

NEWS AND VIEWS

PERSPECTIVE

Puny males punch above their weight to preserve genetic diversity in a declining Atlantic salmon populationJ.-S. MOORE*¹ and D. J. FRASER†**Department of Zoology and Beaty Biodiversity Research Centre and Museum, University of British Columbia, 6270 University Boulevard, Vancouver, BC, Canada V6T 1Z4; †Department of Biology, Concordia University, Montréal, QC, Canada H4B 1R6*

Many salmonid fish populations have anadromous (i.e. migratory) and nonanadromous individuals co-existing in sympatry. The nonanadromous individuals, frequently males, mature at a much smaller size in freshwater without undergoing marine migrations and often successfully fertilize many eggs laid by anadromous females. Because these small males do not recruit to fisheries, they are often not regarded in high esteem by fishers. In this issue of *Molecular Ecology*, Johnstone *et al.* (2013) demonstrate that by substantially contributing to reproduction, such males help maintain genetic diversity in a declining population of Atlantic salmon (*Salmo salar*). Their results show that estimates of effective population size (N_e), obtained by counting the number of anadromous adults returning from sea and correcting for unequal sex ratios, are lower than estimates generated from genetic markers. Many mechanisms are expected to reduce N_e below the adult census population size (N); the opposite pattern of $N_e > N$ observed by Johnstone *et al.* (2013) is difficult to explain unless the reproductive effort of nonanadromous males is accounted for. The results have important implications for the conservation of small populations and highlight the challenges of relating N_e to N in organisms with complex life histories.

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It is not easy being an anadromous Atlantic salmon (*Salmo salar*). Born in freshwater, you are exposed to an array of predators as you migrate to marine feeding grounds in the North Atlantic. Once you attain a large enough size,

typically after one or more winters at sea, you return to natal spawning beds following an arduous upstream migration. It is therefore not surprising that in many populations, a substantial proportion of males – whose reproductive output is less tightly linked to body size than that of females – opt instead for the much easier option of foregoing marine migration and maturing at a small size in freshwater. These males then ‘sneak’ in between their larger anadromous brethren while they are fighting over access to anadromous females, and often successfully fertilize a significant portion of the eggs (Fleming 1996). Much recent work has strongly suggested that the variable life history of Atlantic salmon constitutes a conditional strategy wherein juveniles displaying certain phenotypes (often a larger size at age or growth rate) forego anadromous migrations in favour of freshwater residence (e.g. Hutchings & Myers 1994; Piché *et al.* 2008). In some populations, males adopting freshwater residence far outnumber the larger anadromous males (Fleming 1996). Because fishers do not care much for those small males, their presence has often been seen as having a negative effect on recruitment to the fishery and on the harvestable biomass (Myers 1984). Indeed, nonanadromous males can eventually grow to become anadromous males, but the energy invested in early reproduction often results in increased mortality. For instance, Myers (1984) estimated that precocious male maturation reduced the anadromous male population by 60% in a Newfoundland stream. The study by Johnstone *et al.* (2013) published in this issue of *Molecular Ecology* suggests that, while small mature males do reduce the number of anadromous males, they contribute significantly to the preservation of genetic diversity in a declining population. They could thus contribute to the long-term persistence of populations – and thus to fisheries – that might otherwise suffer from a number of genetic consequences associated with small population size.

Johnstone *et al.* (2013) took advantage of a long-term data set of adult census population size (N) estimates collected between 1985 and 2011 from a small salmon stream in southeast Newfoundland (Fig. 1), which they supplemented with microsatellite data from samples collected over the same period. The authors predicted that, if the nonanadromous males contributed significantly to genetic diversity in the population, effective population size (N_e) estimates based on genetic markers should be higher than those obtained from counting the returning number of anadromous adults (after correcting for unequal sex ratios). Few other mechanisms would be expected to lead to such a pattern. Indeed, a variety of well-known mechanisms reduce N_e compared with N (e.g. variance in reproductive success, biased sex ratios, fluctuating population sizes), but the opposite pattern is difficult to explain

