

1 **Gene flow from domesticated escapes alters the life history of wild Atlantic salmon**

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16 history evolution, maladaptation, *Salmo salar*

17 **Interbreeding between domesticated and wild animals occurs in several species. This**
18 **gene flow has long been anticipated to induce genetic changes in life-history traits of**
19 **wild populations, and thereby influencing population dynamics and viability. Here, we**
20 **show that individuals with high levels of introgression (domesticated ancestry) have**
21 **altered age and size at maturation in 62 wild Atlantic salmon *Salmo salar* populations,**
22 **including seven ancestral populations to breeding lines of the domesticated salmon. This**
23 **study documents widespread changes in life-history traits in wild animal populations**
24 **following gene flow from selectively bred, domesticated conspecifics. The continued high**
25 **abundance of escaped, domesticated Atlantic salmon thus threatens wild Atlantic**
26 **salmon populations by inducing genetic changes in fitness related traits. Our results**
27 **represent key evidence and a timely warning for the potential ecological impacts**
28 **following the globally increasing use of domesticated animals.**

29 Gene flow from domesticated animals into wild conspecific populations is widespread,
30 and documented examples include American mink¹, wolves², wild boars³, wild cats⁴, bison⁵
31 and Atlantic salmon^{6,7}. Domestication commonly entails selection for economically important
32 traits and genetic homogenization due to low effective population sizes⁸. Domesticated
33 organisms, therefore, have altered genetic composition underlying functional traits and
34 theoretical models predict that gene flow from domesticated organisms into wild populations
35 is detrimental for population growth and viability^{9,10}. In plants, the effects of hybridization
36 between domesticated and wild conspecifics include evolution of weeds, increased or new
37 invasiveness, and increased risk of extinction of wild species¹¹. In animals, experimental
38 studies have documented genetic differentiation in phenotypic traits between domesticated
39 organisms and their wild conspecifics, with hybrids often at intermediate values. The animal
40 literature is dominated by studies on salmonid fishes, and particularly on Atlantic salmon.

41 The domestication process of the Atlantic salmon in Norway involved a large-scale
42 national breeding programme beginning in the 1970s, based on several wild populations from
43 Norway, with selection on increased growth and avoidance of early sexual maturation^{12,13}.
44 Later, the breeding goal has included other traits such as disease resistance, flesh colour, and
45 fat content¹²⁻¹⁴. Common garden experiments show that domesticated salmon and hybrids
46 have altered phenotypes, compared with wild salmon. This includes growth^{15,16}, predator
47 avoidance and aggression¹⁷, life-history traits and phenology¹⁸, and probability of precocious
48 male maturation^{19,20}. Three large scale experiments using different rivers controlled by fish
49 traps show that domesticated introgression can alter age at seaward migration (smolt age) and
50 sea age at maturity, and lead to reduced survival and reproductive fitness²¹⁻²⁴. This literature
51 leaves little doubt that domesticated introgression is expected to impact the wild Atlantic
52 salmon in a way that most likely is detrimental for population demography. However, the
53 experimental settings and limited number of whole-river experiments do not necessarily
54 represent the extent or scale of the impact of domesticated introgression on natural
55 populations.

56 Effects of introgression on life history traits, such as age and size at maturation, are of
57 particular concern because of their close connection to fitness and demography²⁵. In Atlantic
58 salmon, the time spent at sea before maturation, called sea age, is closely related to size at
59 maturity^{26,27}. An Atlantic salmon returning to the river to spawn after three winters at sea is 3-
60 5 times heavier than one returning after one winter. Because size is strongly related to
61 reproductive success²⁸ and the survival at sea is low²⁹, the sea age at maturity represents a
62 trade-off between survival and reproductive success. In addition, growth rate at sea affects
63 both adult size (and therefore reproductive success) and survival³⁰. There may also be
64 complex relations between early and late life-history decisions, for example precocious male

65 maturation (or parr maturation) leads to investment in gonad production over somatic growth
66 and a postponed seaward migration^{19,31}.

