SHORT COMMUNICATION

Effective size of an Atlantic salmon (*Salmo salar* L.) metapopulation in Northern Spain

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Abstract The genetic diversity of metapopulations is influenced not only by the effective sizes (N_e) of individual subpopulations, but also by the total effective size of the metapopulation (*meta-N_e*). We estimated *meta-N_e* of four neighbouring Atlantic salmon populations connected by gene flow using genetic estimates of subpopulation N_es and migration rates derived from capture–recapture data. The *meta-$\hat{N}_e$* was lower than the sum of $\hat{N}_e$s of the subpopulations, suggesting that genetic diversity harboured by the four river salmon metapopulation is lower than what would have been expected by viewing individual subpopulations separately. In addition, *meta-$\hat{N}_e$* was found to be sensitive to changes in $\hat{N}_e$ of the subpopulation from which net emigration rate was largest, so as that the genetic diversity of the metapopulation would be best preserved by avoiding any reductions in N_e of this subpopulation. Yet, this subpopulation is the one that has historically—and still is—experiencing the highest exploitation rate in the metapopulation system.

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Introduction

Genetic diversity allows organisms to evolve in response to environmental change and avoid inbreeding depression (Reed and Frankham 2003). The effective population size (N_e) is a metric that predicts the rate of change in genetic diversity and potential for inbreeding in the absence of gene flow, and it has thus become a standard criterion for assessing conservation status and extinction risks of species and populations (Frankham 1995). However, the use of N_e has traditionally been restricted to individual populations, whereas in the real world natural populations are often interconnected by some degree of gene flow (Slatkin 1985), so it becomes necessary to consider the genetic consequences resulting from metapopulation dynamics (reviewed in Whitlock 2004).

In a set of interconnected populations, i.e. a metapopulation (Hanski and Gilpin 1991), genetic diversity depends not only on the N_e and dynamics of individual subpopulations but also rates of gene flow between them (Whitlock and Barton 1997; Wang and Whitlock 2003). Consequently, genetic diversity of a metapopulation should not be only assessed at the level of individual subpopulations, but by considering the total effective size of a metapopulation, *meta-N_e* (e.g. Fraser et al. 2007a;

Palstra and Ruzzante 2008). Theory suggests that meta-N_e is not equal to the sum of N_es of the subpopulations, but that it can be either increased through differentiation slowing down overall genetic drift (Wright 1939, 1943), or substantially reduced due to differences in subpopulation sizes, demography, or asymmetries in sex ratio or gene flow (Whitlock and Barton 1997; Nunney 1999; Whitlock 1999; Waples 2002a; Tufto and Hindar 2003; Fraser et al. 2007a; Palstra and Ruzzante 2008). Such dependencies have implications for species conservation and management, and there is a general need for empirical investigations of meta-N_e and its dynamics in metapopulation systems (Whitlock and Barton 1997; Fraser et al. 2007a). In harvested populations, it has also been shown that considerable gains in meta-N_e can be achieved if the harvesting strategy in interconnected populations accounts for their metapopulation structure (Tufto and Hindar 2003; Hindar et al. 2004).

Atlantic salmon (Salmo salar L.) is an anadromous fish which has declined dramatically over the last decades throughout the world due to overexploitation, habitat change, aquaculture of Atlantic salmon (World Wildlife Fund 2001; Ford and Myers 2008) and potentially also through genetic interactions between wild and escaped farmed salmon (Tufto 2001; Naylor et al. 2005). Despite usually strong homing tendency resulting in genetic differentiation and likely local adaptations (Garcia de Leaniz et al. 2007; Verspoor et al. 2007), some gene flow occurs between neighbouring populations with straying rates ranging between 0 and 19% (reviewed in Stabell 1984; Hendry and Stearns 2004). Recent studies on migratory salmonids have further revealed that asymmetric gene flow amongst populations is common and can play a substantial role in maintaining salmonid genetic diversity (Østergaard et al. 2003; Consuegra et al. 2005; Fraser et al. 2007b; Hansen et al. 2007; Dionne et al. 2008). Therefore, it becomes important to consider metapopulation structure in conservation strategies for Atlantic salmon (Cooper and Mangel 1999; Schtickzelle and Quinn 2007), particularly in order to allocate fishing effort between local populations in a genetically sustainable way (Hindar et al. 2004).

