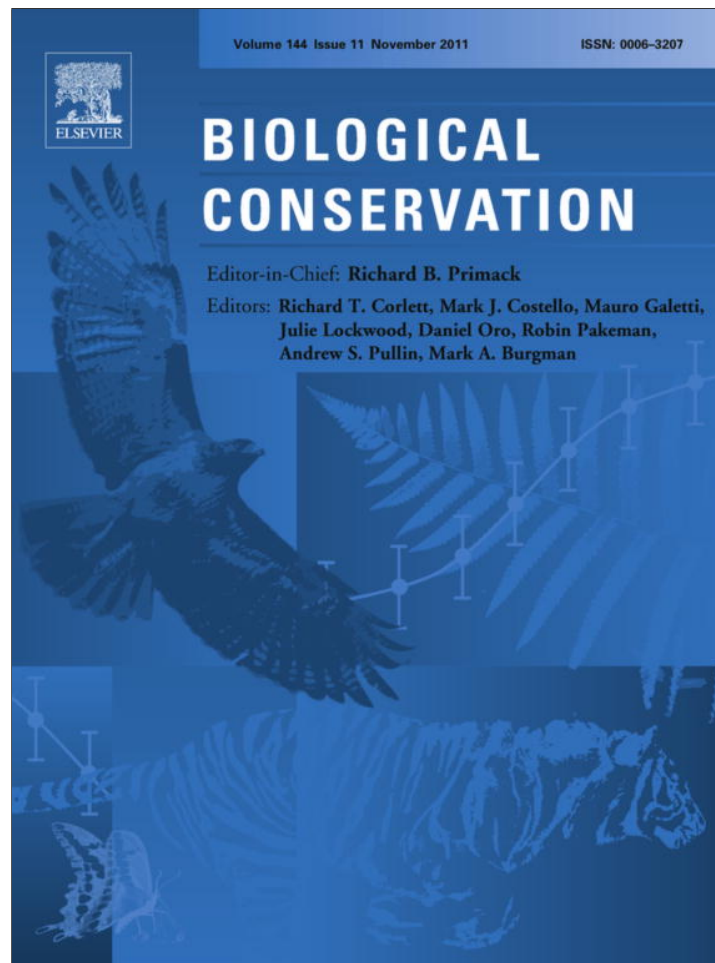


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Short communication

Restoration versus recolonisation: The origin of Atlantic salmon (*Salmo salar* L.) currently in the River ThamesAndrew M. Griffiths^{a,b,*}, Jonathan S. Ellis^{a,1}, Darryl Clifton-Dey^c, Gonzalo Machado-Schiaffino^{d,2}, Dylan Bright^e, Eva Garcia-Vazquez^d, Jamie R. Stevens^{a,*}^a Molecular Ecology and Evolution Group, School of Biosciences, Geoffrey Pope Building, University of Exeter, Stocker Road, Exeter EX4 4QD, UK^b Marine Biological Association of the United Kingdom, The Laboratory, Citadel Hill, Plymouth PL1 2PB, UK^c Environment Agency for England and Wales, Thames Region, UK^d Departamento Biología Funcional, Área de Genética, Universidad de Oviedo, C/ Julian Claveria s/n, 33006 Oviedo, Spain^e Westcountry Rivers Trust, Rain-Charm House, Kyl Cober Parc, Stoke Climsland, Callington, Cornwall PL17 8PH, UK

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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.

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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

* Corresponding authors at: Molecular Ecology and Evolution Group, School of Biosciences, Geoffrey Pope Building, University of Exeter, Stocker Road, Exeter EX4 4QD, UK (J.R. Stevens and A.M. Griffiths). Tel.: +44 1392 723775.

