Home ground advantage: selection against dispersers promotes cryptic local adaptation in wild salmon

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Abstract

Individuals that disperse into new areas for reproduction are potentially at a disadvantage compared to residents that are locally adapted to environmental conditions. Such local adaptation has the potential to drive population divergence and ultimately speciation, yet quantifying the effect of dispersal on fitness is rarely investigated in the wild. Here we capitalize on fine-scale population structure and natural dispersal events to compare the reproductive success, and hence fitness, of local and dispersing individuals in multiple parent-offspring cohorts of wild Atlantic salmon (*Salmo salar*) in the Teno River, Finland. A total of 264 sexually mature adults and 5223 juvenile fish were captured on a large spawning ground of the Utsjoki tributary over four cohort years. Genetic population assignment identified adults that had migrated back to their natal spawning grounds (local) and individuals that originated from other populations within the system (dispersers). Parentage analysis of juveniles sampled on the spawning grounds the following spring demonstrated that local females and males had 9.6 and 2.9 times higher reproductive success than dispersers, respectively. No phenotypic differences in body size between local and dispersers were found. Thus, the forces driving selection against dispersal remain cryptic. Taken together, these results demonstrate that local salmon have a distinct fitness advantage over dispersers, revealing how local adaptation may act to drive population divergence without clear morphological differences or physical barriers to gene flow.

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[1-3]. Local adaptation arises when the optimal phenotype varies geographically, primarily due to environmental heterogeneity. As a result, populations evolve locally advantageous traits under divergent selection[1,2]. Studies of local adaptation can provide insights into the evolution and maintenance of biodiversity, species responses to climate change, and ultimately, the processes of speciation and extinction[4-7]. Therefore, understanding the evolutionary forces such as selection, migration, mutation and genetic drift that may promote or constrain local adaptation is an important aim in biology[2,8-13].

One ecological selection pressure that can limit gene flow between populations and influence local adaptation is immigrant inviability, or selection against dispersers and their offspring[14,15]. Immigrant inviability is the result of pre- and post-zygotic reproductive barriers to dispersal including reduced survivorship and reproductive success of migrants via mortality, mate choice, assortative mating, and reduced survivorship and fitness of hybrid offspring[14]. Consequently, immigrant inviability can be interpreted as a reproductive isolating mechanism that promotes local adaptation and ecological speciation[16].

Natural dispersal events have the potential to illuminate immigrant inviability, yet few studies documenting the effect of selection against migrants have been conducted in the wild (but see refs 17-19). Furthermore, commonly used reciprocal transplant experimental approaches

for demonstrating higher relative fitness of local individuals have several limitation that are rarely recognized[13,14,20]. Current reciprocal transplant experimental approaches 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[14,21]. Second, reciprocal transplant studies rarely, if ever, acknowledge the potential effects of the choice of 'migrant' individuals in reciprocal transplants. Third, randomly selected individuals in reciprocal transplant experiments may not reflect true natural dispersers that may express different behavioural or physiological phenotypes, and thus bias the results of the fitness estimation in non-local environments[22-25]. An alternative approach to investigate local adaptation, particularly in natural systems, is to capitalize on genetic methods to identify natural migrants and compare the fitness of local and migrant individuals.

In recent decades, salmonid fishes have become a model system for studying local adaptation in natural systems[8,11,26-29]. Most salmonids are anadromous, migrating from freshwater spawning grounds to marine habitats, and demonstrate high fidelity to their natal spawning sites on their return migration[30-32]. Atlantic salmon (*Salmo salar*) exhibit extensive variation in life history strategies related to the timing of sexual maturity and migration strategies[30-33]. A small proportion of salmon disperse to new spawning grounds on returning from their marine migration[34-36]. Here, we take advantage of natural dispersal events in a wild Atlantic salmon population complex in the Teno River system of northern Finland[37,38] (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 fitness advantage over dispersers in both males and females. Our results imply that local selection against dispersers may lay the groundwork for local adaptation and population divergence in this species.

