Home ground advantage: local Atlantic salmon have higher reproductive fitness than dispersers in the wild

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Abstract

A long-held, but poorly tested, assumption in natural populations is that individuals that disperse into new areas for reproduction are at a disadvantage compared to individuals that reproduce in their natal habitat, underpinning the eco-evolutionary processes of local adaptation and ecological speciation. Here, we capitalize on fine-scale population structure and natural dispersal events to compare the reproductive success of local and dispersing individuals captured on the same spawning ground in four consecutive parent-offspring cohorts of wild Atlantic salmon (*Salmo salar*). Parentage analysis conducted on adults and juvenile fish showed that local females and males had 9.6 and 2.9 times higher reproductive success than dispersers, respectively. Our results reveal how higher reproductive success in local spawners compared to dispersers may act in natural populations to drive population divergence and promote local adaptation over microgeographic spatial scales without clear morphological differences between populations.

Introduction

The pattern of individuals exhibiting higher fitness in their local habitat compared to individuals originating from others, and the process leading to such a pattern, is known as local adaptation (Williams 1966; Kawecki & Ebert 2004). Local adaptation arises when the optimal phenotype varies geographically, primarily due to environmental heterogeneity. As a result, populations may evolve locally advantageous traits under divergent selection (Williams 1966; Kawecki & Ebert 2004). Studies of local adaptation can provide insights into the evolution and maintenance of diversity, species responses to climate change, and ultimately, the processes of speciation and extinction (Kawecki & Ebert 2004; Savolainen *et al.* 2013). Therefore, understanding the forces such as selection, migration, mutation and genetic drift that may promote or constrain local adaptation is an important aim in biology (Kawecki & Ebert 2004; Hereford 2009; Savolainen *et al.* 2013).

One ecological selection pressure that can limit gene flow between populations and influence local adaptation is selection against immigrants that have dispersed from other populations and their offspring (Hendry 2004; Nosil *et al.* 2005). An important aspect of selection against such dispersers is the relative reproductive fitness advantage of local individuals that may result from pre- and post-zygotic processes including mate choice, assortative mating, and reduced fitness of hybrid offspring (Nosil *et al.* 2005). Consequently, lower reproductive fitness of dispersers can be interpreted as a reproductive isolating mechanism that promotes local adaptation and ecological speciation (Rundle & Nosil 2005).

Natural dispersal events have the potential to illuminate the importance of reproductive success in shaping local adaptation, yet few studies comparing reproductive success between local and migrating individuals are conducted in nature (but see (Orell *et al.* 1999; Hansson *et al.* 2004; Peterson *et al.* 2014)). Rather, reciprocal transplant experiments are commonly employed for testing whether local individuals have higher relative fitness (Kawecki & Ebert 2004; Nosil *et al.* 2005; Hereford 2009; Blanquart *et al.* 2013). However, transplant experiments have several limitations that are rarely recognized. First, for

practical reasons many reciprocal transplant experiments measure fitness-related traits, rather than directly measuring reproductive success of local and foreign pairings, yet this is a key component of the strength of selection against migrants and the cost of adaptation to different environments (Nosil *et al.* 2005; Tobler *et al.* 2009). Second, reciprocal transplant studies rarely, if ever, acknowledge the potential effects of the choice of 'transplant' individuals used in experiments. For example, randomly selected individuals from a population may not reflect true natural dispersers that express different behavioral or physiological phenotypes, and thus bias the results of the fitness estimation in non-local environments (Haag *et al.* 2005; Cote *et al.* 2010; Edelaar & Bolnick 2012). An alternative approach to investigate local adaptation, particularly in natural systems, is to capitalize on genetic methods to identify natural dispersers and compare the fitness between local and migrant individuals.

In recent decades, salmonid fishes have become a model system for studying local adaptation in natural systems (Taylor 1991; Fraser *et al.* 2011; Peterson *et al.* 2014). Many salmonids are anadromous, migrating from freshwater spawning grounds to marine habitats, and demonstrate high fidelity to their natal spawning sites on their return migration (Quinn 1993; Hendry *et al.* 2003; Bett *et al.* 2017). Atlantic salmon (*Salmo salar*) exhibit extensive variation in life history related to the timing of sexual maturity and migration strategies (Quinn 1993; Garant *et al.* 2003; Barson *et al.* 2015; Erkinaro *et al.* 2018). However, a small proportion of salmon disperse to new spawning grounds upon returning from their marine migration (Fleming 1996; Fleming & Einum 2011). Here, we take advantage of such natural dispersal events in a wild Atlantic salmon population complex in the Teno River system of northern Finland (Vähä *et al.* 2017; Erkinaro *et al.* 2018) (Fig. 1) to compare the reproductive success of local individuals spawning in their natal environment versus individuals that have dispersed from other populations within the complex. Using data from four consecutive parent-offspring cohorts in a large spawning ground, we found that local individuals have a distinct and consistent reproductive fitness advantage over dispersers in both males and females. Similar results were observed in a single cohort from a second spawning area. Our results imply that a local reproductive fitness advantage lays the groundwork for local adaptation and population divergence in this species.