67 Interbreeding between domesticated and wild Atlantic salmon occurs in many parts of
68 its natural range on both sides of the Atlantic³²⁻³⁶. Fish farms are common from Ireland and
69 Scotland to the Russian coast of the Barents Sea and from Maine in the US to Newfoundland
70 in Canada. We investigated the effects of gene flow from domesticated salmon in 62
71 populations along the entire Norwegian coastline (Fig. 1a). Norway has both the world's
72 largest Atlantic salmon farming industry and the largest remaining wild population³⁷. The
73 number of farmed escapees is estimated at approximately one million fish annually³⁸. This is
74 more than the total number of fish in the Norwegian salmon run³⁷, and has led to extensive
75 gene flow from domesticated to wild fish^{6,7}.

76 Results

77 Eastern Atlantic phylogenetic group

78 The Norwegian domesticated Atlantic salmon originate from populations along the west coast
79 of Norway³⁹, which represent the Eastern Atlantic phylogenetic group⁴⁰. We estimated the
80 effect of domesticated introgression in 48 populations of this phylogenetic group (Fig. 1a).
81 Seven of these are among the ancestral populations to the breeding lines of domesticated
82 salmon (Fig. 1a, Supplementary Table 1). These ancestral populations are all characterised by
83 a high mean sea age at maturity, and classified as large-salmon populations (Supplementary
84 Table 1). Due to a shared ancestry, the phenotypic effects of introgression in the ancestral
85 populations are expected to be less than in other populations⁴¹⁻⁴³. Yet, we found a strong sex-
86 dependent effect of domesticated introgression on sea age in these populations (Fig. 1b).
87 There was no difference in the effect of introgression between the seven ancestral populations
88 and the 15 non-ancestral large-salmon populations (Supplementary Figure 1). Domesticated

89 introgression increased the number of females attaining maturity at a sea age of two years
90 (proportion changing from 0.43 to 0.65 at full introgression) and the number of males
91 attaining maturity at a sea age of one year (proportion changing from 0.36 to 0.57), while the
92 other sea-age categories correspondingly declined (Fig. 1b).

93 Estimating the level of genetic introgression is difficult, and the discovery of these
94 effects is remarkable considering that our measure of level of introgression in individual fish
95 is inherently imprecise because of the close relatedness between domesticated and wild
96 salmon⁴⁴. This imprecision obscures and leads to underestimates of the effects of
97 introgression, and inflates the observed range of introgression estimates (Supplementary
98 Figure 2). Hence, we only discover effects of introgression when the biological signal is
99 strong, and our results represent conservative estimates of the true effects.

100 Twenty-six of the Eastern-Atlantic populations were qualitatively different from the
101 ancestral populations in that they are dominated by smaller fish maturing at an early age, and
102 thus classified as small-salmon populations (Fig. 1a, Supplementary Table 1). In these
103 populations, we found little or no effect of introgression on sea age (Fig. 1b). There was,
104 however, a strong effect of introgression on sea-age independent size at maturity (Fig. 1c).
105 The increase in mass from no to complete introgression was estimated at 0.171 ln kg, which is
106 equivalent to an increase of 18.6% in these populations. This effect was almost absent (3.4%)
107 in the seven ancestral populations of the domesticated salmon breeding lines, and intermediate
108 (9.5%) in the non-ancestral large-salmon populations (Fig. 1c). Hence, even though the
109 domesticated salmon show strongly increased growth in the captive environment^{15,16}, our
110 results indicate that their genetically high growth potential does not lead to an increased sea-
111 age independent size at maturity in the wild, compared to their ancestral lineages. This can be
112 because either the ancestral populations have already maximized the growth potential possible

113 in nature, or that the fast-growing individuals, with high domestic introgression, die before
114 attaining maturity.

115

116 Barents Sea phylogenetic group

117 We also investigated effects of domesticated introgression in 14 populations of the Barents
118 (and White) Sea phylogenetic group (Fig. 1a, Supplementary Table 1). These populations are
119 more distantly related to the domesticated salmon than the populations of the Eastern Atlantic
120 group⁴⁰. Thus, the effects of introgression in these populations comprise both domestication
121 and phylogenetic effects, and are therefore expected to be more pronounced than in the
122 Eastern Atlantic populations. A relationship between population divergence and effect of
123 introgression has been shown experimentally in the Atlantic salmon⁴⁵. In addition, the
124 environmental differences between the Eastern Atlantic and Barents Sea populations, such as
125 marine feeding grounds and a longer winter, may lead to a different effect of the domesticated
126 introgression.