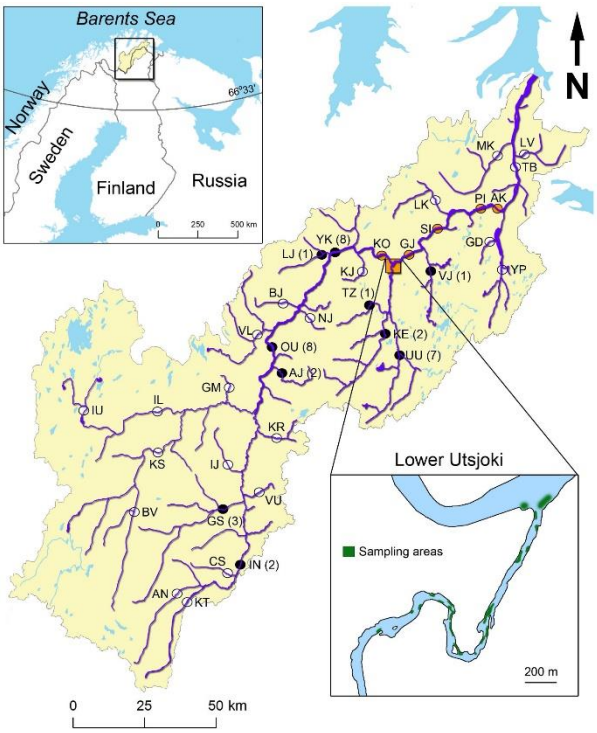

Figure 1: Locations sampled for baseline populations (indicated with circles) in the Teno river basin[38]. The orange square represents the lower Utsjoki study site and orange circles represent locations in the Teno mainstem that were considered as 'local'. Black circles represent locations where spawning 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 adult and juveniles were sampled in the lower Utsjoki sampling location. Abbreviations for sampling locations can be found in supplemental data.

Results

Population assignment. The Teno River system in northern Europe (68–70°N, 25–27°E) is characterized by a high level of temporally-stable and genetically distinct populations within its mainstem and between tributaries. This study focused on a 2km river stretch at the mouth of the Utsjoki tributary at the Teno mainstem (lower Utsjoki: 69°54'28.37"N, 27°2'47.52"E; Fig. 1). A total of 264 adults (230 males and 34 females) and 5223 juveniles (all < one year old) were collected in the lower Utsjoki location over four consecutive parent-offspring cohort years from 2011-2015 (Supplementary Table 1). There was a significant 7:1 male-bias in the sex ratio (two-

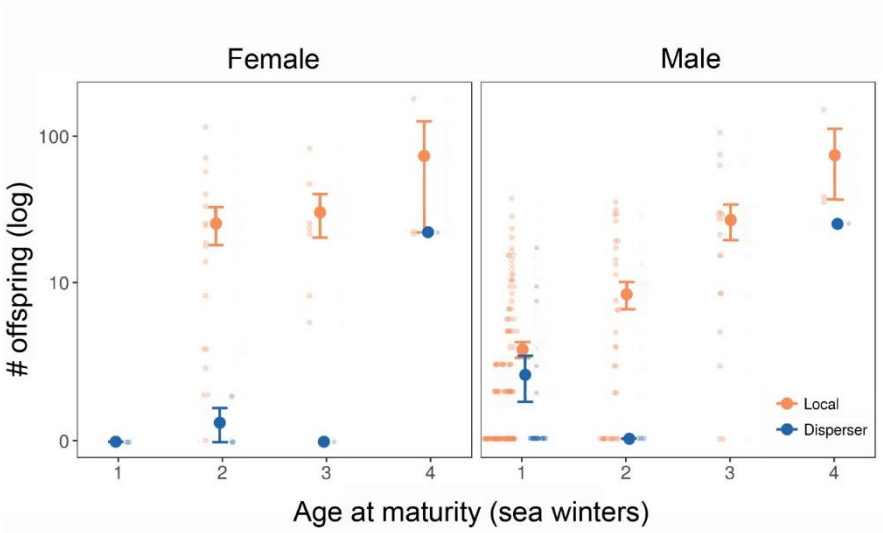

Figure 2. The effect of origin (local or disperser) and age of maturity (sea winters) on reproductive success. Large circles with error bars indicate the mean and ± standard error of the mean, small circles show individual data points. For clarity, points are jittered on the x axis. No very young (1SW)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

