THE EFFECTS OF DAM REMOVAL ON RIVER COLONIZATION BY SEA LAMPREY *PETROMYZON MARINUS*

E. LASNE[a,b,c*], M.-R. SABATIÉ[a], N. JEANNOT[d] AND J. CUCHEROUSSET[e,f]

[a] *UMR 0985 ESE, Agrocampus Ouest/INRA, Rennes cedex, France*
[b] *MNHN—UMR BOREA, CRESCO, Dinard, France*
[c] *UMR CARRTEL, INRA/Université de Savoie, Thonon-les-Bains Cedex, France*
[d] *INRA—U3E, Pont-Scorff, France*
[e] *CNRS, Université Paul Sabatier, ENFA—UMR 5174 EDB (Laboratoire Évolution and Diversité Biologique), Toulouse, France*
[f] *Université de Toulouse, UMR 5174 EDB, Toulouse, France*

ABSTRACT

Habitat fragmentation is an important cause of biodiversity loss in freshwater systems, as worldwide rivers have been fragmented by dams and other hydraulic structures. To restore freshwater fish populations, some barriers have been removed, but the long-term ecological effects of this removal have been rarely quantified. In the present study, we quantified the effects of barrier removal on river colonization by anadromous sea lamprey (*Petromyzon marinus*) by analyzing the spatial distribution and nest density in a small coastal river (France) from 1994 to 2011. Our results demonstrated the benefit of dam removal within few years after restoration. Indeed, the spatial distribution of nests shifted significantly upstream and was more uniform throughout the river after removal. Our results also suggest that the spatial patterns of habitat colonization were affected by the density of nests, river flow and connectivity. Finally, although the number of nests was significantly higher after removal, it was not possible to clearly identify the contribution of intrinsic versus external factors involved in this pattern. Further investigations are therefore needed to quantify the potential subsequent effects on juvenile recruitment and the overall population dynamics. Copyright © 2014 John Wiley & Sons, Ltd.

KEY WORDS: diadromous fish; river connectivity; habitat restoration; colonization; spawning

Received 21 August 2013; Revised 19 February 2014; Accepted 12 May 2014

INTRODUCTION

Most temperate rivers have been highly fragmented by impoundments through the construction of mill weirs, barrages and dams for hydropower production, flood protection and water supply for human consumption or agriculture (Dynesius and Nilsson, 1994; Nilsson *et al.*, 2005; Liermann *et al.*, 2012). These barriers have caused an important loss of hydrological connectivity, that is, the 'water-mediated transfer of matter, energy, and/or organisms within or between elements of the hydrologic cycle' (Pringle, 2001), between the upstream and downstream parts of rivers. The alteration of hydrological connectivity has been advocated as a major source of biodiversity loss and changes in freshwater ecosystem functioning (Pringle *et al.*, 2000; Pringle, 2003). Most specifically, impoundments may prevent the displacement and migrations of organisms within the riverine networks and between habitats necessary for life-cycle completion (Lucas *et al.*, 2009). This can subsequently modify gene flow within and between populations (Horreo *et al.*, 2011; Alp *et al.*, 2012), species abundance and community composition (Nislow *et al.*, 2011; Rolls *et al.*, 2013). Therefore, restoring hydrological connectivity is of utmost importance for the maintenance and conservation of aquatic biodiversity (Liermann *et al.*, 2012).

Restoring hydrological connectivity can be achieved principally by installation of fish passes (Prato *et al.*, 2011) and removal of barriers (Hart *et al.*, 2002). Although fish passes may be a cost-effective approach to improve the downstream and/or upstream movements of fish while maintaining human activities associated with the presence of a barrier (e.g. hydropower production, fishery, recreational activity and water withdrawal), the efficiency of most of the fish passes is limited for most of the weak swimmer species (Noonan *et al.*, 2012). Barrier removal is a more holistic alternative as it restores longitudinal connectivity for many organisms (Hart *et al.*, 2002). The number of barriers that have been removed has dramatically increased during the last decades (Bednarek, 2001; Hart *et al.*, 2002; Bernhardt *et al.*, 2005), and the costs associated with their removal are context dependent and mainly related to the size and nature of the barrier (Bernhardt *et al.*, 2005; de Leaniz, 2008). When the barrier that is planned to be

---

*Correspondence to: E. Lasne, UMR CARRTEL—INRA/Université de Savoie, 75 avenue de Corzent, BP 511 F-74203 Thonon-les-Bains Cedex, France.
E-mail: emilien.lasne@thonon.inra.fr

removed is also associated with socio-economic activities, its social acceptance is often challenging (Hart and Poff, 2002; Lejon *et al.*, 2009). To improve this social acceptance, the ecological effects of barrier removal should therefore be quantified and communicated (Kibler *et al.*, 2011; Rolls *et al.*, 2013). However, to date, long-term studies providing such information are still scarce (Bernhardt *et al.*, 2005; Roni *et al.*, 2008).