127 The effects of introgression in the Barents Sea populations were in several cases
128 qualitatively different and to some degree stronger compared with the Eastern Atlantic group
129 (Fig. 1d and e). However, the results in the two phylogenetic groups are not directly
130 comparable due to the difference in uncertainty in estimated introgression (Supplementary
131 Figure 2), and the smaller sample size of the Barents Sea dataset makes these estimates more
132 uncertain. In females, the effect of introgression on sea age was qualitatively similar to the
133 corresponding Eastern Atlantic large- and small-salmon populations, but there was no
134 statistical support for the observed changes (Fig. 1d). In males, there was a strong decline in
135 one-sea-winter fish and a corresponding increase in two-sea-winter fish, these changes had
136 strong statistical support in the small-salmon populations (Fig. 1d). Interestingly, the large-
137 salmon populations of the Barents Sea group had a decreased sea-age-independent mass but

138 an increased length at maturation (Fig. 1e). However, these effects were uncertain and not
139 statistically different from zero. On the other hand, in the small-salmon populations there was
140 a very strong effect on sea-age independent size: an individual with half of its genome
141 originating from domestication was on average 24% heavier and 5% longer at maturation than
142 the wild type (Fig. 1e).

143 Discussion

144 The present results are solely observational and no experimental manipulations have been
145 performed. The advantage of this approach is that it provides estimates and can document
146 effects arising from a naturally occurring introgression process in a large number of wild
147 populations. The disadvantage is that factors correlated with level of introgression may create
148 a spurious relationship between level of introgression and the investigated traits. For example,
149 level of introgression may change over time and therefore be correlated with environmental
150 changes affecting the phenotype of the salmon. Similarly, environmental differences between
151 populations may affect both susceptibility to introgression and phenotypic characteristics.
152 However, we control for both among population differences and among year differences. Our
153 analysis, therefore, compares individuals the same year within the same population, but with
154 different level of introgression. Because there is limited scope for environmental factors to
155 create a spurious correlation between level of introgression and trait values in a given year
156 within a population, we regard this problem as little in our case.

157 The size and sea age at maturity increase with river size²⁶, and there is also genomic
158 evidence supporting that these traits are selected to fit the natural environment of each
159 population⁴⁶. Introgression affecting these traits is therefore expected to lead to fitness
160 reduction in the wild, which has been shown experimentally^{22,23}. The life history changes will
161 also alter the demography of the populations, and may lead to homogenization of populations.
162 The Eastern Atlantic populations become more similar to small-salmon populations when it

163 comes to sea age, with low proportions of three sea-winter fish, and more similar to large-
164 salmon populations when it comes to growth, with high sea-age independent size at
165 maturation. Hence, the difference between these two classes of populations is less
166 pronounced, which may have negative consequences for the temporal stability in total stock
167 abundance, known as the portfolio effect⁴⁷.

168 Fish aquaculture has had a steady increase in production, and reached 73.8 million
169 tonnes globally in 2014⁴⁸. This involves more than 350 species of finfishes⁴⁸, and in many
170 instances escapees potentially interbreed with wild conspecifics⁴⁹. Lab experiments have long
171 suggested that there potentially are substantial functional genetic effects of interbreeding
172 between wild and domesticated conspecifics. This study documents such an effect on a broad
173 geographic scale for a culturally and economically important species. Taken together, our
174 study and the extensive experimental literature on the subject provides solid evidence that
175 domesticated introgression have strong effects on important biological characteristics of wild
176 Atlantic salmon, and we would expect similar effects for gene flow from other genetically
177 altered domesticated animals on their wild conspecifics.

178 Methods

179 Data

180 The data consist of 4101 individuals of Atlantic salmon captured in 62 rivers along the entire
181 Norwegian coastline from 59 to 71 degrees North (Fig. 1, Table S4). The large majority of the
182 data was collected by anglers fishing the entire salmon producing stretch during the
183 recreational fishing season that covers most of the run time in Norway (mainly June through
184 August; see Supplementary Figure 3). We therefore regard our data as representative for the
185 adult populations we are studying. There may still be biases in the data regarding size, age or
186 level of introgression. Biases can arise from fishing regulation on fish size, bag limits, fishing

187 gear or fishing season. These biases can affect population means and can potentially also
188 weaken the observed phenotypic effect of introgression, but they are not expected to create a
189 spurious increase in the effect of introgression on the phenotypic traits within populations and
190 years.