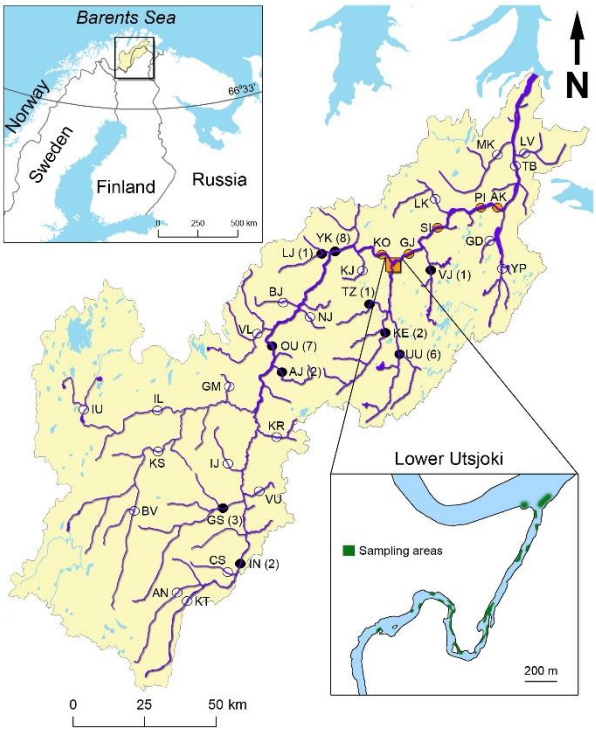

Fig. 1. Locations sampled for baseline populations (indicated with circles) in the Teno river basin (Vähä et al. 2017). The orange square represents the lower Utsjoki study site and orange circles represent locations in the Teno mainstem that were considered as 'local'. Black circles represent locations where spawning adults were assigned as dispersers with the number of assigned individuals noted in parentheses. Open circles represent baseline populations to where none of the breeding adults were assigned. Lower right inlay shows areas in green where adults and juveniles were sampled in the lower Utsjoki sampling location. Abbreviations for baseline sampling locations can be found in Fig. S2.

Results

Population assignment. A total of 264 adults (230 males and 34 females) and 5223 juveniles (all less than one year old) were collected in the lower Utsjoki location of the Teno River over four consecutive parent-offspring cohort years from 2011-2015 (see **Appendix S1**, Table S1). There was a significant 7:1 male-bias in the sex ratio (two-sided χ^2 =

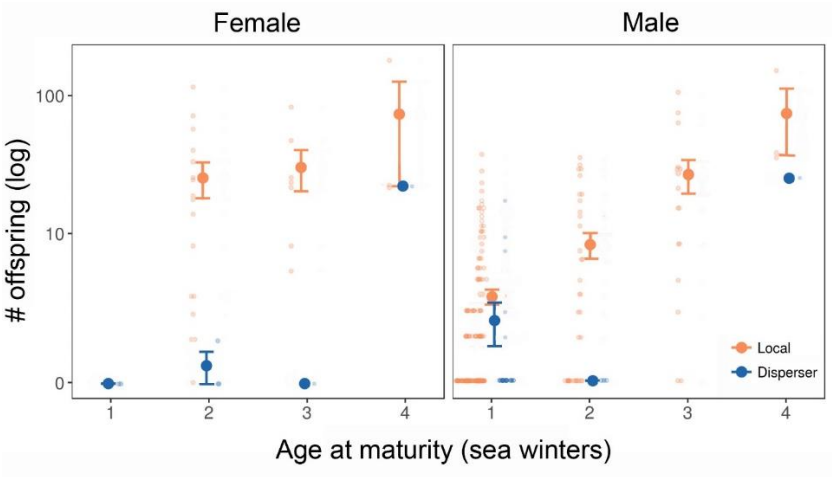

Fig. 2. The relationship of origin (local or disperser) and age at maturity (sea-winters) with reproductive success (# of offspring). Large circles with error bars indicate the mean ± SE, small circles show individual data points. For clarity, points are jittered on the x axis. No very young (1 SW) local females and only one old (3-4 SW) disperser male were recorded.

55.06, P < 0.0001) that was consistent over the four cohort years.