Diadromous fish are amongst the organisms that are the most impacted by barriers because these species need to migrate between marine and freshwater ecosystems at least twice during their life cycle (Lucas and Baras, 2001). The negative ecological impacts of barriers on diadromous fish have been well documented (Cote *et al.*, 2009; Lassalle *et al.*, 2009; Liermann *et al.*, 2012). Connectivity alteration by barriers reduces river colonization from downstream areas, and suitable upstream habitats may remain inaccessible for diadromous populations (McDowall, 1998). Here, we used the removal of a barrier in a coastal river (Scorff River, France) as a unique opportunity to quantify the ecological effects of river connectivity restoration on diadromous fishes using sea lamprey (*Petromyzon marinus*) as a model organism. Sea lamprey are anadromous and spend their first years as filter feeding, blind larvae burring into soft sediments of rivers. After 4–7 years, they undergo a metamorphosis and migrate out of rivers where they forage on various marine vertebrates (Lança *et al.*, 2013; Silva *et al.*, 2013). Adults return in fresh waters to spawn and then die. Sea lampreys are distributed along the North American and European coasts in rivers and also in some case in land-locked populations (Hardisty and Potter, 1971). As many other diadromous fishes (Limburg and Waldman, 2009), sea lamprey populations face various threats: habitat fragmentation, pollution, habitat loss, overexploitation and climate change (Beaulaton *et al.*, 2008, Lassalle *et al.*, 2008). Lampreys are known to be sensitive to connectivity alteration and notably to low-head barriers (i.e. small barriers, generally <5-m height) because of their relatively poor swimming ability (Lucas *et al.*, 2009; Jackson and Moser, 2012; Nunn and Cowx, 2012). Although such low-head barriers are generally known to allow fish migration under specific environmental conditions, such as high flow discharge (Andrade *et al.*, 2007; Lucas *et al.*, 2009), they may also hamper fish movement when located downstream of catchment areas (Lucas *et al.*, 2009; Rolls, 2011; Gardner *et al.*, 2013). A recent work showed that they could nonetheless (re-)colonize upstream reaches after low-head barrier removal (Hogg *et al.*, 2013). Using temporal and spatial patterns of sea lamprey nest distributions collected over an 18-year period (6 years before and 5 years after barrier removal), the aim of the present study was to quantify the effects of barrier removal on the density and distribution of sea lamprey nests. Specifically, we tested whether increased river connectivity through barrier removal

modified distribution patterns by decreasing nest density below the barrier leading to a more uniform distribution along the river and by increasing the relative proportion of nests in the upstream sections.

MATERIAL AND METHODS

Study area

The Scorff River is a small (75 km long, Figure 1) coastal river located in Southern Brittany, France, that was selected as a study site because it hosts the Moulin des Princes field station that is monitoring salmonid populations and environmental conditions in the river. The Scorff River drains a 480-km^2 watershed with a mean annual flow of $5.16 \, m^3 \, s^{-1}$ (ranging from 1.39 in late summer to $10.1 \, m^3 \, s^{-1}$ in the winter/spring, period of 1994–2011). Sea lamprey is only present in the main river and does not colonize tributaries. The study area includes a 35 km-long reach located upstream of the tidal influence limit (Figure 1). A fish farm weir (3 m in height) located 25 km from the river mouth was removed in 2000 as farming activity ceased. It was suspected to have a major impact on catchment colonization, although some lampreys could migrate upstream by a small side channel that was designed to supply water for the fish farm in high flow conditions. Several disused mills, which have no visible impact on lamprey migration (except at the upmost part of the study sector between sections 9 and 10), were used to delimit the monitoring sections (Figure 1). No lamprey nests have ever been observed upstream of section 9.