191 The data are a subset of that used in Karlsson et al.⁷, where the magnitude of
192 introgression for the different populations are reported. We categorized the data depending on
193 whether the population was dominated by small- or large-sized salmon, and phylogenetic
194 group (Eastern Atlantic or Barents/White Sea, cf. Bourret et al.⁴⁰). The large-salmon
195 populations (dominated by multi-sea-winter spawners) are qualitatively similar to the
196 ancestral populations of the breeding lines of the domesticated salmon in that they attain
197 maturity at an older sea age and at a larger age independent size than the small-salmon
198 populations (dominated by one- and two-sea-winter spawners). We assigned populations to
199 large- and small-salmon populations along the lines of Jensen⁵⁰: large-salmon populations
200 have less than 60% of their catch below 3 kg, while small-salmon populations have more than
201 60% of their catch below 3 kg (in the catch data statistics from 1993 through 2012).

202 A subset of the Eastern Atlantic large-salmon populations dominated the domesticated
203 salmon breeding lines after the initial generations of selection. These rivers are (from south to
204 north): Suldalslågen, Vosso, Årøyelva, Driva, Surna, Gaula, and Namsen^{12,39}.

205 [Measurement of introgression](#)

206 We used 48 single nucleotide polymorphic (SNP) loci previously identified as differentiating
207 between wild and domesticated Atlantic salmon in Norway⁵¹ to estimate genomic proportion
208 of domesticated origin for each individual following the method of Karlsson, et al.⁴⁴. In short,
209 we estimated for each individual the proportional ancestry in domesticated reference
210 population relative to the wild reference population using STRUCTURE⁵². Two *in silico* wild
211 and domesticated reference populations were generated from the genotypes of a pool of

212 samples from historical wild populations and the major breeding kernels in Norway
213 (AquaGen, Salmobreed and Mowi), respectively, followed by random mating as implemented
214 in HybridLab⁵³. The historical wild samples represent Atlantic salmon of wild origin because
215 they were conceived in the early- to mid-eighties, at an early stage of salmon farming. The
216 domesticated reference samples from the breeding kernels were sampled between 1998 and
217 2008^{7,11}. These breeding kernels have been kept isolated since they were founded from wild
218 salmon in the 1970s^{12,39}. We analysed single individuals together with the wild and the
219 domesticated reference populations in STRUCTURE using the admixture model, 50 000
220 repetitions as burn in, and 100 000 repetitions after burn in, and no *a priori* information of
221 sample designation. For each individual we recorded the proportional ancestry in the
222 domesticated reference population (P_{ind}). The level of introgression, or proportion of
223 domesticated genome relative to the domesticated and wild reference population means, was
224 calculated as $(P_{ind} - P_W)/(P_D - P_W)$, where P_W and P_D are the mean proportional ancestry
225 in the domesticated reference population for the wild and the domesticated reference samples,
226 respectively. These values were estimated at $P_W = 0.060$ and $P_D = 0.903$ for the Eastern
227 Atlantic phylogenetic group and $P_W = 0.016$ and $P_D = 0.992$ for the Barents/White Sea
228 phylogenetic group.

229 Phenotypic measurements

230 At capture, the angler measured total length (in mm, from the tip of the snout to the end of the
231 caudal fin) and wet mass (in g), recorded sex and took a scale sample of each fish. A
232 professional scale reader analysed the growth pattern of the scales, excluded escaped farmed
233 salmon, and recorded the time the wild fish had spent at sea before attaining maturity (sea
234 age)^{54,55}.