Genetic population assignment using a conditional maximum likelihood approach based on 30 microsatellite markers indicated that 231 (87.5%) of the adults (88.7% of males and 79.4% of females) originated from the same genetic population near the sampling location and were thus considered local (Table S2). The remaining 33 individuals (26 males and seven females) were assigned to 10 genetically distinct populations 3 to 183 km from the spawning area and were classified as dispersers (Table S2). Average individual assignment probabilities to baseline populations (Vähä *et al.* 2017) were 92.7% ± 0.7 (local: 94.0% ± 0.7; dispersers: 84.1% ± 3.0).

Teno river salmon show considerable variation in sea age at maturity, where spending more years at sea results in larger body size and higher fecundity (Heinimaa & Heinimaa 2004; Pritchard *et al.* 2018). Indeed, a range of sea ages at maturity, and therefore sizes, were observed in both local and disperser fish (Table S3). As is common in many Atlantic salmon populations, the average sea age at maturity of females was higher than males (2.4 ± 0.1 vs. 1.4 ± 0.0 sea-winters (SW), respectively). Local and dispersers did not differ in sea age at maturity (females: t = 1.55, P = 0.132, effect size 0.5 ± 0.3; males: t = 0.98, P = 0.326, effect size 0.1 ± 0.1) or weight within sex (females: t = 1.01, P = 0.322, effect size 0.58 ± 0.57; males: t = 0.64, P = 0.525, effect size 0.17 ± 0.27; Table S3). Local and dispersing fish showed no difference in condition (effect of origin, in addition to sea age, on condition: in females, -0.7 ± 0.5, t = -1.4, P = 0.167; in males, 0.1 ± 0.2, t = 0.4, P = 0.662).

Reproductive success. Bayesian parentage analysis using 13 microsatellite loci assigned 1987 of the 5223 offspring (38%) to at least one sampled adult with confidence (Table S4). Missing data for parentage analysis was 2.2% ± 0.3 in adults (mean number of loci genotyped: 12.72 ± 0.03) and 1.9% ± 0.1 in offspring (mean number of loci genotyped: 12.76 ± 0.01).

On average, local females were assigned 9.6 times more offspring than dispersing females (32.5 vs 3.4 offspring, respectively) and local males were assigned 2.9 times more than dispersing males (6.6 vs 2.3 offspring, respectively; Fig. 2, Table S3). These results were significant for both sexes (Table 1). This pattern of higher reproductive success among local females and males remained significant when restricting analyses to only include those adults that successfully reproduced at the site, i.e. only individuals confidently assigned as parents to offspring (Table S5).

The advantage of local spawners compared to dispersers was observed across all sizes and maturation ages (sea age). Both males and females showed greater reproductive success with increasing sea age at maturity (Table 1). In females, the difference in reproductive success between locals and dispersers was less pronounced in later maturing females (sea age class and origin interaction in addition to main effects of sea age, origin and number of adults and juveniles: -4.44 ± 1.03, z = -4.29, P < 0.0001, Fig. 2). Males, on the other hand, showed no evidence of different effects of origin in different sea age classes with local and dispersing males being consistently more successful within each sea age maturation class (sea age class and origin interaction: 0.13 ± 0.27, z = 0.492, P = 0.623; Fig. 2). Condition did not influence the effect of

Term	Parameter estimate	Std. error	z value	P
Females				
(intercept)	-6.58	0.31	-20.94	<0.0001
Sea age	0.61	0.05	13.09	<0.0001
# adults	0.02	0.02	1.29	0.199
# offspring	-0.02	0.01	-1.63	0.103
Origin	1.38	0.22	6.18	<0.0001
Zero-inflation	-8.83	0.49	-18.17	<0.0001
Males				
(intercept)	-6.75	0.20	-33.88	<0.0001
Sea age	0.83	0.03	32.40	<0.0001
# adults	-0.02	0.00	-7.56	<0.0001
# offspring	0.06	0.02	4.22	<0.0001
Origin	0.54	0.14	3.75	<0.0001
Zero-inflation	-7.28	0.14	-53.38	<0.0001

Table 1. Summaries of models for lower Utsjoki females and males testing the effects of sea age at maturity (sea age), annual adult sample size (# adults), annual offspring sample size (# offspring) and adult origin (local or disperser) on reproductive success. The "zero-inflation" term accounts for the large number of adults with zero reproductive success in our sample.

origin on reproductive success (effect size of origin in model also including condition as a predictor, in females: 1.57 ± 0.22; in males, 0.56 ± 0.14).

Consistency across cohort years In both sexes, the fitness advantage of local spawners was robust across all cohort years, and remained significant when any single cohort year was removed from the dataset (i.e., on all three year subsets of the data with males and females pooled, the smallest effect of origin as a main effect on number of offspring was 1.79 ± 0.23 and all P < 0.001).