In Southern Europe, the abundance of Atlantic salmon has declined drastically, and several populations are endangered and may face extinction (World Wildlife Fund 2001; Hindar et al. 2007). Here we focus on four neighbouring Atlantic salmon populations in Northern Spain that are connected by gene flow (Consuegra et al. 2005; Consuegra and Garcia de Leaniz 2007). Our aim was to estimate the meta-N_e of this four-river metapopulation and identify the relative importance of each subpopulation in determining meta-N_e.

Methods

Migration between the rivers

The Rivers Deva, Nansa, Pas and Ason are located in Northern Spain and drain into the Atlantic Ocean (Fig. 1). During the period 1996–2000 a mark-recapture study was conducted in the Rivers Nansa, Pas, and Ason by stocking 605 847 coded wire tagged juveniles into these rivers and recapturing them as adult spawners (Consuegra et al. 2005). In total 208 marked individuals were recaptured over the study period. During the same period, similar mark-recapture studies were conducted in other salmon rivers of N. Spain with similar stocking and fishing efforts as in our four study rivers (data in Garcia de Leaniz et al. 2001). Yet, only one marked immigrant (from neighbouring river Sella) was recaptured in our study rivers (in River Nansa) while three emigrants were recaptured in neighbouring river Bidasoa, and one emigrant was recaptured in neighbouring river Lea (Garcias de Leaniz, unpublished data), suggesting that the study rivers can be treated as a fairly isolated metapopulation system.

We utilized the recapture data (Table 1) to predict rates of migration between the four rivers. Migration rates can be assumed to decrease as a function of distance x between the rivers (Jonsson et al. 2003; Hendry and Stearns 2004), so we modelled the probability using a double-exponential distribution

$$f(x) = \frac{1}{\sqrt{2}a}e^{-\frac{\sqrt{2}}{a}|x|} \tag{1}$$

that peaks at the natal river, where a is a free model parameter equal to the standard deviation of the dispersal displacements x. The probability of entering a river was calculated by taking the integral of the probability density function, using points half the distance between the rivers $z_i = (x_{i+1} + x_i)/2$ as intermediate cut points, and $-\infty$ and $+\infty$ as the left- and rightmost cut points. The probability of migrating from river j to river i is then
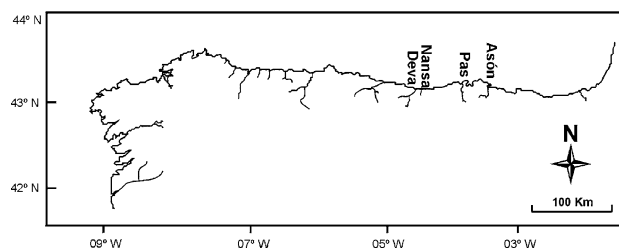
Fig. 1 Locations of the study rivers in Northern Spain. The distance between Deva and Nansa is 3 km, between Nansa and Pas 39 km, and between Pas and Ason 50 km

Table 1 Backward migration rates between the rivers predicted by the migration model

Expected and observed (bold font) numbers of recaptures are given inside brackets

River of capture	River of origin			
	Deva	Nansa	Pas	Ason
Deva	0.929	0.049	0.016	0.006
Nansa	0.068	0.817 (69.3, **69**)	0.082 (21.3, **24**)	0.032 (4.4, **2**)
Pas	0.016	0.043 (1.4, **2**)	0.915 (88.3, **88**)	0.026 (1.3, **1**)
Ason	0.001	0.003 (0.04, **0**)	0.005 (0.2, **0**)	0.991 (21.8, **22**)

$$m_{ij} = F(z_{i+1} - x_i; a) - F(z_i - x_i; a) \tag{2}$$

where $F(x)$ is the cumulative density function.