E-mail addresses: andiff@MBA.ac.uk (A.M. Griffiths), jonathan.ellis@plymouth.ac.uk (J.S. Ellis), darryl.clifton-dey@environment-agency.gov.uk (D. Clifton-Dey), gonzamachado@yahoo.com (G. Machado-Schiaffino), dylan@wrt.org.uk (D. Bright), egv@fq.uniovi.es (E. Garcia-Vazquez), J.R.Stevens@exeter.ac.uk (J.R. Stevens).

¹ Present address: School of Biomedical and Biological Sciences, University of Plymouth, Drake Circus, Plymouth PL4 8AA, UK.

² Present address: Laboratory for Zoology and Evolutionary Biology, Department of Biology, University of Konstanz, D-78457 Konstanz, Germany.

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

Table 1

Capture details and assignment probability (prob) for adult salmon ascending the River Thames; for each individual the river of most likely origin is given.

Sample Name	Date	Length (mm)	Weight (kg)	Sex	Marked	Location	Complete Baseline				Reduced Baseline			
							ONCOR	Prob	BAPS	Prob	ONCOR	Prob	BAPS	Prob
THAMES.01	16/07/03	680	3.0	M	Yes	Molesey	Shannon (hatchery)	1	Shannon (hatchery)	1	Shannon (hatchery)	1	Shannon (hatchery)	1
THAMES.02	18/07/03	790	5.1	F	Yes	Sunbury	Moy(Ireland)	0.62	Lomond (Scotland)	0.30	Laune (Ireland)	1	Delphi (hatchery)	0.36
THAMES.03	18/07/03	680	3.6	M	Yes	Molesey	Laune (Ireland)	0.99	Delphi (hatchery)	0.19	Laune (Ireland)	1	Laune (Ireland)	1
THAMES.04	23/07/03	620	2.7	F	Yes	Molesey	Derwent (N. England)	0.96	Eden (N. England)	0.20	Shannon (hatchery)	0.92	Shannon (hatchery)	0.48
THAMES.05	06/08/03	640	2.7	M	Yes	Molesey	Laxford (Scotland)	0.84	Laxford (Scotland)	0.36	Dart (SW England)	0.69	Shannon (hatchery)	0.27
THAMES.06	11/11/03	755	3.55	M	Yes	Molesey	Nith (Scotland)	0.96	Nith (Scotland)	0.23	Laune (Ireland)	1	Shannon (hatchery)	0.35
THAMES.07	14/11/03	800	5.4	F	Yes	Molesey	Blackwater (Ireland)	0.83	Shannon (hatchery)	0.50	Laune (Ireland)	0.94	Shannon (hatchery)	0.52
THAMES.08	24/11/03	830	5.3	F	Yes	Molesey	Laune (Ireland)	0.44	Fleet (Scotland)	0.34	Laune (Ireland)	1	Laune (Ireland)	1
THAMES.09	24/11/03	780	4.0	F	Yes	Molesey	Nith (Scotland)	0.98	Elorn (France)	0.27	Sée (France)	0.95	Sée (France)	1