Habitat availability for sea lamprey

Sea lampreys require specific habitat to spawn (Hardisty and Potter, 1971; Andrade *et al.*, 2007). Suitable substrate is composed of gravel and cobbles [i.e. particles ranging from 9.5 to 50 mm according to Applegate (1950) or from 15 to 115 mm according to Morman *et al.* (1980)], while suitable flow ranges from 0.4 to 1.6 m s^{-1} (Applegate, 1950) or from 0.15 to 0.6 m s^{-1} (Igoe *et al.*, 2004). Water depth is less limiting as spawning can occur across a wide range (e.g. from 5 to 152 cm in Morman *et al.*, 1980). Following Andrade *et al.* (2007), suitable spawning habitat was defined as riffles and runs with at least 30% gravel or cobble substrate. Suitable habitat for larvae consists of sand or silt/mud possibly with organic debris in pools and fine particle deposit area (Applegate, 1950; Hardisty and Potter, 1971). To quantify the suitable habitat for sea lamprey in Scorff River, homogenous hydrodynamic habitat units (i.e. riffles, run and pool) were mapped in August 2010 and the surface of each habitat in each section quantified using a geographic information system (GIS; refer to succeeding texts). Substrate was visually classified into
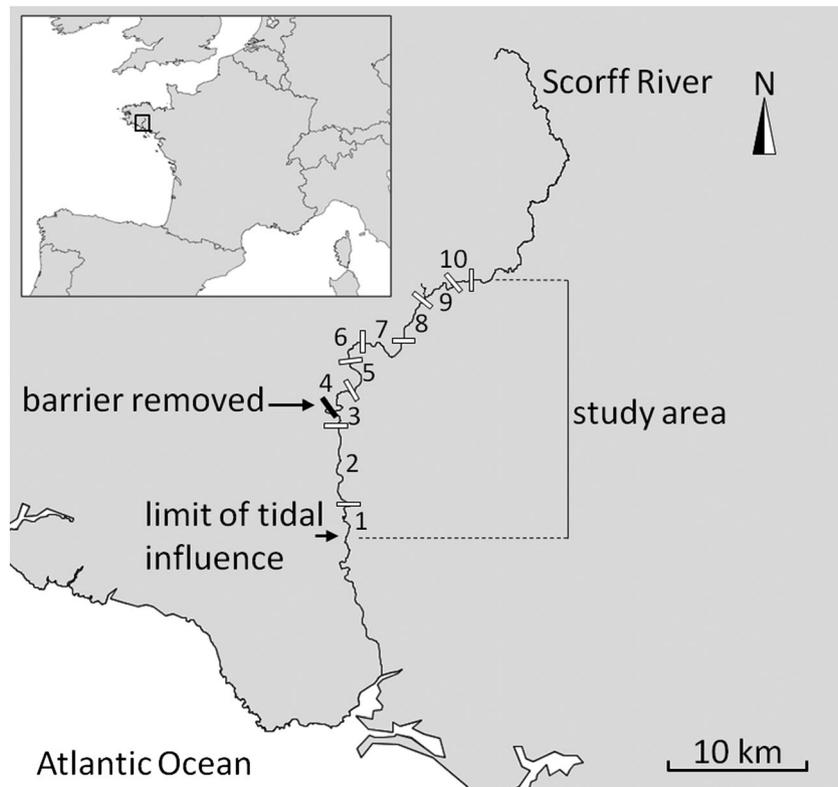
Figure 1. The Scorff River and location of the monitored sections. The black bar represents the barrier removed in 2000

six categories (rock, >500 mm; boulders, 200–500 mm; cobbles, 100–200 mm; gravels/pebbles, 2–100 mm; sand, 0.2–2 mm and silt/mud, <0.2 mm) and quantified as a percentage of surface area. Using substrate and hydrodynamical characteristics of the sections, $14.98 \cdot 10^4 \, m^2$ was classified as suitable for spawning and $8.86 \cdot 10^4 \, m^2$ as suitable for larvae among the $46.52 \cdot 10^4 \, m^2$ of aquatic habitat in the river (refer to details for each river section in the Supplementary Material 1). No longitudinal gradient was detected for spawning habitat, whereas larval habitat surface tended to slightly decrease upstream.