The 'attractiveness' of a river to Atlantic salmon may affect migration and also sizes of annual returns have been observed to increase rates of immigration to a river (Jonsson et al. 2003). To account for this, migration probabilities were weighted with census sizes of the anadromous river populations ($N_{c,i}$) that, in addition to correlating with annual run sizes (Consuegra et al. 2005), were considered good proxies of the general preference of salmon to reproduce in each river. Weighting was done through a term $N_{c,i}^b$ in which b was a free model parameter. During the period 1996–2000 harmonic means (and their 95% CIs) of the census anadromous population were 151 (±50), 393 (±143), 202 (±135) and 86 (±66) in Deva, Nansa, Pas and Ason, respectively (Consuegra et al. 2005). Furthermore, the model was designed to have a parameter c describing the minimum homing probability, representing an inherited tendency of a salmon to return to its natal river. The probability of migration from river j to river i then becomes

$$m'_{ij} = \delta_{ij}c + (1-c)\frac{m_{ij}N_{c,i}^b}{\sum\limits_{i=1}^{4} m_{ij}N_{c,i}^b} \tag{3}$$

where $\delta_{ij} = 1$ for $i = j$ and 0 otherwise. Since recaptures only occurred in a subset S of the rivers in the system (i.e. Nansa, Pas and Ason), the probability of being recaptured in river i, conditional on being recaptured in one of the rivers $i \in S$ becomes $m''_{ij} = m'_{ij} / \sum_{i \in S} m'_{ij}$. Assuming that the observed recapture counts (X_{2j}, X_{3j}, X_{4j}) follow a multinomial distribution with parameters $\left(m''_{2j}, m''_{2j}, m''_{2j}, \sum_{i \in S} X_{ij}\right)$, the log likelihood function, omitting constant terms, becomes

$$\ln L(a, b, c) = \sum_{i \in S} \sum_{j \in S} X_{ij} \ln m''_{ij} \tag{4}$$

The migration rate model was fitted to the mark-recapture data numerically using the maximum likelihood method.

Estimation of the effective metapopulation size (meta-N_e)

Estimates of N_e per generation are reported by Consuegra et al. (2005) for Deva, Nansa, Pas and Ason for years 1996–2000. Genetic estimates (microsatellite analyses based) of N_e with their 95% confidence intervals (CI) derived using the method by Wang and Whitlock (2003) were 28 (22–37), 31 (24–42), 29 (23–37), and 12 (11–16) assuming open populations with immigration ($\hat{N}_{eOPEN}$), and 84 (42–506), 74 (38–313), 98 (81–645), and 38 (27–87) assuming closed populations ($\hat{N}_{eCLOSED}$), respectively. We estimated meta-N_e of the four-river metapopulation system using the method developed by Tufto and Hindar (2003). Unlike Whitlock and Barton's (1997) method which requires information about correlations between and within populations, this method calculates meta-N_e from a backward migration matrix M and subpopulation N_es. For a system of four subpopulations, the meta-N_e is defined based on the dominant eigenvalue of a 10×10 matrix A (a function of M and local N_es) describing the transition of the 10 variances and covariances of subpopulation allele frequencies from one generation to the next. For details see Tufto and Hindar (2003). While the method assumes a constant migration matrix and constant subpopulation N_es it should provide a reasonable estimate of meta-N_e (meta-$\hat{N}_e$) also in cases with some temporal variation in local population sizes and the pattern of migration (R-code is available from the second author). Based on a normal approximation, a 95% CI around meta-$\hat{N}_e$ was computed from the corresponding standard error using the delta method (see e.g. Bolker 2008, p 366) with partial derivates calculated numerically. To investigate relative amounts of uncertainty in meta-$\hat{N}_e$ arising from uncertainty associated to $\hat{N}_{eOPEN}/\hat{N}_{eCLOSED}$ and the migration model, we estimated 95% CI by 1) only considering uncertainty in $\hat{N}_{eOPEN}/\hat{N}_{eCLOSED}$ and 2) by considering uncertainty in both $\hat{N}_{eOPEN}/\hat{N}_{eCLOSED}$ and the migration model. To investigate sensitivity of meta-N_e to changes in a subpopulation, we assessed how meta-$\hat{N}_e$ would change if $\hat{N}_{eOPEN}/\hat{N}_{eCLOSED}$ of one subpopulation increased or decreased with up to ±20%.