235 Statistical analyses

236 The effect of introgression on sea age, measured as the probability of maturing at different
237 sea-ages for individual m captured at year l in population k of sex j and in population category
238 i , was analysed in a multinomial (logit) mixed effect model:

239

$$\ln \frac{\Pr(y_{ijklm} = 1)}{\Pr(y_{ijklm} = 3+)} = a_{1ij} + b_{1ij}x_{ijklm} + d_{1ij}(x_{ijk**} - x_{ij***}) + r_{1ijk} + u_{1ijl},$$

$$\ln \frac{\Pr(y_{ijklm} = 2)}{\Pr(y_{ijklm} = 3+)} = a_{2ij} + b_{2ij}x_{ijklm} + d_{2ij}(x_{ijk**} - x_{ij***}) + r_{2ijk} + u_{2ijl},$$

240

241 where a is the intercept term, b is the within population effect of level of introgression (x), d
242 is the among population effect (as a contrast to the within population effect b), r is the
243 random effect of river, u is the random effect of year nested within category and sex, and
244 asterisks (*) in the subscript mean the average taken over these levels. The different outcomes
245 of y were maturation at sea age one ($y = 1$), maturation at sea age two ($y = 2$) and maturation
246 at sea age three or older ($y = 3+$). The random effects were assumed independent and
247 identically normally distributed, and a multinomial distribution was assumed for the response
248 variable y . The population categories “Ancestral” and “Large” in the Eastern Atlantic
249 Phylogenetic Group were pooled in this analysis, as there were no differences between these
250 two categories in sea age and the effect of introgression (Supplementary Figure 1). To
251 evaluate the statistical support for an effect of the level of introgression on sea age, we
252 compared the model above with a model excluding the effect of sea age for each sex within
253 each population category (i.e. parameters b_1 and b_2 were set to zero for the respective sex
254 within each category). A decrease in AIC value of more than two when the effect of sea age
255 was included was considered as strong statistical support⁵⁶. This model was fitted using the
256 statistical software package Template Model Builder⁵⁷ implemented in R⁵⁸.

257 The length or mass at maturity of individual m migrating out to sea at year l from
258 population k belonging to sea age group j and population category i was log transformed and
259 analysed in a linear mixed effect model:

260

$$\ln y_{ijklm} = a_{ij} + b_i x_{ijklm} + d_i (x_{ijk**} - x_{i****}) + r_{ik} + u_{il} + e_{ijklm}$$

261

262 The parameters a , b , d , r , and u mean the same as in the model for sea age, while e is the
263 residual term. For the effect of year nested within category, u , river category “Ancestral” and
264 “Large” in the Eastern Atlantic Phylogenetic Group were pooled. Both random effects and
265 residuals were assumed independent and normally distributed. Sex was not included in the
266 models because the two sexes had very similar estimates, and AIC did not support inclusion
267 of sex difference in the model. The linear mixed models were implemented in the lme4 R-
268 package⁵⁹. Diagnostic plots were used to assess statistical assumptions of the models.

269 [Data Availability](#)

270 The data supporting the findings of this study are available in the Dryad digital repository
271 with the identifier doi:10.5061/dryad.gh721

272 [Code Availability](#)

273 R-code for the statistical models are available in Dryad digital repository with the identifier
274 doi:10.5061/dryad.gh721

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428

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434

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436 generated and conducted bioinformatics on the molecular data. K.H., H.S., P.F., A.J.J., K.U.,
437 T.N., B.B., B.F.-L, H.L. and E.N. coordinated the collection of phenotypic data. G.H.B.
438 analysed data. G.H.B., K.H., G.R., B.J. and S.K. wrote the manuscript. All authors read and
439 commented on the manuscript.

440

441 **Competing financial interest:** The authors declare no competing financial interest.

442

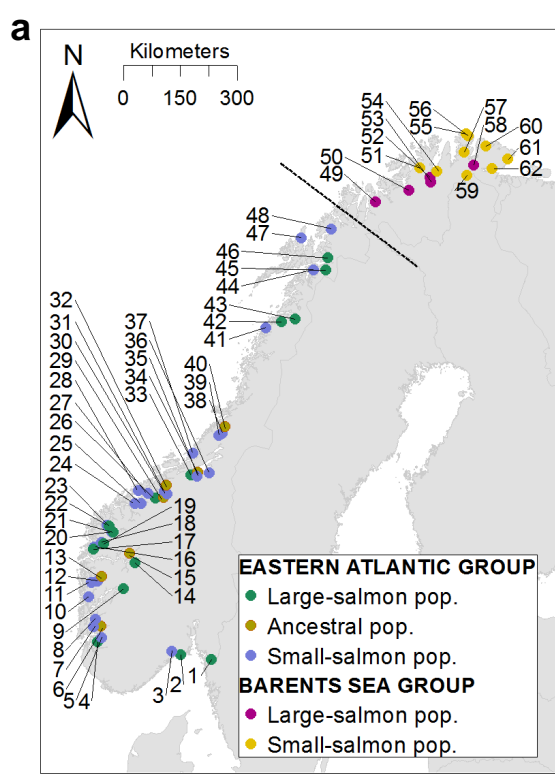
443 **Supplementary Information** is available for this paper.