THAMES.10	24/11/03	660	2.2	M	Yes	Molesey	Usk (Wales)	0.70	Shannon (hatchery)	0.40	Shannon (hatchery)	0.99	Shannon (hatchery)	0.45
THAMES.11	15/09/06	590	–	M	No	Molesey	Avon (S. England)	0.95	Avon (S. England)	1	Itchen (S. England)	1	Itchen (S. England)	0.76
THAMES.12	15/09/06	665	–	M	No	Molesey	Avon (S. England)	1	Avon (S. England)	1	Itchen (S. England)	1	Itchen (S. England)	1
THAMES.13	07/09/07	625	–	F	No	Molesey	Itchen (S. England)	0.97	Test (S. England)	1	Itchen (S. England)	1	Itchen (S. England)	1
THAMES.14	07/09/07	735	–	–	No	Old Windsor	Avon (S. England)	0.93	Avon (S. England)	1	Itchen (S. England)	1	Itchen (S. England)	0.55
THAMES.15	14/09/07	620	–	M	No	Molesey	Avon (S. England)	0.60	Itchen (S. England)	0.45	Itchen (S. England)	1	Itchen (S. England)	0.74
THAMES.16	18/09/07	600	–	M	No	Molesey	Itchen (S. England)	1	Itchen (S. England)	1	Itchen (S. England)	1	Itchen (S. England)	1
THAMES.17	01/12/07	600	–	M	No	Tilbury	Esk (Scotland)	0.97	Sella (Spain)	0.31	Sée (France)	0.65	Sée (France)	0.42
THAMES.18	22/07/08	640	2.86	M	No	Molesey	Itchen (S. England)	1	Itchen (S. England)	1	Itchen (S. England)	1	Itchen (S. England)	1
THAMES.19	01/08/08	623	2.1	M	No	Molesey	Itchen (S. England)	0.82	Avon (S. England)	0.31	Itchen (S. England)	1	Itchen (S. England)	1
THAMES.20	04/08/08	575	2.8	M	No	Molesey	Avon (S. England)	1	Avon (S. England)	1	Itchen (S. England)	0.99	Itchen (S. England)	0.68
THAMES.21	28/08/08	665	3	M	No	Molesey	Itchen (S. England)	0.84	Itchen (S. England)	1	Itchen (S. England)	1	Itchen (S. England)	1
THAMES.22	01/09/08	555	1.35	F	No	Molesey	Itchen (S. England)	0.98	Itchen (S. England)	0.48	Itchen (S. England)	1	Itchen (S. England)	0.76
THAMES.23	01/09/08	575	1.83	M	No	Molesey	Itchen (S. England)	1	Itchen (S. England)	1	Itchen (S. England)	1	Itchen (S. England)	1
THAMES.24	01/09/08	580	1.8	F	No	Molesey	Itchen (S. England)	0.90	Itchen (S. England)	1	Itchen (S. England)	1	Itchen (S. England)	1
THAMES.25	23/09/08	620	2.6	–	No	Shepperton	Avon (S. England)	0.85	Avon (S. England)	0.45	Itchen (S. England)	1	Itchen (S. England)	0.73
THAMES.26	24/09/08	560	1.8	F	No	Sunbury	Itchen (S. England)	0.69	Avon (S. England)	1	Itchen (S. England)	1	Itchen (S. England)	1

