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Short communication

Restoration versus recolonisation: The origin of Atlantic salmon (*Salmo salar* L.) currently in the River Thames

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ABSTRACT

Since the 1970s, when major improvements to the water quality were made, the River Thames has been subject to a high-profile project aimed at restoring Atlantic salmon to the catchment. Whilst initially successful, with hundreds of salmon returning each year in the late 1980s, the number of adults returning to the river has declined steeply again in recent years, reaching a low in 2005 when no salmon were recorded. Using a baseline of genetic information gathered from 3830 salmon from throughout their southern European range, and incorporating samples from the hatchery fish used to stock the Thames, all 10 tagged hatchery fish captured in 2003 and all 16 returning untagged adult salmon captured between 2005 and 2008 were assigned to their most likely river of origin. The results suggest that untagged salmon currently ascending the river originate not from exogenous fish stocked into the Thames, but predominantly from other rivers in southern England. This highlights the potential for natural processes of recolonisation to operate in rivers where salmon have become locally extirpated. These findings also underscore several important considerations when undertaking species restoration projects: (i) previous causes of declines must be sufficiently ameliorated to allow new/translocated individuals to thrive, (ii) introduced individuals should originate from a stock that is closely related to the extirpated population, according to the principles of contemporary conservation biology, and (iii) dispersal and gene-flow from neighbouring populations may play a significant role in establishing new populations.

1. Introduction

Restoration of single species of plants and animals is becoming more frequent around the world, but these attempted reintroductions have often been met with mixed success (Fischer and Lindenmayer, 2000; Frankham, 2008; Wolf et al., 1996, 1998). This is certainly the case for the Atlantic salmon (*Salmo salar* L.), which has been subject to numerous restoration efforts (Fraser et al., 2007; Fraser, 2008; Hesthagen and Larsen, 2003; O'Reilly and Doyle, 2007; Ward et al., 2008). These have occurred in response to serious declines that have been experienced by many populations of salmon in rivers across their native range, including their complete extirpation from some rivers (Parrish et al., 1998). Whilst the reasons for these continued declines appear to be multifactorial, historically they can be tied to anthropogenic environmental changes occurring within rivers, primarily the exploitation of land and water resources without regard for effects on aquatic ecosystem health (MacCrimmon and Gots, 1979). Yet, the Atlantic salmon has considerable sporting and commercial value, and it remains an important keystone species in freshwater habitats and provides a valuable indicator of good water quality and ecosystem health (NASCO, 2009). Therefore, attempts have been made to artificially support such populations through stocking of hatchery-bred fish, and this approach has also been extended to cases where salmon have become locally extinct. However, the outcomes of such practices have been both controversial and extremely variable, and confounding factors make it very difficult to conclude if

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captive-bred lines of salmonids can be reintroduced as self-sustaining populations (see Fraser, 2008).

Historically, the River Thames had a significant and well-documented run of salmon; it is mentioned as far back as the Magna Carta (1215), and a substantial fishery existed on the river until the early 19th Century. The industrial revolution and urbanization of London led to increased levels of pollution in the river and the last record of a Thames salmon was made in 1833 (Wheeler, 1979). After previous unsuccessful attempts to restore salmon to the Thames, in 1974 a lone salmon was caught downstream of London, following significant improvements in water quality. This discovery acted as a primer for restoring salmon to the Thames and stocking of juveniles began in 1975. In 1979 the Salmon Rehabilitation Scheme was established, which released salmon into a variety of Thames tributaries. The predominant origin of these stocked fish was salmon farm seconds from Scottish hatchery lines (although occasional releases of fish from other rivers in southern England, e.g. River Avon, were also made). The numbers of adult salmon recorded in the river gradually rose, reaching a peak of 338 in 1993 (Supplementary Material 1). In 1994 the scheme focused on restoring a self-sustaining population of salmon to the River Kennet, identified as the tributary of the Thames with the largest amount of breeding and nursery habitat. The source of the stocked fish was also changed to utilise supportively-bred fish (i.e. only one generation of captive breeding) from the Rivers Shannon and Delphi in Ireland; around the same time, a programme of fish pass construction began to allow returning adults to negotiate the 36 weirs between the tidal limit and the spawning habitat on the Kennet. However, in 1997 the numbers of adult salmon recorded in the Thames declined significantly, reaching a low in 2005 when no salmon were captured (Supplementary Material 1).