444

445 **Figure legend**

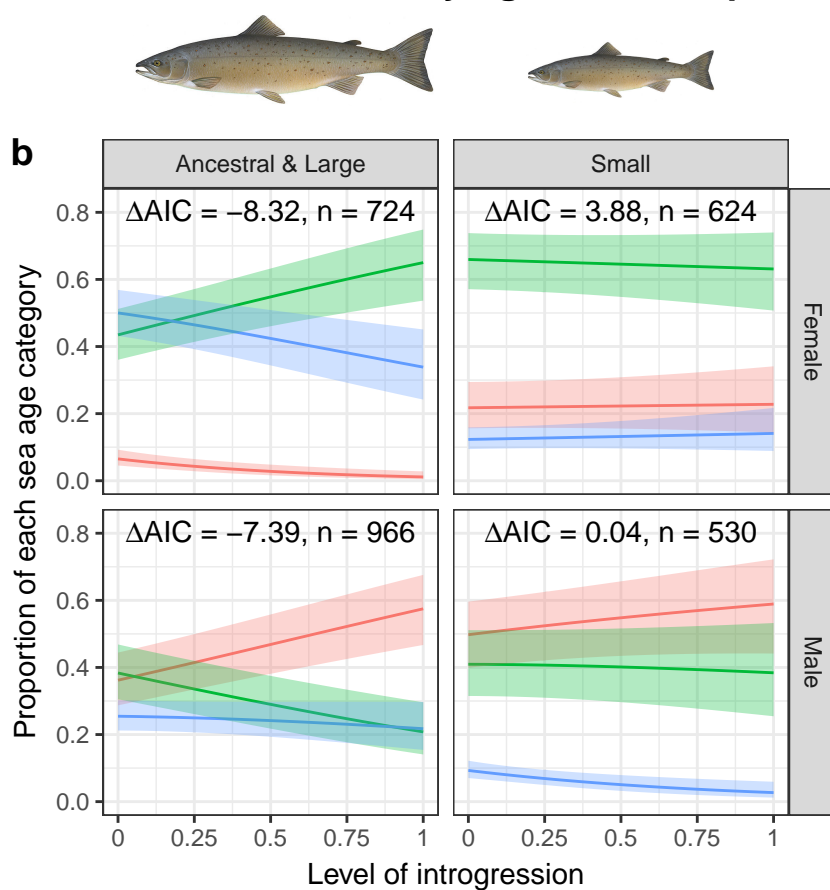
446 **Figure 1 | Effect of introgression (proportion of domesticated genome) on life history. a,**
447 map of the populations. See Supplementary Table 1 for population info. **b,** the effect of level
448 of introgression on sea age at maturation (proportion of each sea age category: 1, 2, and 3
449 years or older) for females and males in the Eastern Atlantic Phylogenetic group. Shaded
450 areas give \pm one standard error (symmetrical on the logit scale). The statistical support is given

451 by the change in *Akaike's Information Criterion* (ΔAIC) from a model excluding the effect of
452 introgression to a model including the effect. (A ΔAIC -value more negative than -2 is
453 considered strong statistical support⁵⁶.) See Supplementary Table 2 for parameter estimates. **c**,
454 the effect of introgression on the mass and length at maturation within each sea age category
455 in the Eastern Atlantic group. The mass (kg) and length (cm) at no introgression and
456 maximum observed introgression are given for each sea age category. The slope of the
457 regressions \pm one standard error gives the effect of introgression and its precision. See
458 Supplementary Table 3 and 4 for parameter estimates. **d** and **e**, show the same as **b** and **c**, but
459 for the Barents Sea Phylogenetic Group. Illustration of *Salmo salar* by Timothy Knepp,
460 distributed under a CC-PD-Mark 1.0 licence.



Sea age 1 2 3+

Eastern Atlantic Phylogenetic Group



Barents Sea Phylogenetic Group