Nest density and spatial distribution

The density and spatial distribution of sea lamprey nests were quantified by monitoring each river section after the spawning season that typically started in May and ended in July (Sabatié *et al.*, 2011) and counting each individual nest. Nest density was calculated as the number of nests per unit of suitable spawning habitat surface. Monitoring dates were selected to obtain clear water conditions once spawning activity was finished (i.e. no or very few spawners still present in the spawning habitats) as nests could be detected several weeks after construction as they are built with large stones (Sousa *et al.*, 2012). No other species

was spawning in these habitats at this season. Monitoring was performed by boat or wading from 1994 to 1999 and in 2001, 2002, 2009 and 2011. In 2005, only total river abundance of nests was measured. Although most of the nests are built and occupied by a single pair (Hardisty and Potter, 1971), the number of adults involved in a nest is variable, and an individual may spawn and build several nests (Harvey and Cowx, 2003; Moser *et al.*, 2007; Sousa *et al.*, 2012). However, a recent study combining nest counts and mark-recapture analysis suggests that nest count could provide a reliable and strong proxy of spawner abundance (Hogg *et al.*, 2013). Additionally, river flow, known to influence river colonization by lampreys (Almeida *et al.*, 2002; Andrade *et al.*, 2007; Lucas *et al.*, 2009), has been measured every hour at an automated gauging station all along the entire study period (Direction Régionale de l'Environnement, de l'Aménagement et du Logement Bretagne). Using these measurements, mean daily flow was calculated from April to June during each study year and used as a metric of hydrological conditions during the spawning run.

Statistical analyses

The limits of hydrodynamic habitats, the locations of nests, the removed barrier and section limits along the Scorff River

were integrated into a GIS database (gvSIG©, http://www.gvsig.org). Five metrics were then calculated to quantify the spatial distribution of nests: first quartile, mean, median, third quartile and maximal distance of the nests to the river mouth. Spatial distribution metrics were compared before and after barrier removal using Wilcoxon non-parametric tests. The relationships between the number of nests and distribution metrics were then tested using a linear regression on model log-transformed data. Data were too scarce to statistically explore the combined effects of the number of nests, barrier removal and flow on the spatial distribution of nests. Therefore, bivariate plots were used to examine potential trends. All statistical analyses were performed using R (R Core Team, 2012).

RESULTS

Number of nests in the river

The number of nests in the river was highly variable during the study period, with a mean value of 223.82 nests (±193.20 SD) and ranging from 21 in 1996 to 661 in 2011 (Figure 2). Overall, the number of nests after barrier removal (mean = 348.00 nests (±211.7 SD), range: 180–661) was significantly higher (Wilcoxon test, $W = 2$, $p < 0.05$) than that before barrier removal [mean = 120.33 (±102.40 SD), range: 21–311].

Spatial distribution

Nest distribution was spatially (i.e. downstream versus upstream) and temporally (i.e. before versus after removal) variable (Figure 3). The most downstream nests occurred at 13.90 km from the river mouth, that is, just upstream of the tidal limit. Downstream of the removed barrier, mean nest density did not differ significantly before and after
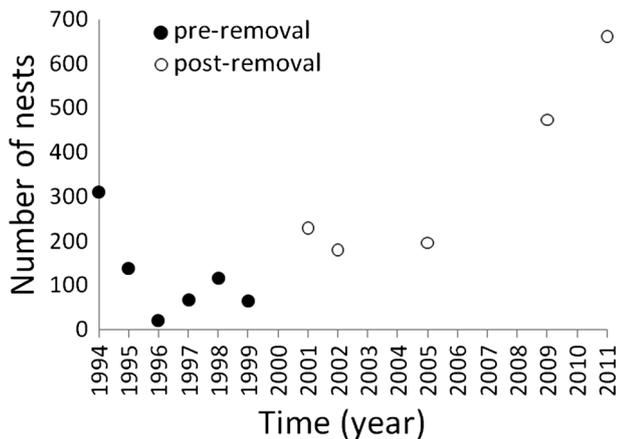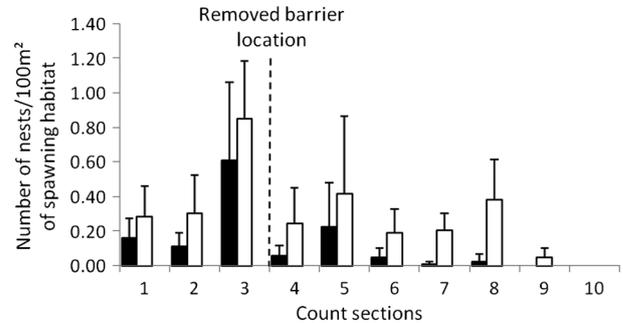