Mating success and assortative mating. We examined the mating success (number of unique mates per individual identified within our sample) and whether mating was assortative according to origin (locals or dispersers). Among the 28 adult females and 115 males with at least one mate identified including unsampled mates, males had fewer mates than females on average (male mating success 1.4 ± 0.1 female mating success 3.0 ± 0.4, pooled across both locals and dispersers for each sex; effect of sex on mating success as a single main effect in a Poisson GLM: -0.74 ± 0.13 log(mates), z = -5.54, P < 0.001). Among the 55 pairs in which both mates were identified, the majority consisted of two local individuals, whereas no successful disperser-disperser pairs were identified (50 pairs local-local, five mixed, four of which had a local mother). Hence, there was no indication of assortative mating with respect to origin, with local and dispersing parents having similar proportions of dispersing mates (effect sizes as logit(proportion of mates disperser): in males 14.7 ± 3269, z = 0.005, P = 0.996; in females, 15.5 ± 3097, z = 0.005, P = 0.996). Local and dispersing parents also did not differ in the weight of their mates (effect of origin on sea age at maturity-controlled weight of mates in males: 2.6 ± 0.6 kg, t = 1.06, P = 0.291; in females: 0.2 ± 0.4 kg, t = 0.61, P = 0.550) nor in mating success, although males had fewer mates than females overall (in a single model of number of mates: effect of origin 0.20 ± 0.30 log(mates), z = 0.69, P = 0.490; effect of sex -0.74 ± 0.13 log(mates), z = -5.57, P < 0.001). Despite the small number of mixed-origin pairs, such pairs had significantly lower reproductive success than local-local pairs (-0.85 ± 0.35, z = -2.45, P = 0.014).

Discussion

It has been hypothesized that decreased reproductive success among migrants influences local adaptation by selecting against dispersal of adults and their offspring into new environments (Hendry 2004; Nosil *et al.* 2005). Our aim in this study was to utilize natural dispersal events to assess the relative reproductive success of dispersers in the wild. Although the majority of adults sampled had indeed returned to their natal spawning grounds, there was nevertheless considerable potential for gene flow between genetically distinct populations with dispersing adults accounting for approximately 12.5% of the potential parental pool. Despite this, only 3.7% of juvenile parentage assignments were matched to dispersing adults. Thus, the home

ground advantage of locals resulted in several times higher reproductive success for both males and females over dispersers. We also found an increase in reproductive success with sea age at maturity, indicating that the older, and therefore larger, fish tend to have higher reproductive potential, regardless of origin.

Dispersal and migration likely play important roles in phenotypic trait divergence (Kinnison *et al.* 2003; Edelaar & Bolnick 2012). However, we found no phenotypic differences in size and sea age at maturity between local and dispersing individuals. Costs of dispersal in terms of physical migration to new locations, arrival precedence on the spawning grounds, and familiarity with the natal environment may give local breeders an advantage, yet these factors are difficult to measure in the wild (Kinnison *et al.* 2003; Peterson *et al.* 2014). On the other hand, sex-specific and juvenile straying may promote adult dispersal (Hamann & Kennedy 2012), but evidence for factors that cause these behavioral differences is limited (Quinn 1993; Hendry *et al.* 2003; Peterson *et al.* 2016; Bett *et al.* 2017). If phenotypic differences between local and dispersing individuals were observed (e.g., Peterson *et al.* 2014) then assortative mating by phenotype may reinforce genetic and phenotypic differentiation. Alternatively, environmental variation may influence the degree of assortative mating between salmonid populations (Gauthey *et al.* 2016). Our examination of mate choice, albeit constrained by the low number of mating pairs including dispersers, gave no clear evidence of assortative mating based on origin, be it local or disperser. This result implies that mating preferences for local mates is sufficiently low to allow dispersers to obtain mates in non-natal localities.

In our study, dispersers almost exclusively originated from localities further upstream of our study location (34 dispersers from 25 possible upstream localities, 1 disperser from 7 possible downstream localities, Fig. 1). It is therefore worth considering the possibility of whether dispersers may have been still migrating upstream to spawn. We believe this is an unlikely scenario given that water temperatures are colder in upstream locations resulting in an earlier peak spawning activity in these areas compared to that of our study site (Heggberget 1988) (Fig. S1). Thus, adults leaving the lower Utsjoki spawning site after sampling would be less likely to find active spawning sites elsewhere. Moreover, studies in other salmonids show that movements in male sockeye salmon (*Oncorhynchus nerka*) decreases as the spawning season progresses (Rich *et al.* 2006), and that most dispersers first homed to their natal streams before dispersing to new spawning grounds (Peterson *et al.* 2016). Studies of Atlantic salmon caught in the Teno river show that movement of individuals to other areas is rare close to spawning (Økland *et al.* 2001) and radiotelemetry of individuals has also shown very limited movement during the breeding season (Karppinen & Erkinaro 2009). Thus, long distance movement of individuals visiting this spawning site close to spawning time is highly unlikely. Finally, in the unlikely event that dispersers were to spawn in several locations within a year, their reproductive success on non-natal spawning grounds remains demonstratively lower than local spawners based on our models that exclude adults with no offspring assigned in our sample (Table S5). Therefore, reduced reproductive success need not be a universal feature of an individual disperser, but one that is specific to reproductive success in the non-natal location even if the disperser potentially still produces more offspring, and thus obtains higher fitness, in their natal habitat.