The objective of this study was to identify the origins of wild (untagged) adult salmon that have ascended the Thames since 2005. Additionally, tagged adult fish sampled from the river in 2003, which originated from the restoration programme (i.e. fish of known origin), were used to provide a benchmark for assessing the accuracy of assignment. Between 2005 and 2008, no tagged fish were recovered and two potential sources for untagged fish within the river appear most probable: (i) a hitherto undocumented naturally reproducing population derived from the stocked hatchery fish; (ii) straying of adults from other rivers; a further possibility, of which we also need to be mindful, is that untagged fish derive from other unrecorded, untagged releases of fry. Adult salmon caught within the Thames between 2005 and 2008 have been genotyped with a suite of 12 microsatellite markers used previously to assemble a baseline of genetic data from populations of salmon across the southern part of their European range (Griffiths et al., 2010). Genetic assignment tests were then used to determine the probable origins of these adult fish.

2. Materials and methods

Twenty-six adult salmon were characterised in the study; most were sampled at Molesey and Sunbury Weir (Table 1 and Fig. 1); including all 10 tagged fish captured in 2003 and all 16 untagged fish captured between 2005 and 2008 (two in 2006, five in 2007 and nine in 2008). Total length, weight and sex were collected for each individual, alongside some scale samples for genetic analysis. In 2007, 50 randomly selected juvenile fish were also sampled from each of the two stocks of fish released into the Thames (bred directly from wild salmon collected from the Rivers Shannon or Delphi). Individual genotypes were generated for 12 microsatellite loci, following Griffiths et al. (2010).

Genepop v3.4 (Raymond and Rousset, 1995), was used to test for linkage disequilibrium and Hardy–Weinberg equilibrium (HWE) in the hatchery samples. These samples were added to an existing baseline of 3730 salmon, originating from 55 rivers in the southern part of the European range of Atlantic salmon (encompassing northern Spain, western France, Ireland, southern England and the Atlantic coast of Britain, Griffiths et al., 2010). Assignment testing of the Thames fish was conducted using a maximum likelihood approach implemented by ONCOR (Kalinowski et al., 2008), and a Bayesian method, BAPS (Corander et al., 2003). Previous data analysis has shown that this baseline is robust for regional assignment (Griffiths et al., 2010), but that in some geographical areas (in particular, northern England, western Scotland and Ireland) the database may not be suitable for reliable assignment of fish to the level of individual rivers. Therefore, following the recommendations of Hansen et al. (2001) to maximise assignment power by minimising the number of samples included in the analysis (by using samples most relevant to the problem), a reduced baseline of eight sample collections was also used. The selection of baseline samples was based on maximising sample size and levels of differentiation between samples, whilst still retaining samples that are likely origins for the Thames salmon. Therefore, samples from the Cares (northern Spain; $N = 75$), Sée (northern France; $N = 50$), Itchen (southern England; $N = 53$), Dart (southwest England; $N = 84$), Ayr (Scotland; $N = 68$), Laune (Ireland; $N = 47$), Delphi hatchery ($N = 50$) and Shannon hatchery ($N = 50$) were selected as representative of rivers from across the sampled region. The reduced baseline was subsequently used to test the assignment of Thames fish in a broader collection of software, to ensure the consistency of the results (Supplementary Material 2).

3. Results

The Delphi and Shannon hatchery samples were both associated with highly significant deviations from HWE (at 8 and 9 of the loci, respectively, $P < 0.05$) and significant linkage disequilibrium (out of 66 pair-wise tests in each population 45 and 61, respectively, showed $P < 0.05$).

The maximum likelihood and Bayesian approaches generated a good consensus for the most likely rivers of origin for Thames salmon. Whilst ONCOR generally produced a higher probability of assignment than BAPS, it was less consistent and more prone to significant changes in assignment when the reduced baseline was employed (Table 1). All the tagged fish captured in 2003 assigned back to baseline samples originating from the northern regions of the study area (except Thames 09 that demonstrated a high probability of originating from northern France). The more recent captures of untagged salmon nearly all demonstrated consistent and high probabilities of originating from rivers in southern England. The one exception to this was a single untagged sample (Thames 17) caught in 2007, which was associated with a low probability and did not assign to samples from southern England. A similar pattern of assignment was demonstrated in the other software utilised (Supplementary Material 2), although assignment probabilities were often lower in GeneClass and, in a number of instances, its assignments diverged noticeably from the other packages (perhaps due to its contrasting assignment methodology, i.e. the ability to exclude baseline samples as the source of an individual).

4. Discussion

Overall, the results from genetic assignment testing of adult salmon returning to the Thames demonstrated a generally consistent picture: all but one of the tagged fish captured in 2003 assigned to rivers in the northern part of the study area, and all but one of the untagged fish assigned to rivers in southern England. That the assignments of tagged fish were generally associated with lower