of sire
724 life history (1: anadromous form, 2: precocious form), egg size of dam, and offspring
725 sex (1: female, 2: male), plus interactions among these parameters. The body size of
726 offspring was included in the dispersal and maturation models. Data were analysed by
727 multiple regressions based on a Bayesian hierarchical approach.

728 **Fig. 3** Mean and 95% credible intervals of standardized covariates associated with
729 offspring traits, with analyses based only on fish captured both in June and September:
730 distance moved and growth rate between June and September, and probability of
731 precocious maturation of male offspring. Parameters of each model estimate the
732 influence of sire life history (1: anadromous form, 2: precocious form), egg size of
733 dam, and offspring sex (1: female, 2: male), interactions among these parameters, and
734 the body size and captured location of offspring in June. The growth rate between June

735 and September was only included in the maturation model. Data were analysed by
736 multiple regressions based on a Bayesian hierarchical approach.
737

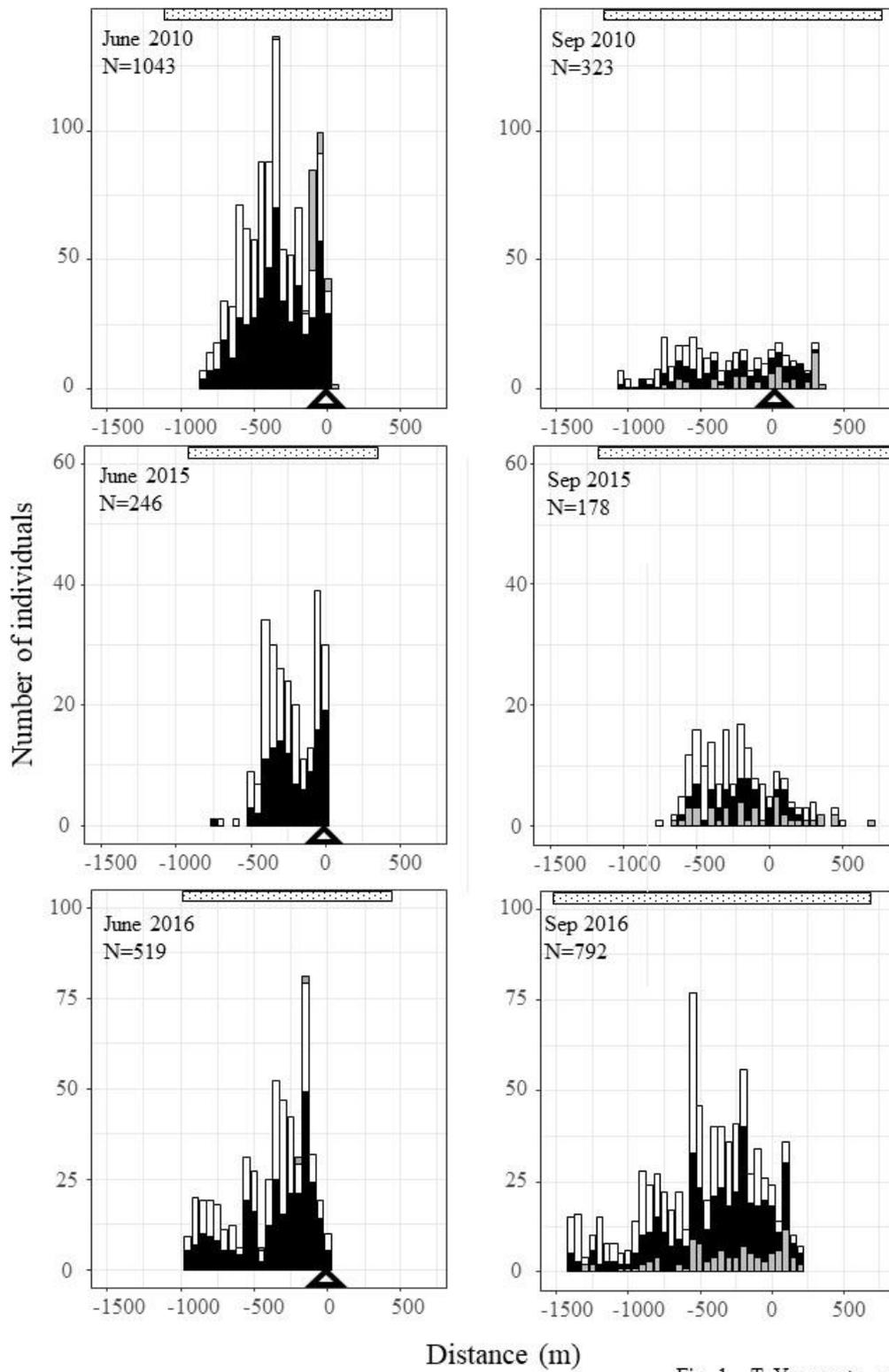


Fig. 1 T. Yamamoto et al.