Local adaptation. Reduced reproductive success in dispersers raises the strong possibility that local adaptation is reinforced if this pattern is observed throughout the system. A similar assessment of reproductive success in a single cohort at a second location in the Teno system (Akujoki, see **Appendix S1** Supplementary materials, Tables S1-4, S6, Figs. S2-3) allowed us to partially test for local adaptation. Mirroring our main results from lower Utsjoki, local individuals from Akujoki also had higher reproductive success over dispersers (local vs. dispersing females, 11.7 vs. 8.2 offspring; local vs. dispersing males, 9.0 vs 1.6 offspring; Table S3, Fig. S3). However, this effect was significant in males but not in females, possibly due to low sample sizes (Table S6, Fig. S3)

A key advantage of the current study compared to traditional reciprocal transplantation experiments is that we assessed reproductive success of natural dispersal events. However, our natural

dispersal approach also precluded a reciprocal design, and hence unambiguous identification of local adaptation. We did not identify any clear phenotypic differences between locals and dispersers in either study location and thus specific factors responsible for this pattern remain unclear. However, previous population genetics studies provide some insight regarding important differences between the lower Utsjoki site and the populations of origin of some of the dispersers. For example, using genomic screening, a recent study identified river flow volume as a potential adaptively-important environmental characteristic in Teno River Atlantic salmon (Pritchard *et al.* 2018). Flow volume is considerably higher in the lower Utsjoki study site compared to most of the disperser populations (Pritchard *et al.* 2018). Further, marked differences in juvenile growth rates, as well as differences in body size at age at maturity, have been observed between individuals from the lower Utsjoki location and the disperser population in the upper Teno mainstem (Aykanat *et al.* 2015). These observations suggests that there may be additional population-specific demographic or environmental factors that potentially influence local adaptation within the Teno River system.

Conclusion. This study provides convincing empirical support for fine-scale local selection against dispersal in a large Atlantic salmon meta-population, signifying that local individuals have a marked home-ground advantage in reproductive fitness. These results emphasize the notion that migration and dispersal may not be beneficial in all contexts and highlight the potential for selection against dispersal and for local adaptation to drive population divergence across fine spatial scales.

Methods and Materials

Study system. The Teno River is a large river in northern Europe (68–70°N, 25–27°E) that forms the border between Finland and Norway and drains north into the Tana Fjord at the Barents Sea (Fig. 1). The Teno River supports one of the world's largest and most phenotypically diverse Atlantic salmon stocks (Niemelä *et al.* 2006; Erkinaro *et al.* 2018). Up to 50,000 individuals are harvested by local fishers and recreational fisheries annually (Erkinaro *et al.* 2018), representing up to 20% of the riverine Atlantic salmon catches in Europe. The Utsjoki river is one of the largest tributaries of the Teno river system (length 66 km, catchment area 1652 km^2), draining into the main stem 108 km from the Barents sea.

Our focal sampling location covered the first kilometers from the mouth of the Utsjoki tributary, referred to hereafter as lower Utsjoki (69°54'28.37"N, 27°2'47.52"E; Fig. 1). This area includes large gravel beds suitable for spawning in the Teno river mainstream (Fig. 1). The lower Utsjoki harbors several distinctive spawning grounds (c. 150–400 m) which are separated by 150–600 m river sections with pools and slow flowing reaches. Wetted widths of the spawning areas vary from 30-50 m and the maximum spawning site depth is ~300 cm, although most nests (redds) are at depths between 70-150cm. Thermal conditions in lower Utsjoki are strongly influenced by Lake Mantojärvi (194 ha, max depth 60 m), situated approximately 5 km upstream from the river mouth: the lowest river stretch freezes over usually 1–2 weeks later than in the Teno main stem or in other tributaries. The daily mean water temperatures typically drops below 7°C by the end of September and the peak spawning activity usually takes place during the first week of October (Fig. S1).

The lower Utsjoki location includes permanent monitoring sites where annual electrofishing surveys have been conducted since 1979. Therefore, it is highly unlikely that areas with substantial numbers of juvenile salmon would be overlooked in our juvenile sampling. Regions with both high and low juvenile density were sampled each year with a view to ensuring the sampling of offspring produced by individuals spawning in different quality habitats.