sided $\chi^2 = 55.06$, $P < 0.0001$) that was consistent over the four cohorts.

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 (Fig. 1, Supplementary Table 1). The remaining 33 individuals (26 males and seven females) were assigned to 10 genetically distinct populations 25 to 161 km from the spawning area and were classified as dispersers (Supplementary Tables 1 & 2).

Teno river salmon show significant variation in the number of years they spend at sea before returning to spawn (referred to as age at maturity and measured as seawinters or SW), where spending longer at sea results in larger body size and higher reproductive success[39,40]. A range of age at maturity classes, and therefore sizes, were observed in both local and disperser fish (Supplementary Table 3). As is common in many Atlantic salmon populations, the average age at maturity of females was higher than males (2.4 vs. 1.2 years, respectively). Local and disperser fish did not differ in age at maturity (females: 2.5 ± 0.1, $t = 1.55$, $P = 0.132$, effect size 0.5 ± 0.3; males: 1.3 ± 0.1, $t = 0.98$, $P = 0.326$, effect size 0.1 ± 0.1) or weight within sex (females: 8.06 ± 0.63, $t = 1.01$, $P = 0.322$, effect size 0.58 ± 0.57; males: 3.81 ± 0.24, $t = 0.64$, $P = 0.525$, effect size 0.17 ± 0.27; Supplementary Table 3).

Reproductive success. Bayesian parentage analysis assigned 1987 of the 5223 offspring (38%) to at least one sampled adult with confidence (Supplementary Table 4). 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, Supplementary Table 3). These results were significant for both sexes (females, effect of origin as main effect: 1.38 ± 0.22, $z = 6.18$, $p < 0.001$; males, effect of origin: 0.54 ± 0.14, $z = 3.75$, $p < 0.001$; all models include main effects of maturation age and number of sampled individuals, Supplementary Tables 3 & 5).

The advantage of local spawners compared to dispersers was observed across all sizes and maturation ages. Both males and females showed greater reproductive success with increasing age at maturity (males: 0.83 ± 0.03, $z = 32.4$, $p < 0.001$; females: 0.61 ± 0.05, $z = 13.1$, $p < 0.001$). In females, the difference in reproductive success between locals and dispersers was less pronounced in larger, later maturing females (maturation age class and origin interaction in addition to main effects of age, origin and number of adults and juveniles: -0.44 ± 1.03, $z = -4.29$, $p < 0.001$, Fig. 2, Supplementary Table 5). Males, on the other hand, showed no evidence of different effects of origin in different maturation age classes (maturation age class and origin interaction: 0.13 ± 0.27, $z = 0.492$, $p = 0.623$; Fig. 2, Supplementary Table 5).

Consistency across years. Across both sexes, the fitness advantage of local spawners was robust across all sampling years, remaining significant when any single 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 mates per individual) 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 (mean of 1.4 vs. 3.0 mates across both locals and disperses, Supplementary Table 3; effect of sex on number of mates as single main effect in 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 age of 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 the number of mates they had, 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, they displayed a visibly lower reproductive success than local-local pairs (-0.85 ± 0.35, $z = -2.45$, $p = 0.014$).