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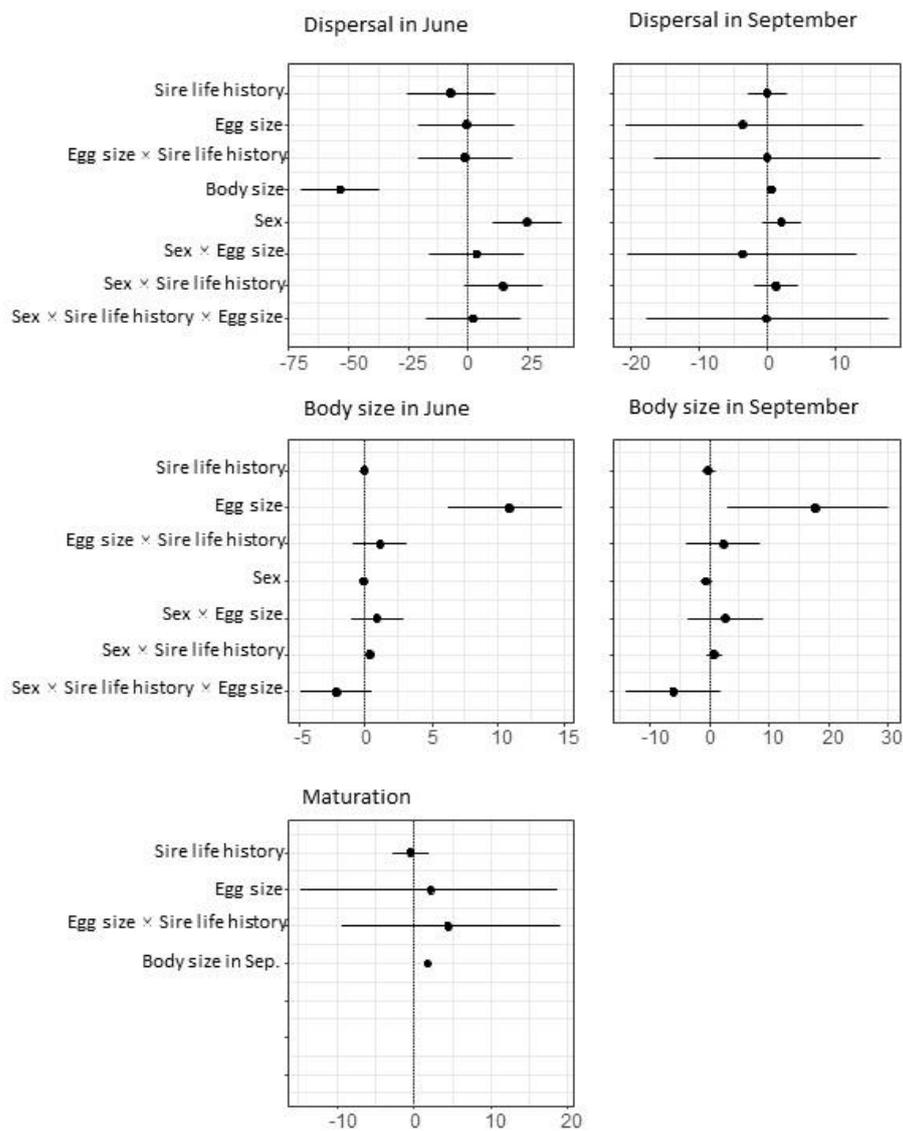


Figure 2 T. Yamamoto et al.