The Teno river is characterized by a high level of temporally-stable genetic sub-structuring throughout the river system (Vähä *et al.* 2008), and genetically distinct populations within the mainstem are also reported (Vähä *et al.* 2017). Fish from the lower Utsjoki are genetically identical to individuals captured from the lower Teno mainstem (Vähä *et al.* 2017) (Fig. 1). We also sampled adults and offspring at a second spawning location, Akujoki River over one cohort year (2011-2012; Fig. S2) but for simplicity, we only present results from lower Utsjoki in the maintext.

Sampling. Anadromous adults were sampled in mid September-October on the spawning grounds, which is approximately 1-2 weeks prior to the commencement of spawning. All adults were assessed for signs of maturity during sampling (presence of secondary sexual characteristics, presence of sperm from milking males and visual inspection of females) and all adults appeared to be in, or very near, spawning condition. Throughout the study, "cohort year" refers to the spawning year when adults were captured and offspring were fertilized, although offspring were sampled in the subsequent calendar year. In total, four parent-offspring cohorts were sampled between 2011 and 2015.

Adults were caught using gill nets except for a few males caught by angling. Fish were transported into large keep nets by boat and then sexed, weighed and measured for total length (tip of snout to end of caudal fin). Scale and fin tissue samples were taken for phenotypic and molecular analyses, respectively. We released fish back into the river after sampling. During sampling, four adults died in the net (two disperser females, one disperser male and one local male). One of the dead females (caught October 1st) was observed to already have released her eggs and was therefore retained as a potential parent. The other three dead individuals were excluded from all analyses.

Juveniles were sampled 10-11 months later (around 2-3 months after they are expected to have emerged from the nests in the stream bed gravel) by comprehensively electrofishing all accessible river sections on or close to the spawning areas (Fig. 1). Genetic samples were collected from all juveniles by sampling a portion of the adipose fins or adipose- and anal fins. After sampling the juveniles were returned into the river.

Sea age at maturity. Sea age at maturity, defined as the number of years an individual spent at sea before returning to spawn (measured in sea-winters, SW) was determined for adults captured on the spawning ground using scale growth readings as outlined in (Aykanat *et al.* 2015). For one female and 15 males from which scales could not be obtained, sea age at maturity was estimated based on their weight. Briefly, data from known-sea age fish were used to define a normal distribution of weight in each sea age class, the likelihood of the weight of each unknown-age individual occurring in each sea age class was calculated, and each of these individuals was assigned the most likely sea age class for their weight (Fig. S4).

DNA extraction. DNA of adults and juveniles was extracted from 1-2 mm^3 of ethanol-preserved fin tissue with the QIAamp 96 DNA QIAcube HT Kit using Qiacube HT extraction robot using the recommended tissue extraction protocol with the following modifications: washing with the AW2 buffer was conducted twice, top elute buffer was not used and samples were incubated for 5 minutes before vacuum in the elution step. The final elution volume (AE buffer) was 100 µl.

Microsatellite genotyping. All adults and juveniles were genotyped using 13 microsatellite loci (panel 1 as outlined in Aykanat *et al.* (2014)) excluding locus *Sssp2210*) for parentage assignment. Adults were genotyped with an additional 17 loci (30 total loci) in order to improve the population assignment power (panel 2 as outlined in Aykanat *et al.* (2014) plus *Sssp2210* from panel 1 and *MHCII* as outlined in Ozerov *et al.* (2017)). PCR amplification was performed in 6µl (panel 1) or 8 µl (panel 2) volume using Qiagen multiplex master mix (Qiagen Inc. Valencia, CA, USA) with 0.1 to 0.4 µM of each primer. The amplification was carried out according to the manufacturer's standard protocol with annealing temperatures of 59 °C (Panel 1 MP1) or 60 °C. Visualisation of PCR products was achieved on a capillary electrophoresis-based ABI PrismTM 3130xl instrument (Applied Biosystems). Samples were prepared by pooling 1.6 µl of MP1 and 1.7 µl MP2 with 100 µl of MQ-H_2O (panel 1) and 1.5 of MP1 and 1.5 µl of MP2 with 100 µl of MQ-H_2O (panel 2). HiDi formamide (Applied Biosystems) and GS600LIZ size standard (Applied Biosystems) were mixed by adding 10 µl of HiDi and 0.1 µl of size standard/reaction. 10 µl of this mix was added in each well together with 2 µl of pooled PCR products. Before electrophoresis samples were denatured at 95 °C for 3 minutes. Alleles were visually inspected with Genemarker v.2.4 (SoftGenetics).