Results

The estimated migration rate model parameters were a: 77.12 (SE $\pm$ 87.56) km, b: 3.85 (SE $\pm$ 0.91) and c: 0.76 (SE $\pm$ 0.05). Estimated standard errors (SE) indicated uncertainty in the rate parameter of the double-exponential distribution, whereas the exponent of N_c and the minimum homing probability were estimated with a good level of certainty. Comparison of model predictions with recapture data (Table 1) as well as a goodness of fit test based on the deviance (McCullagh and Nelder 1989) of the model both indicated that the model fitted the data well ($D = 3.15$, $df = 2$, $P = 0.21$). Therefore, the model was considered to provide a reasonable proxy of salmon migration between the rivers, and the backward migration matrix predicted by the model (Table 1) was used to calculate $meta\text{-}\hat{N}_e$.

When calculations were based on $\hat{N}_{eOPEN}$ the $meta\text{-}\hat{N}_e$ was 45.6, whereas when being calculated using $\hat{N}_{eCLOSED}$ the $meta\text{-}\hat{N}_e$ was 95.8. 95% CIs around these estimates were 42.2–48.9 and 54.3–137.3, respectively, when only considering uncertainty in $\hat{N}_{eOPEN}/\hat{N}_{eCLOSED}$, whereas including uncertainty in the migration model yielded the corresponding 95% CIs being 6.2–87.9 and 0–232.4. Thus, $meta\text{-}\hat{N}_e$ was in both cases smaller than the sum of estimated effective subpopulation sizes [100 for $\hat{N}_{eOPEN}$; 294 for $\hat{N}_{eCLOSED}$]. $meta\text{-}\hat{N}_e$ was very robust to changes in Deva, Nansa, and Pas subpopulations, so that even $\pm20\%$ change in either $\hat{N}_{eOPEN}$ or $\hat{N}_{eCLOSED}$ changed $meta\text{-}\hat{N}_e$ with less than ±0.5 individual (Fig. 2). In contrast, a change of $\pm20\%$ in $\hat{N}_{eOPEN}$ for Ason population changed $meta\text{-}\hat{N}_e$ with ±3.5 individuals (Fig. 2a), and for $\hat{N}_{eCLOSED}$ the corresponding change was ±14.1 individuals (Fig. 2b).