Discussion

Immigrant inviability influences local adaptation by selecting against dispersal of adults and their offspring into new environments[14,15]. Our aim in this study was to utilize natural straying events to offer a unique glimpse of selection against dispersal in the wild. Although the majority of adults sampled had indeed returned to their natal spawning grounds, there was nevertheless potential for gene flow between genetically distinct populations with dispersers accounting for approximately 12.5% of the parental generation. Despite this, 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 age at maturity, indicating that the older, larger fish tend to have higher reproductive potential, regardless of origin.

We found no obvious phenotypic differences in size and age between local and dispersing individuals. Hence, it is difficult to separate the potential mechanisms favouring local breeders, such as lower fitness costs of physical migration, precedence, and familiarity on dispersers from selection for particular environments[17]. A number of factors may promote dispersal within salmon populations, but evidence of factors that cause dispersal is limited[30-32]. However, it is interesting to note that dispersers almost exclusively originated from localities upstream of the main study location. If phenotypic differences between local and dispersing individuals had been observed (e.g. ref 17) then a potential explanation could be assortative mating by phenotype that may then reinforce genetic and phenotypic differences. Our examination of mate choice, albeit constrained by the low number of mating pairs including dispersers, gave no 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.

Cryptic local adaptation? A fitness disadvantage to dispersal raises the strong possibility that local adaptation will evolve if this pattern is observed throughout the system. A similar assessment of reproductive success in a second location in the Teno system (Akujoki, see Supplementary Methods) 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 (Supplementary Fig. 2, Supplementary Tables 1, 3-4, 6-7). A key advantage of the current study compared to traditional reciprocal transplantation experiments is that we assessed reproductive success of natural dispersal events. However, this also limited our natural dispersal approach from allowing a reciprocal design, and hence unambiguous identification of local adaptation. Because we find no clear phenotypic differences between local and dispersers in either of these locations, it is unclear what factors may be responsible for such a clear fitness dispersal disadvantage. Thus, the potential for cryptic local adaptation is likely high in spite of appreciable adult dispersal, although the ecological factors

driving such local adaptation remain unresolved in this case. Using genomic screening, a recent study identified river flow volume as a potentially adaptively important environmental characteristic in Teno River Atlantic salmon[41]. Future research on ecological differences between localities may reveal whether habitat preferences may drive local adaptation.

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 success. These results emphasise the notion that migration and dispersal may not be beneficial in all contexts and further highlight the potential for selection against dispersal and cryptic local adaptation to drive population divergence across very fine geographic scales.

Methods

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[42,43]. Up to 50,000 individuals are harvested by local fishermen and recreational fisheries annually[42], representing up to 20% of the riverine Atlantic salmon catches in Europe[44]. The river is characterized by a high level of temporally-stable genetic sub-structuring between tributaries[45,46], and genetically distinct populations within the mainstem are also reported[38,47].

The study focused on a 2km river stretch at the mouth of the just before connecting with Teno mainstream including large gravel beds suitable for spawning (Fig. 1, additional details concerning sampling locations and a second spawning location, Akujoki River can be found in the Supplementary Methods). Fish from this location are genetically identical to individuals captured from the lower Teno mainstem[38] (Fig. 1, Supplementary Table 2).

Sampling. Adults were sampled in September-October on the spawning grounds, approximately 1-2 weeks prior to the commencement of spawning, and had attained full secondary sexual characteristics. Throughout the study, "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. All sampling was approved by local environmental agencies and water management co-operatives, and conducted according to the relevant national guidelines.

Adults were caught using gill nets except for a few 1SW males caught by angling. We transported fish 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 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 assessable river sections on or close to the spawning areas (Fig. 1). Genetic samples were collected for all juveniles by removing a portion of the adipose fins or adipose- and anal fins. After sampling the juveniles were returned into the river.

Age at maturity. Each adult individual's age at maturity was determined using scale growth readings following internationally agreed guidelines[41] as outlined in ref 47. For one female and 15 males from which scales could not be obtained, age at maturity was estimated based on their weight. Briefly: data from known-age fish were used to define a normal distribution of weight in each age class, the likelihood of the weight of each unknown-age individual occurring in each age class was calculated, and each of these individuals was assigned the most likely age class for their weight (Supplementary Figure 1).