confidence is in agreement with the results from previous work suggesting lower power of the baseline to distinguish between stocks of fish in Scotland, Ireland and northern England (Griffiths et al., 2010). In many of these cases, the use of a reduced baseline helped increase the assignment probabilities to either the hatchery stocks or rivers within Ireland, confirming the utility of the baseline data for genetic assignment in this case. There are also a number of confounding factors unique to the hatchery samples that may explain the inability to assign released fish back to their hatchery stocks. First, there is a longer period of time separating the collection of returning adults and baseline fish for the hatchery stocks, when compared to the other samples. If stocks demonstrate shifts in allele frequencies over time, there is more potential for this process to affect the power of assignment to the hatchery stocks. Second, despite efforts to collect representative samples from the hatchery stocks, they did deviate strongly from HWE. Given that hatchery processes are unlikely to satisfy the assumptions underlying HWE, e.g. random mating and

no selection, and supportively bred stocks of salmonids can demonstrate rapid changes in allele frequencies (e.g. Griffiths et al., 2009) this is not surprising. However, deviations from HWE and genotypic equilibrium in the hatchery samples could bias the results of assignment tests compared to wild populations with more stable genetic composition.

Of the 16 untagged fish analysed, 15 were assigned to southern English rivers, the other was assigned to northern France. When interpreting this result it is important to note that only a minority of fish released into the Thames over the last 30 years originated from rivers in these southern regions. Whilst it has proven impossible to accurately work out how many of the released hatchery fish shared this origin (particularly as juveniles from multiple sources were mixed before release), we do know from Environment Agency records that the release of fish from southern England into the Thames ceased in 1994. Therefore, it would appear unlikely that the returning adults captured since 2006 could result

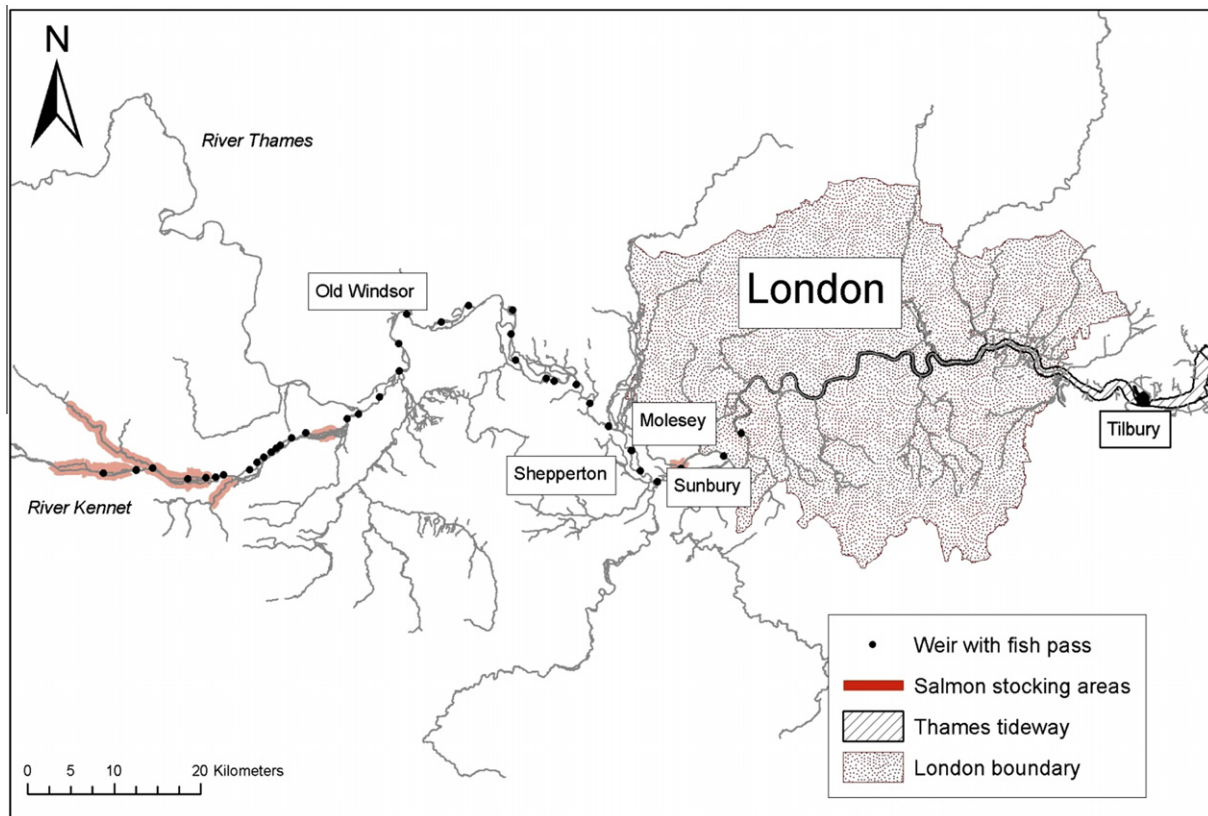


Fig. 1. Map of the Thames catchment.

from untagged releases or tag-loss, as too much time has elapsed between these events. The alternative explanation, that stocked fish originating from southern England successfully formed a reproducing population, also seems implausible because extensive surveying has failed to identify any evidence of salmon reproduction in the Thames. Moreover, the majority of untagged adults also had very high assignment probabilities (and admixture coefficients) to southern England, suggesting little or no evidence of introgression from the other more northerly hatchery stocks which were used predominantly in stocking the Thames – i.e. it appears unlikely that no influence of other numerically dominant hatchery stocks of northerly origins would be detected if an extant natural population had established from the restoration efforts.