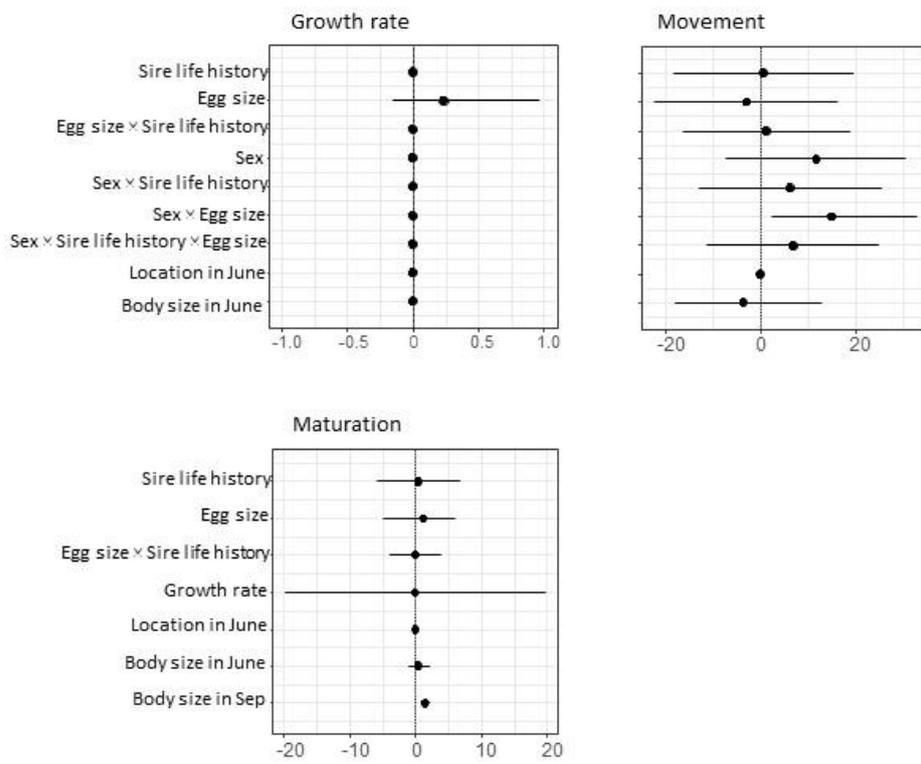


Figure 3 T. Yamamoto et al.

Table 1 Body size (cm \pm SD), sex and location relative to nest (negative values indicate movement downstream) of masu salmon from anadromous and precocious fathers, captured in June and September. Also given is the number and percentage of males that had matured precociously in September.

Year	Sire	Sex	n	June		September			Number (%) of Maturation
				Body size	Location	n	Body size	Location	
2010	Anadromous	M	210	4.46 \pm 0.50	-313.6 \pm 211.0	85	8.61 \pm 1.91	-161.2 \pm 333.9	29 (34.1%)
		F	222	4.49 \pm 0.48	-372.7 \pm 196.4	63	8.50 \pm 1.61	-394.4 \pm 335.5	
	Precocious	M	265	4.56 \pm 0.50	-390.0 \pm 199.1	107	8.79 \pm 1.68	-239.7 \pm 373.3	
		F	227	4.63 \pm 0.49	-451.1 \pm 174.4	68	8.69 \pm 1.64	-519.9 \pm 314.9	
2015	Anadromous	M	51	4.80 \pm 0.42	-194.1 \pm 155.1	43	9.01 \pm 1.18	-189.5 \pm 259.9	23(53.5%)
		F	61	4.76 \pm 0.37	-233.6 \pm 145.7	52	9.49 \pm 1.17	-278.8 \pm 255.6	
	Precocious	M	62	4.75 \pm 0.39	-216.1 \pm 162.2	43	8.50 \pm 1.15	-133.7 \pm 297.4	
		F	72	4.78 \pm 0.41	-263.2 \pm 170.1	40	9.60 \pm 1.04	-230.0 \pm 277.5	
2016	Anadromous	M	101	4.63 \pm 0.46	-387.1 \pm 257.7	154	7.64 \pm 1.23	-414.3 \pm 348.4	34(22.1%)
		F	64	4.59 \pm 0.49	-368.0 \pm 251.6	128	8.06 \pm 1.12	-655.1 \pm 370.0	
	Precocious	M	173	4.74 \pm 0.51	-342.2 \pm 253.6	268	7.95 \pm 1.30	-363.8 \pm 373.2	
		F	169	4.69 \pm 0.53	-433.1 \pm 256.7	235	8.36 \pm 1.27	-550.0 \pm 393.1	

745