Figure 3. Mean density of nests (number per 100 m² of suitable habitat surface area) in each monitored section along the Scorff River before (black bars) and after (white bars) barrier removal. Error bars represent standard deviations

removal [before removal: 0.20 nests $100\,\text{m}^{-2}$ suitable spawning habitat (±0.13 SD); after removal: 0.39 nests $100\,\text{m}^{-2}$ suitable spawning habitat (±0.21 SD); Wilcoxon test, $W = 5$, p-value > 0.10]. However, the density of nests located upstream of the barrier significantly increased after barrier removal [before removal: 0.04 (±0.05 SD); after removal: 0.22 (±0.14 SD); Wilcoxon test, $W = 1$, p-value 0.05]. This change in spatial distribution upstream was observed in 2001 and 2002 (i.e. the years following barrier removal) when the number of nests in the river was within the range of the values observed before removal (Supplementary Material 2). Except for the first quartile distance and median distance, all spatial distribution metrics significantly increased after barrier removal (refer to details in Table I), demonstrating an increased proportion of nests in the upstream sections. For instance, the maximum colonized distance increased by approximately 20% (i.e. 7.2 km) after barrier removal. Additionally, mean, third quartile and maximum distance of nests significantly increased as the number of nests in the river increased (Figure 4).

Before removal, low spatial distributions were observed in four (1995, 1996, 1997 and 1999) of the six monitored years (Figure 5a–b). In 1994 and 1998, spatial distribution was close to the median value measured throughout the study. During this period, low spatial distributions were associated with low number of nests in the river (Figure 5a)

Figure 2. Number of sea lamprey nests in the Scorff River before (black symbols) and after (white symbols) barrier removal

Table I. Colonization metrics (mean ± SD) before and after barrier removal

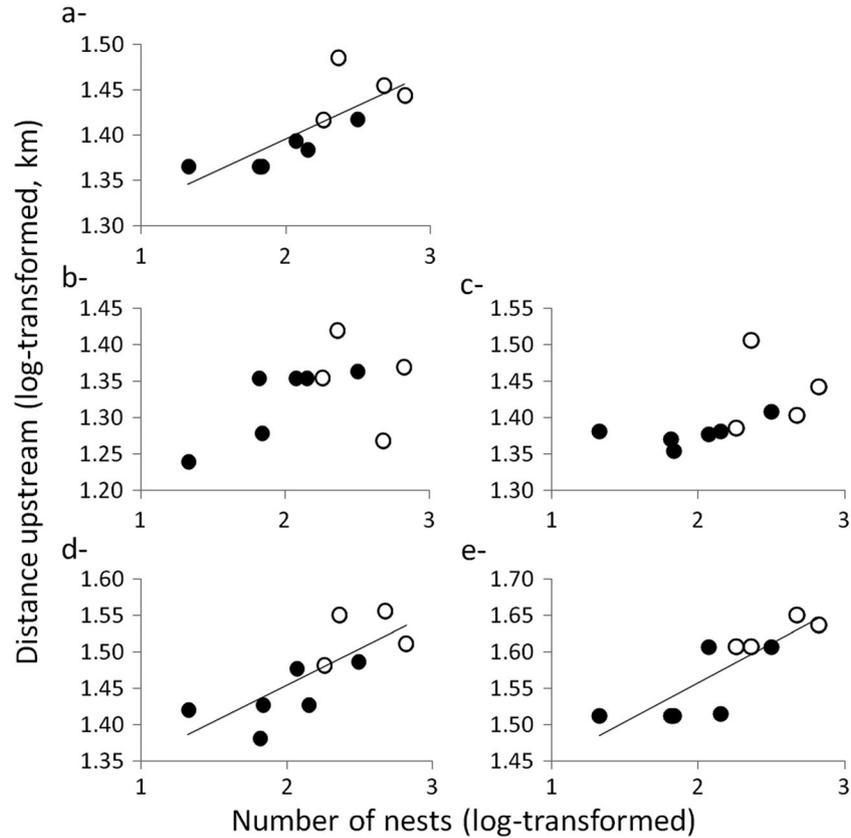| Spatial distribution metric	Distance upstream (km)		Wilcoxon test	
	Pre-removal	Post-removal	W	p
Mean	24.2 ± 1.2	28.3 ± 1.9	1	0.02
First quartile	21.1 ± 2.4	22.7 ± 3.2	7.5	0.38
Median	24.0 ± 1.0	27.3 ± 3.5	2	0.04
Third quartile	27.4 ± 2.5	33.6 ± 2.7	1	0.03
Maximum	35.2 ± 4.1	42.3 ± 2.2	2	0.03