Population assignment. Adults were assigned to their population of origin using the

ONCOR program (Kalinowski *et al.* 2007). Population baseline data for individual assignment consisted of 3323 samples originating from 36 locations as described in Vähä *et al.* (2017). Allelic richness averaged 6.4 ± 0.1 across baseline sampling locations (range 4.5-7.3) and genetic assignment success as predicted from single stock simulations in ONCOR averaged 91.1 ± 2.1% (range 54-100%) (Vähä *et al.* 2017 *Supplementary Data*). Microsatellite data indicated that the baseline sampling sites extending 45km downstream and 5km upstream of the lower Utsjoki sampling location were not significantly differentiated from each other (Vähä *et al.* 2017) (Fig. 1). Therefore, microsatellite data from these five sampling sites were pooled to form one baseline population (the 'mainstem lower' baseline in Vähä *et al.* (2017) and adults assigned to this baseline sample were considered local (Fig. 1, Table S2).

Reproductive success. Reproductive success was quantified as the number of offspring assigned to an adult, following parentage assignment of all offspring. Pedigrees were constructed for each parent-offspring cohort separately using the package MasterBayes (Hadfield *et al.* 2006) V2.55 in the program R (R Core Team 2018). MasterBayes implements a Bayesian approach using MCMC sampling to estimate the most likely pedigree configuration while simultaneously estimating the unsampled population size, thus reducing bias in parentage assignments by allowing for uncertainty in all model parameters.

The pedigree model used fixed genotyping error rates in a two-level model, calculated by re-extracting and re-genotyping 190 randomly chosen samples from 24 initial plate runs and comparing the two runs. Allelic drop-out (E1) was calculated as the frequency of genotypes that were homozygous in one run and heterozygous in the other, which yielded more conservative error rates than MicroDrop, a dedicated tool to estimate allelic drop-out in genetic data without repeat samples. Stochastic error rate (E2) was calculated as the frequency of alleles that were scored differently in the two runs, conservatively also including one allele from all putative cases of allelic dropout. E1 and E2 were calculated separately for each locus. Across all 13 loci, mean E1 was 0.20% and mean E2 was 0.24%.

We calculated allelic frequencies from the parental genotypes to prevent skewing by family groups produced by particularly fecund parents. Alleles from unsampled parents, present in the offspring but not in the parental genotypes, were added manually to the parental genotypes at low frequency. A simulation analysis showed that, among offspring with confidently assigned parents, this marker panel identified the true (positively identified or unsampled) mother with 96.6% accuracy and true father with 93.3% accuracy (10 pedigree runs on genotypes simulated from the final pedigree). Errors in the simulation involved unsampled parents or low-confidence assignments, with different known parents assigned in different runs in only 0.2% of dam assignments and 0.3% of sire assignments. For offspring with 10 or 11 loci typed, one mismatch with potential parents was allowed, and for those with 7-9 loci typed, no mismatches were allowed. Among 2552 offspring typed at 10 or more loci and confidently assigned at least one parent, 30 of the 1192 dam assignments and 22 of the 1581 sire assignments had one mismatch between parent and offspring. Of 264 adults and 5341 offspring, 118 offspring with fewer than 7 loci successfully genotyped were excluded; all parents were successfully typed with at least 11 loci (204 at all 13 loci). Final sample sizes and assignment probabilities are shown in Tables S1 and S4.

Priors for the Bayesian inference were chosen to be broad but informative. The number of unsampled parents (unsampled population size) was estimated for both mothers and fathers in association with the pedigree estimation through MCMC sampling from the prior distribution, specified with a mean of four times the sampled population size (Aykanat *et al.* 2014), and variance calculated as 1.5 – 0.25 * sampled population size, which encompassed likely parameter space. The model was run for 70,000 iterations after a burn-in of 5,000, thinning every 2 iterations (Link & Eaton 2012). The modal pedigree configuration was extracted from the posterior distribution of pedigrees, and assignments with a likelihood of at least 90% were considered confident and used in the analyses.

A total of 13 individuals (6 female, 7 male) that had spawned in a previous year as adults were identified based on scale morphology (repeat spawners, or kelts) were captured at

the lower Utsjoki location (4.9% of all adult individuals captured in this location). The mean sea age at maturity of repeat spawning females was 3.2 ± 0.4 SE (range 2-4 SW) and all repeat spawning males had spent one year at sea before the first spawning migration and another year at sea before returning to spawning for the second time (all repeat spawners were 2 SW). Only one repeat spawning female was a disperser, all other individuals were local. Additionally, adult genotypes were screened for recaptures using allelematch (Galpern *et al.* 2012). Allelematch identifies full and partial genotype matches based on genotype data. Using the criterion of up to two allele mismatches, we found no recaptured adults pooled across all cohort years (2010-2014).