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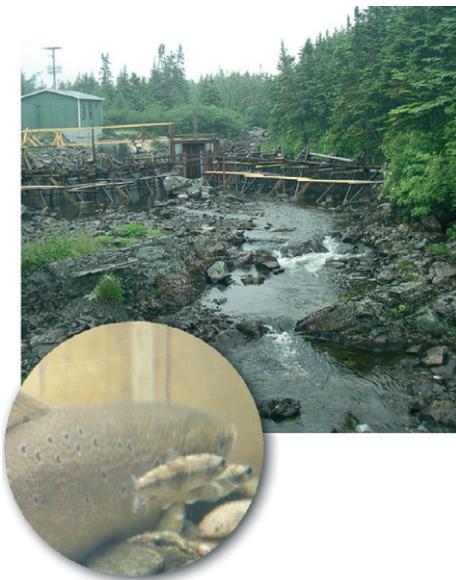


Fig. 1 The counting fence set up on Northeast Brook, Trepassy in southeast Newfoundland, Canada, used by Johnstone *et al.* (2013) to obtain estimates of the anadromous adult Atlantic salmon run sizes between 1985 and 2011. The inset shows two nonanadromous small mature male parr Atlantic salmon swimming next to a much larger anadromous male. Photo credits: top: D. Ruzzante, bottom: L. Weir & J. Hutchings.

unless one considers the contribution of nonanadromous males. Because of the prevalence of early maturation in males, the sex ratio of returning anadromous adults was female-biased; N_e was therefore estimated based on theoretical predictions of the effect of biased sex ratio on N_e . Note that, many other phenomena not taken into account here (e.g. high variance in reproductive success) would also reduce effective population size, but this only renders the conclusions of the study more conservative. Estimating N_e using genetic markers can be challenging and estimates often vary between methods or can have large confidence intervals (Luikart *et al.* 2010; Palstra & Fraser 2012). The authors mitigated this potential problem by generating many estimates from a variety of estimation methods (for a recent review of available genetic methods, see Luikart *et al.* 2010). The data set allowed the use of several different temporal methods on samples separated by roughly five generations. These temporal estimates were supplemented with those generated from a single year of sampling. In this case again, multiple methods were used, but only the linkage disequilibrium method was found to give reliable results. Variation among estimates generated with different methods was considerable (between 290 and 584). Nevertheless, in all cases, the N_e estimates obtained from microsatellites were 34–420% higher than the demographic estimate of N_e obtained using the information on the sex ratio of the anadromous run.

Conditional mating strategies are widespread among salmonids and other taxa (Gross 1996), and the results of Johnstone *et al.* (2013) have implications for the conserva-

tion of small populations of other species of salmonids. It remains to be seen whether the contribution of these puny males to the preservation of genetic diversity is a widespread phenomenon, but in the population studied by Johnstone *et al.* (2013), they certainly punch above their weight class. The study also highlights some of the challenges associated with calculating N_e/N ratios in organisms with complex life histories. Estimates of N_e are easily obtained from molecular markers and offer the promise of a simple and cost-effective tool to estimate N in conservation programs strapped for cash (Luikart *et al.* 2010). But a simple conversion factor based on N_e/N ratios remains elusive (Palstra & Fraser 2012), and such ratios are likely to vary among species, among populations within species and even over time within populations. More studies that provide reliable estimates of both N_e and N are needed to understand the relationship between the two parameters. Reliable estimates of census population size are particularly hard to come by (Palstra & Fraser 2012), and the study by Johnstone *et al.* (2013) suggest that they may be particularly unreliable in species where one component of the population is more difficult to catch or survey than the remainder.

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J.-S.M. and D.J.F. are both interested in salmonid evolutionary ecology, molecular ecology and conservation genetics, and they both enjoy working at the inter-phase between fundamental and applied problems. Neither of them is particularly interested in boxing.

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