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 ref 48 excluding locus *Sssp2210*) for parentage assignment. Adults were genotyped with an additional 17 loci in order to improve their assignment to their population of origin (panel 2 as outlined in ref 48 plus *Sssp2210* from panel 1 and *MHCII* as outlined in ref 49). 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[50,51]. Population baseline data for individual assignment consisted of 3323 samples originating from 36 locations as described in ref 38. Microsatellite data indicated that the baseline sampling sites extending 45km downstream and 5km upstream of the spawning location were not significantly differentiated from each other[38] (Fig. 1). Therefore, microsatellite data from these five sampling sites were pooled to form one baseline population (the 'mainstem lower' baseline in ref 38) and adults assigned to this baseline sample were considered local.

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[52] V2.55 in the program R[53]. 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[54], calculated by 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[55]. 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%.

Allele frequencies were obtained 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 the candidate parent population, 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). Most changes 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. Of 2552 offspring typed at 10 or more loci and confidently assigned at least one parent, none showed any mismatches with the assigned parent(s). 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 are shown in Supplementary Table 4.

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[48], 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[56]. The modal pedigree configuration was extracted from the posterior distribution of pedigrees, and assignments with a likelihood of at least 90% were used in the analyses.

Statistical modelling. Relationships between parental traits including age at maturity, body size, origin (local or disperser), water distance and reproductive success were tested in a generalized linear modelling framework using a zero-inflated model from the R package pscl[57,58]. The distributions of number of offspring contained a large proportion of zeros, which could arise if parents did not attempt to breed in the sample area but instead migrated elsewhere, and/or if parents 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 breed) 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 regression with a log link. The response was the number of offspring produced 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). Males and females were analysed separately to account for expected differences in the distributions of reproductive success. In addition, variation in phenotypes (age at maturity and weight) between local and disperser parents was tested using Gaussian linear models in the R package lme4[59].

All models of reproductive success included a main effect of age of maturity as older fish tend to be more successful breeders, and indeed, later-maturing fish of both sexes produced more offspring (Fig. 2, Supplementary Table 3). 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 (Supplementary Table 3). In models including these background variables, we tested for a main effect of individual origin (local or disperser). To further examine the role of age at maturity, the interaction between individual origin and age was tested, using age at maturity as a two-level factor (termed "age class"; 1 and 2SW vs. 3SW or older in females, 1SW vs. 2SW or older in males) to account for the low numbers of older disperser fish. 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.

Local and disperser mating patterns were investigated by examining the mating success and whether breeding was assortative according to origin. Mating success was calculated the number of unique mates for each parent identified through parentage analysis (Supplementary Table 4). Mate choice was examined only among the 55 pairs where both parents were positively identified; for each individual in these pairs, the proportion of mates who were local and the mean weight of mates were calculated. The relationship of all responses with individual origin was tested in the R package nlme[60] V3.1-137 using a Poisson generalized linear model (GLM) for the number of mates, a Poisson mixed model (GLMM) for the number of offspring per pair with mother ID fitted as a random effect to account for many females being represented more than one pair, a Gaussian model including a main effect of mate age for mate weight, and a quasibinomial GLM for the proportion of local mates. In the latter two,

the response was weighted by the number of mates.

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Author contributions C.R.P., J.E., P.O., T.A. & ME designed the study. M.E., J.-P.V., P.O., S.J. & C.R.P. collected samples. M.E. & J.-P.V. performed laboratory work. H.G.-W. & J.-P.V. analysed the data, K.B.M., C.R.P. & H.G.-W. wrote the manuscript, with input and final approval from all other authors.

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Supplementary Information Supplementary Methods, Supplementary Figures 1-2, Supplementary Tables 1–7, Supplementary References.

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