Statistical modelling. Relationships between parental traits including sea age at maturity, body size, origin (local or disperser), and reproductive success were tested in a generalized linear modelling framework using a zero-inflated model from the R package pscl (Jackman 2017). The distributions of number of offspring per adult contained a large proportion of zeros, which could arise if adults did not attempt to breed in the sample area but instead migrated elsewhere, and/or if adults bred but did not produce any offspring that were sampled or survived to swim up. The zero-inflated model was a two-component mixture model, accounting for zeros both in a binary term for the probability of the unobserved state (did or did not reproduce) and as zero counts as part of the proper count distribution. The zero-inflation probability was modelled in a binomial model with a logit link and the counts in a Poisson model with a log link. The response was the number of offspring assigned and all effect sizes are presented on the scale of the predictor in this log-linear model. Annual differences in sampling effort were addressed by offsetting both parts of the model by log(number of offspring sampled in that parents' sampling year). Different models testing effects on reproductive success were run separately for males and females to account for expected differences in the distributions of reproductive success. Phenotypic differences (sea age at maturity, weight and condition, calculated as the residual from a linear model of weight predicted by length for each sex and spawning cohort (Patterson 1992)) between local and disperser parents were tested using Gaussian linear models in the R package lme4 (Bates *et al.* 2015).

All models of reproductive success included a main effect of sea age at maturity as older fish tend to be more successful breeders, and indeed, later-maturing fish of both sexes produced more offspring (Fig. 2). In addition, between-year differences in the number of adults and juveniles sampled could affect reproductive success measures by influencing the likelihood that parents and offspring are identified in the pedigree. Hence, the number of offspring and adults of the relevant sex sampled each year (annual sample size) was included in all models. In models including these background predictors, we tested for a main effect of individual origin (local or disperser). To further examine the role of sea age at maturity, the interaction between individual origin and sea age was tested, using sea age at maturity as a two-level factor (termed "age class"; 1 and 2 SW vs. 3 SW or older in females, 1 SW vs. 2 SW or older in males) to account for the low numbers of older disperser fish. We also tested whether individual condition explained variation in reproductive success by repeating the main models with condition as an additional predictor. All these effects were tested only in the count component of the model. In all models, zero-inflation was addressed using a constant (intercept-only) binomial component of the mixture model.

To assess between-year consistency in the effect of origin, the modelling of origin as a main effect was repeated with each sampling year removed in turn, using a dataset that combined males and females, to allow for very small annual sample sizes of females and/or disperser fish. This model was the same as the main model except that it included an interaction between origin and sex, to allow for differences in effect size between males and females, and annual sample size was taken as the total number of adults (rather than of each sex) sampled each year.

We investigated local and disperser mating patterns by examining the mating success and whether breeding was assortative according to origin. We calculated mating success as the minimum number of unique mates for each parent identified through parentage analysis. Whenever only one parent was identified, we assumed one mate. However, it is possible that

additional pairings occurred but that we did not recover offspring from those reproductive events in our sample. We examined mate choice among the 55 pairs where both parents were positively identified; for each individual in these pairs, the weight and age of each mate was noted and the proportion of mates who were local was calculated. The relationship of all responses with individual origin was tested in the R package nlme (Pinheiro *et al.* 2017) V3.1-137 as follows: mating success (number of mates) was tested in a Poisson generalized linear model (GLM); number of offspring per pair was tested in a Poisson mixed model (GLMM) including mother ID as a random effect to account for multiple mating by females; mate weight was tested in a Gaussian GLMM including a main effect of mate sea age; and the proportion of mates that were local was tested in a quasibinomial GLM weighted by the number of mates.

To investigate whether local reproductive fitness advantage remains significant among only breeding individuals, we repeated our main analyses on a dataset including only those adults assigned as parents to offspring, i.e. excluding individuals that did not have offspring assigned to them in our sample. In our main analyses, reproductive success was modelled in a mixture model that allowed instances of zero reproductive success to be considered both due to parents not attempting to breed at all and due to a spawning attempt being made but failing to produce any offspring surviving to, or detected at, sampling. However, using only breeding individuals did not change the main conclusions of the study. Using the reproductive success of the 115 males and 28 females that had offspring assigned to them as parents, we tested for a main effect of origin alongside main effects of sea age at maturity and annual sample size of adults and offspring as in the main analyses. As these data were not zero-inflated, we used Poisson GLMs; effect sizes were log-transformed, as fitted by the model. Among both males and females that produced offspring, local individuals had higher reproductive success, with a more pronounced effect in females, just as in the full analyses, with local males producing, on average, 9.8 offspring compared to 7.7 for dispersers, and local females 30.9 compared to 12.0 for dispersers (effect of origin on number of offspring: in males, 0.51 ± 0.14, $z = 3.70$, $P = 0.001$; in females, 1.33 ± 0.21, $z = 6.37$, $P < 0.001$).

All statistical models were performed in R (R Core Team 2018) and all means are reported ± one standard error of the mean throughout the text.

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Appendix S1: Supplementary materials, Figures S1-4, Tables S1–6.

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