Figure 4. Relationship between spatial distribution metrics and the number of nests before (black symbols) and after (white symbols) removal years: (a) mean distance (R^2 adjusted (adj.) = 0.58, $p < 0.01$), (b) first quartile distance (R^2 adj. = 0.13, $p > 0.10$), (c) median distance (R^2 adj. = 0.20, $p > 0.10$), (d) third quartile distance (R^2 adj. = 0.56, $p < 0.01$) and (e) maximum distance (R^2adj. = 0.68, $p < 0.01$). Data were log-transformed

and low flow conditions (Figure 5b), while 1994 and 1998 were characterized by high flow conditions. After removal, spatial distribution was above the median values measured throughout the study (Figure 5a), while flow conditions ranged from very low flow (2011) to very high flow (2001). This suggests that the spatial distribution of nests was less dependent of flow after than before barrier removal.

DISCUSSION

Determining the efficiency of river restoration programmes such as barrier removal in improving biodiversity and ecological processes is crucial because such actions are costly, and to do so, before/after approaches are needed (Kibler *et al.*, 2011). Additionally, studies dealing with fish (Catalano *et al.*, 2007; Maloney *et al.*, 2008; Gardner
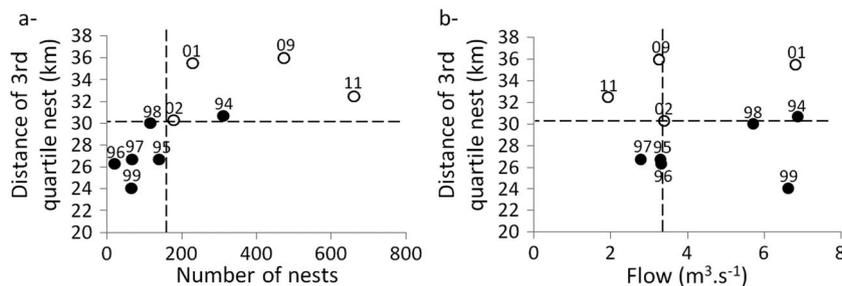

Figure 5. Relationships between the spatial distribution of nests (third quartile) and (a) the number of nests and (b) river flow before (black symbols) and after (white symbols) barrier removal. For each variable, the dashed line represents the median value

et al., 2013) or macroinvertebrates (Maloney *et al*., 2008; Chiu *et al*., 2013; Renofalt *et al*., 2013) have principally focused on community composition changes but rarely on population parameters (Stanley *et al*., 2007; Hogg *et al*., 2013). In the present study, we demonstrated that the spatial distribution of sea lamprey nests increased significantly upstream in the Scorff River after the removal of a barrier located in the middle part of the river as a result of improved connectivity between growing areas at sea and spawning grounds in fresh waters. Before removal, the barrier modified the relationship between spawning habitat availability and nest distribution because accessibility to suitable spawning habitat located upstream was limited (e.g. McDowall, 1998). Nests were principally located downstream of the barrier (66.2% of nests on average) although a fraction of adults were able to swim and spawn above the barrier. High flow might have reduced head loss between upstream and downstream parts and may have increased river width, creating alternative pathways for sea lamprey. In addition, high flow can be a cue stimulating upstream migration (Andrade *et al*., 2007). The distribution of river lamprey *Lampetra fluviatilis* has been demonstrated to be negatively impacted by the cumulative effects of barriers, and spawners were able to colonize stretches located upstream of small barriers (2–3-m head loss) mainly during high-flow conditions (Lucas *et al*., 2009). Here, although it is difficult to fully explore the effect of flow conditions on the spatial distribution of nests, we observed that, before barrier removal, the distribution was slightly enhanced upstream of the barrier under high-flow conditions when the number of nests and spawners was not too low. After removal and irrespective of river flow and the number of nests in the river, most of the nests (62.5% on average) were located upstream of the removed barrier. Except for the most upstream section that was equipped with another dam and the section located immediately downstream the barrier, the distribution of nest density along the river was relatively even, that is, nests were distributed proportionally to the available spawning habitat. These findings confirmed the recent observations of Hogg *et al*. (2013) conducted at a smaller spatial and temporal scale (i.e. 5.2 km of the Sedgeunkedunk River and 1-year pre-removal and a 2-year post-removal). Because spawning in densely occupied habitats probably induces costs associated with competition for mates or nest destruction by subsequent spawners (nest superimposition), migrating upstream might decrease these costs and increase spawning success and the survival and growth of larvae through decreased competition (Murdoch *et al*., 1992). Therefore, colonization patterns might result from complex trade-offs that impoundments could perturb, but sea lamprey response to removal could be intense and rapid (Hogg *et al*., 2013).