Thus, the most parsimonious explanation for recent captures of untagged salmon being assigned with very high probability to southern England would appear to be straying. Geographically, the rivers identified by assignment analysis as the origin of untagged adult Thames salmon are those closest to the Thames in the genetic baseline, making them the most likely source of straying salmon; they are also some of the closest rivers with viable salmon populations. This result highlights the importance of straying, sharing much in common with other studies that have also demonstrated the role of natural recolonisation of previously extirpated rivers (Perrier et al., 2010; Saura et al., 2008; Vasemagi et al., 2001). What makes this result particularly interesting is the persistence of potential colonisers from proximate rivers despite a major long-term stocking programme. Such a result suggests that, although stocked fish previously failed to found a reproducing population in the river, if conditions on the river were to improve, natural processes could establish a population of salmon in the Thames once again, perhaps without the need for stocking. It is also interesting to speculate that straying from proximate rivers

may provide colonisers with adaptations that are already suitable to local environmental conditions (Dionne et al., 2008).

A number of significant questions remain to be addressed: why did the number of stocked salmon fall in the mid-1990s and what is preventing salmon from recolonising the river now? In particular, the effects of mixed-stock exploitation on weaker stocks, have been suggested as a contributing factor in declines of salmon (e.g. Griffiths et al., 2010). Approximately 100 tagged fish from the Thames were intercepted in the Irish drift net fisheries in 1998 and 1999 (CEFAS and EA, 2003), suggesting exploitation at a number of scales may impact on Thames salmon. Alabaster et al. (1991), identified a number of environmental conditions, particularly relating to temperature, dissolved oxygen and flow, that need to be met in order to have a successful run of salmon up the Thames. It has been shown that between 1989 and 2006 the number of storm sewage releases (associated with summer storms in London which overwhelm the treatment plants), increased significantly (EA, 2010, also see Supplementary Material 3). Thus, large volumes of material with a high biological oxygen demand were released into the Thames tideway, potentially reducing the levels of dissolved oxygen and creating a barrier to fish migration. Low flows may also be a significant barrier to fish migration. In 2005, when no salmon were recorded in the Thames, summer flows did not exceed the minimum rates suggested by Alabaster et al. (1991) for migration to occur (EA, 2010). In addition, 2005 was also associated with a very high number of releases of sewage on the Thames (Supplementary Material 3), suggesting that low flows and low water quality may interact to prevent salmon ascending the river. The failure to restore salmon to the Thames must also be viewed in the broader context of (a) general declines in the numbers of salmon returning to many UK rivers from the sea, and (b) the effects of climate change, which, increasingly, may

impact negatively on salmon runs (Horreo et al., 2011), particularly in rivers towards the southern edge of their range, such as the Thames (Davidson and Hazelwood, 2005). However, this has not prevented the recolonisation of extirpated rivers located further southwards than the Thames (Perrier et al., 2010; Saura et al., 2008), suggesting that although conditions in the Thames are currently unsuitable for a self-sustaining population of salmon, planned improvements in tideway water quality and habitat through the Water Framework Directive may increase the likelihood of success in the future.