Discussion

While some metapopulation models predict a higher $meta\text{-}\hat{N}_e$ than the sum of the effective population sizes of the subpopulations (e.g. Wright 1943), this does not seem to be the case in our study system. We found that the $meta\text{-}\hat{N}_e$ of the Atlantic salmon metapopulation was much lower than the sum of effective subpopulations sizes, regardless of whether open ($\hat{N}_{eOPEN}$) or closed ($\hat{N}_{eCLOSED}$) estimates were considered. This result suggests that the amount of genetic diversity harboured by the four-river metapopulation is lower than what would have been expected by analysing individual subpopulations separately (Consuegra et al. 2005). Such a pattern can come about if subpopulations contribute differently to the pool of migrants in the metapopulation (e.g. Whitlock and Barton 1997; Waples 2002b; Tufto and Hindar 2003). This was found to be the case with the Atlantic salmon populations considered here: rates of migration differed between the
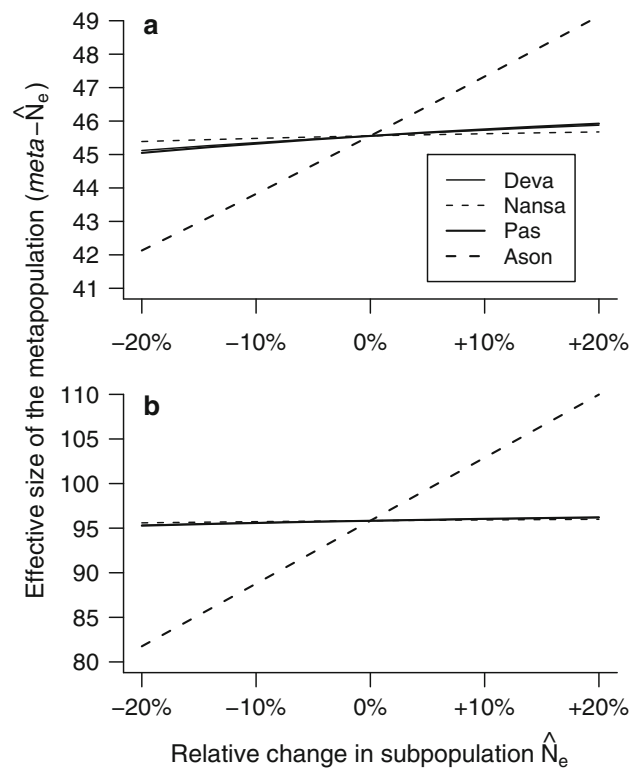
Fig. 2 Change in the effective size of the four-river metapopulation ($meta\text{-}\hat{N}_e$) of Atlantic salmon, when $\hat{N}_e$ of one subpopulation increases/decreases with up to $\pm20\%$. In panel a $meta\text{-}\hat{N}_e$ is calculated based on $\hat{N}_{eOPEN}$, whereas in panel b calculation is based on $\hat{N}_{eCLOSED}$

four populations, with the backward migration rates into River Ason being generally lower than corresponding migration rates out of Ason (Table 1). Such asymmetries in the pattern of migration are known to lower the total effective size towards the size of the subpopulation with the largest net emigration rate (Tufto and Hindar 2003; Hindar et al. 2004). This, and Ason's higher degree of isolation, makes $meta\text{-}\hat{N}_e$ more sensitive to changes in $\hat{N}_{eOPEN}/\hat{N}_{eCLOSED}$ of the Ason population and less dependent on the effective size of other subpopulations (Fig. 2). Our results emphasize the importance of using realistic estimates of migration patterns when estimating metapopulation N_e. This contrasts with practise (e.g. Fraser et al. 2007a) where each population is considered to receive a similar fraction of migrants drawn randomly from the migrant pool.

The $meta\text{-}\hat{N}_e$ estimates derived in this study are well below the critical limit of 500 suggested necessary to avoid loss of genetic variability (Franklin 1980). The observation is not surprising given that estimated effective sizes of populations in the Rivers Deva, Nansa, Pas and Ason were all fairly low (Consuegra et al. 2005), but evokes concerns about the long term persistence of the salmon populations in question. Our analyses were based on N_e estimates and