After removal, we also expected a decrease in the density of nests in the section located downstream of the barrier

(e.g. Hogg *et al*., 2013). It was, however, not the case, and high suitability of spawning habitat in this section might have caused the observed pattern. Specifically, sea lamprey might have acted as an ecosystem engineer in this section. By spawning every year in high density in this section, sea lamprey might have durably modified the river bed and improved the suitability for spawning of the local habitat (Sousa *et al*., 2012). An alternative and non-mutually exclusive hypothesis is that the presence of the barrier, by increasing the density of nests in this section during several years, has led to the presence of an important density of larvae in the vicinity. Because larval pheromones are a cue for adults to select habitat for spawning at large (i.e. river selection) and locally (i.e. nest location selection within 3 m and choice of a redd; Wagner *et al*., 2009; Meckley *et al*., 2012; Neeson *et al*., 2012), increased larval density might have locally increased nest density. Therefore, long-term monitoring of spawning activity should provide information to determine the relative importance of the interacting mechanisms driving sea lamprey nest distribution.

In addition to the modification in the spatial distribution of nests, we also observed that the average number of nests in the river increased after barrier removal. Although the relationship between the number of nests and the number of sea lamprey spawners is not necessarily linear because the number of adults involved in a nest might be variable (Harvey and Cowx, 2003; Moser *et al*., 2007) and assuming that the number of spawners per nest did not changed before and after removal, it is likely that the total number of spawners in the river has increased after barrier removal. Combining a mark-recapture approach and nest counts, Hogg *et al*. (2013) demonstrated that the estimated number of spawners and the number of nests were highly correlated, and they increased within 2 years after dam removal, showing clear links between these two metrics. Sea lampreys do not display homing (Waldman *et al*., 2008), and the entrance of spawners in a river is largely driven by olfactive cues (pheromones) produced by larvae (Polkinghorne *et al*., 2001; Vrieze and Sorensen, 2001; Sorensen *et al*., 2003; Vrieze *et al*., 2010; Meckley *et al*., 2012). Some authors have suggested the existence of a positive feedback between spawner abundance and larvae abundance: An increased abundance of spawners is expected to increase the number of larvae that, in turn, is expected to improve the attractiveness of the river for spawners (Neeson *et al*., 2011; Neeson *et al*., 2012). By improving the access to suitable spawning sites located upstream, barrier removal might have triggered such a feedback. Although no information is available in the studied river, this might have resulted in an increased number of spawners and spatial distribution of nests, as larval habitat was also available upstream. However, the observed increase in the number of nests in the Scorff River might

have been influenced, to some extent, by a general increased number of sea lamprey at a broader European scale that was observed from the end of the 1990s to 2005 (Beaulaton et al., 2008). It is difficult here to disentangle the relative role of local (restoration action) versus global factors in driving the number of nests in the studied river. It is clear that the use of a reference site is important when monitoring the restoration effects (Kibler et al., 2011; Gardner et al., 2013; Rolls et al., 2013). Nevertheless, after barrier removal, the spatial distribution of nests improved upstream irrespective of the number of nests and flow conditions.

Dam removal is becoming a more and more common practice for restoring the ecological integrity of rivers (Bednarek, 2001; Hart et al., 2002; Bernhardt et al., 2005). Nevertheless, understanding how it affects local populations and ecological processes is difficult. In the present study, we observed that barrier removal increased the upstream distribution of sea lamprey nests, irrespective of flow conditions and the number of nests, and these effects were observed rapidly. It allowed the colonization, every year, of suitable spawning habitats that were available upstream, with potential subsequent effects on the distribution of larvae in the river. Because the distribution and number of larvae in a river can affect the number of spawners, further investigations are needed to quantify the effects on the population dynamics.

REFERENCES

Almeida PR, Quintella BR, Dias NM. 2002. Movement of radio-tagged anadromous sea lamprey during the spawning migration in the River Mondego (Portugal). Hydrobiologia 483: 1–8.

Alp M, Keller I, Westram AM, Robinson CT. 2012. How river structure and biological traits influence gene flow: a population genetic study of two stream invertebrates with differing dispersal abilities. Freshwater Biology 57: 969–981.

Andrade NO, Quintella BR, Ferreira J, Pinela S, Posova I, Pedro S, Almeida PR. 2007. Sea lamprey (Petromyzon marinus L.) spawning migration in the Vouga river basin (Portugal): poaching impact, preferential resting sites and spawning grounds. Hydrobiologia 582: 121–132.