Whilst this study is based on a relatively modest set of samples, the results do act to highlight a number of general considerations for attempting reintroductions of extirpated populations. The first concerns the importance of mitigating factors that led to the original decline (IUCN, 1998). Despite efforts at habitat improvement in the River Kennet and a programme of fish pass construction, conditions on the Thames in recent years appear to have prevented salmon from ascending the Thames. This suggests that the previous causes of salmon declines, i.e. pollution associated with the city of London, may not have been ameliorated sufficiently to permit a self-sustaining population of salmon. The second consideration is associated with the suitability of the stocked fish. It has been widely recognised that domestication selection and reduction of genetic diversity in captive bred stocks may affect the success of reintroductions (e.g. Frankham, 2008). Whilst efforts to restore salmon back to the Thames initially focused on the use of Scottish hatchery fish, since 1994 supportively-bred salmon from populations in Ireland have been utilised. Arguably, such an approach is more consistent with contemporary principles of conservation biology, e.g. by reducing the period of captive breeding and maintaining high effective population sizes. However, as seen in this and other studies (Griffiths et al., 2009; Horreo et al., 2008), hatchery samples can demonstrate severe deviations from HWE indicative of selection and/or bottlenecking in the hatchery, with associated negative impacts on the fitness of such captive-bred individuals. The IUCN guidelines on reintroductions (IUCN, 1998), also suggest that the source for restoring an extirpated population should ideally be closely related genetically to the native stock. Given the highly differentiated population structure of Atlantic salmon (Griffiths et al., 2010; King et al., 2001; Stahl, 1987), Irish stocks may be deemed too distant to be a suitable source for the reintroductions. The identification of strays from southern England in the current study would seem to underscore their potential for release on the Thames. Furthermore, the identification of straying from proximate populations of salmon to a river that has been the focus of a major restoration programme emphasizes that potential role of natural dispersal. Several studies on the successful restoration of extirpated salmonid populations have now demonstrated a potentially important role for gene-flow from neighbouring wild populations (Fraser et al., 2007; Withler et al., 2000).

Many of the issues touched on in this study are common to those faced by conservation managers planning reintroduction and translocation programmes for a diverse range of other organisms, for example, reintroduction of the bumblebee *Bombus subterraneus* to southern Britain (Natural England, 2009), 'headstarting' programmes for turtles in the Caribbean (Bell et al., 2005) and freshwater mussels (Thomas et al., 2010). Unlike some of these other organisms, however, Atlantic salmon (and salmonids in general), have a long-standing and important recreational place in many societies. Therefore, in addition to their biological role as apex species in many freshwater ecosystems, substantial financial benefits to the successful reestablishment of a salmon population within a river system may exist (Peirson et al., 2001). For example, when the benefit of having salmon in the Thames was assessed, via a "willingness to pay" questionnaire, the value of having salmon in the river was approximated to £12 million per year (Peirson et al.,

2001), compared with the £3 million spent on the rehabilitation scheme up to that time. Thus, while we do not propose that the primary drivers for salmon conservation are economic, it would appear naïve to suggest that the anticipated financial benefits of having salmon in a river have not, at least in part, played a role in encouraging some stakeholders to support active stocking policies, rather than focusing their efforts on generally longer-term improvements to facilitate natural recovery and recolonisation of salmon populations. Certainly, the results of this study and a previous analysis of the river Tyne hatchery programme in northeast England (Milner et al., 2004) suggest that while stocking may have a role to play in short term mitigation, ultimately improvements in river quality and natural recolonisation by straying from proximal rivers may represent the dominant processes in salmon population recoveries.

In conclusion, there are a number of limitations to attempts at genetically assigning Thames salmon; a single tagged salmon of hatchery origin was assigned back to rivers in northern France and many tagged fish were not successfully assigned back to the hatchery stocks (reflecting perhaps constraints in the baseline data set and departures from HWE in the hatchery stocks). Despite these issues, tagged fish were consistently assigned back to northern salmon populations and untagged individuals currently ascending the river were indicated to originate predominantly from proximate rivers within southern England. Significantly, these results support the hypothesis that untagged salmon caught in the Thames are the result of straying from other rivers, rather than the return of untagged hatchery fish (or successful reproduction by such individuals). This identifies the potential for natural recolonisation of rivers where salmon have become locally extirpated, whilst simultaneously highlighting the futility of long-term stocking without corresponding improvements in river navigability, habitat and water quality. In this sense, conservation strategies for salmon, as for most other organisms, should seek to restore ecosystem function and continuity, not apex species and their immediate habitat (Lawton et al., 2010), whereupon it seems likely that populations of salmon will reestablish naturally.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2011.07.017.

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