migration rates detected between 1996 and 2000, but the study populations are known to have declined in their census sizes throughout the second half of the twentieth century (Consuegra et al. 2005; Ciborowski et al. 2007; Kuparinen et al. 2009), so that our estimates of *meta-N_e* may not reflect long-term state of the metapopulation. However, even though being currently low, the estimated *meta-N_e* of the four river system does not imply that the populations would be doomed to extinction. Several analyses of Atlantic salmon populations have shown that despite declines in census sizes, populations have still managed to preserve much of their neutral genetic diversity (Consuegra et al. 2005; Saura et al. 2006; Fraser et al. 2007b; Ribeiro et al. 2008), suggesting that genetic compensation mechanisms can buffer against loss of genetic diversity at low population sizes (Fraser et al. 2007b). Precocious male maturation that generally supports multiple paternity and thus enhances N_e is common to southern salmon populations (Martinez et al. 2000) and reproductive success of mature male parr can further increase at low population sizes (Fraser et al. 2007b). Preservation of neutral diversity however does not guarantee that adaptive variation unique to these particular populations has not been lost (Willi et al. 2007). Nevertheless, the detected sensitivity of *meta-N_e* to changes in the N_e of Ason population suggests that preservation of genetic diversity of the four-river system in the future is closely linked to future changes in the Ason population.

The message emerging from our study and those previously conducted on genetic diversity of subdivided salmonid populations (Østergaard et al. 2003; Hindar et al. 2004; Fraser et al. 2007a, b; Hansen et al. 2007; Dionne et al. 2008) is that detection of possible population substructuring and connectivity of local populations are vital for successful population conservation and genetically sustainable harvesting (Cooper and Mangel 1999; Schtickzelle and Quinn 2007; Palstra et al. 2007; Palstra and Ruzzante 2008). Patterns of migration between populations can be detected using mark-recapture experiments or molecular genetic analyses (Avise 1994; Tessier and Bernatchez 1999), but both the methods have their drawbacks. Mark-recapture studies measure straying, which may differ from realized gene flow, because strayers may return back to their natal river prior to spawning, or be unsuccessful in their reproduction (Hindar et al. 2004). Also, if marked individuals are of hatchery origin they may stray more than wild ones (Quinn 1993). Genetic analyses would reveal realized amount of gene flow, but particularly in small populations, sample sizes will necessarily remain low, weakening the inference. Furthermore, distinguishing first generation migrant from descendants of earlier migrants can be challenging (Paetkau et al. 2004).

Difficulties in quantifying migrations also apply to the investigated four Spanish rivers. Number of recaptures was low and this adds uncertainty to our model estimates. In particular, due to the low number of recaptures rare migrants into the River Ason could not be detected, yet genetic analyses have indicated those to occur (Consuegra et al. 2005). However, straying rates estimated earlier using genetic assignments (28–39%; Consuegra et al. 2005) were much higher than typically expected for Atlantic salmon (Stabell 1984; Hendry and Stearns 2004), suggesting that sample sizes or the number of molecular markers employed were not sufficient to distinguish migrants. Qualitatively, the pattern of migration detected by the two methods is still the same, with migration being asymmetric and net emigration rates from Ason population being largest (Consuegra et al. 2005; Consuegra and Garcia de Leaniz 2007). Therefore, the findings that the *meta-N_e* is lower than sum of subpopulation N_es and that it is regulated by N_e of Ason population are expected to hold (Tufto and Hindar 2003; Hindar et al. 2004), despite some uncertainty associated to numeric migration rate estimates.

Knowledge about the metapopulation structure of Atlantic salmon is not only needed for estimating *meta-N_e*, but also to identify the subpopulations that are in key to regulate it. In the absence of methods to increase gene flow from these populations (as would be the case with migration of wild salmon), a genetically sustainable option for fisheries management would be to reduce their harvesting, as this would enhance the genetic diversity of the metapopulation (Fig. 2, Tufto and Hindar 2003; Hindar et al. 2004). The four Atlantic salmon populations in the present study have been exploited exclusively by rod and line (Consuegra et al. 2005), with exploitation rates in the Ason being typically higher than in the other rivers (Garcia de Leaniz et al. 1992; Hindar et al. 2007). Such strategy is opposite to the recommendation emerging from the results of this study, i.e. that the genetic diversity of the four Atlantic salmon populations would be best preserved by reducing fishing effort in the River Ason.

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