Applegate VC. 1950. Natural history of the sea lamprey (Petromyzon marinus) in Michigan. U.S. Department of the Interior, Fish and Wildlife Service Special Scientific Report: Fisheries 55. 237 pp.

Beaulaton L, Taverny C, Castelnaud G. 2008. Fishing, abundance and life history traits of the anadromous sea lamprey (Petromyzon marinus) in Europe. Fisheries Research 92: 90–101.

Bednarek AT. 2001. Undamming rivers: A review of the ecological impacts of dam removal. Environmental Management 27: 803–814.

Bernhardt ES, Palmer MA, Allan JD, Alexander G, Barnas K, Brooks S, Carr J, Clayton S, Dahm C, Follstad-Shah J, Galat D, Gloss S, Goodwin P, Hart D, Hassett B, Jenkinson R, Katz S, Kondolf GM, Lake PS, Lave R, Meyer JL, O'Donnell TK, Pagano L, Powell B, Sudduth E. 2005. Ecology – Synthesizing US river restoration efforts. Science 308: 636–637.

Catalano MJ, Bozek MA, Pellett TD. 2007. Effects of dam removal on fish assemblage structure and spatial distributions in the Baraboo River, Wisconsin. North American Journal of Fisheries Management 27: 519–530.

Chiu M-C, Yeh C-H, Sun Y-H, Kuo M-H. 2013. Short-term effects of dam removal on macroinvertebrates in a Taiwan stream. Aquatic Ecology 47: 245–252.

Cote D, Kehler DG, Bourne C, Wiersma YF. 2009. A new measure of longitudinal connectivity for stream networks. Landscape Ecology 24: 101–113.

Dynesius M, Nilsson C. 1994. Fragmentation and flow regulation of river systems in the northern third of the world. Science 266: 753–762.

Gardner C, Coghlan SM Jr., Zydlewski J, Saunders R. 2013. Distribution and abundance of stream fishes in relation to barriers: Implications for monitoring stream recovery after barrier removal. River Research and Applications 29: 65–78.

Hardisty MW, Potter IC. 1971. The biology of lampreys. Academic Press: London, New York.

Hart DD, Poff NL. 2002. A special section on dam removal and river restoration. Bioscience 52: 653–655.

Hart DD, Johnson TE, Bushaw-Newton KL, Horwitz RJ, Bednarek AT, Charles DF, Kreeger DA, Velinsky DJ. 2002. Dam removal: Challenges and opportunities for ecological research and river restoration. Bioscience 52: 669–681.

Harvey J, Cowx I. 2003. Monitoring the river, brook and sea lamprey, Lampetra fluviatilis, L. planeri and Petromyzon marinus. Conserving Natura 2000 Rivers Monitoring Series No. 5. English Nature, Peterborough.

Hogg R, Coghlan SM Jr., Zydlewski J. 2013. Anadromous sea lampreys recolonize a Maine coastal river tributary after dam removal. Transactions of the American Fisheries Society 142: 1381–1394.

Horreo JL, Martinez JL, Ayllon F, Pola IG, Monteoliva JA, Heland M, Garcia-Vazquez E. 2011. Impact of habitat fragmentation on the genetics of populations in dendritic landscapes. Freshwater Biology 56: 2567–2579.

Igoe F, Quigley DTG, Marnell F, Meskell E, O'Connor W, Byrne C. 2004. The sea lamprey Petromyzon marinus (L.), river lamprey Lampetra fluviatilis (L.) and brook lamprey Lampetra planeri (Bloch) in Ireland: general biology, ecology, distribution and status with recommandation for conservation. Biology and Environnement : Proceeding of the Royal Irish Academy 104B: 43–56.

Jackson A, Moser M. 2012. Low-elevation dams are impediments to adult pacific lamprey spawning migration in the Umatilla River, Oregon. North American Journal of Fisheries Management 32: 548–556.

Kibler KM, Tullos DD, Kondolf GM. 2011. Learning from dam removal monitoring: Challenges to selecting experimental design and establishing significance of outcomes. River Research and Applications 27: 967–975.

Lanca MJ, Machado M, Ferreira R, Alves-Pereira I, Quintella BR, De Almeida PR. 2013. Feeding strategy assessment through fatty acid

profiles in muscles of adult sea lampreys from the western Iberian coast. *Scientia Marina* **77**: 281–291.

Lassalle G, Beguer M, Beaulaton L, Rochard E. 2008. Diadromous fish conservation plans need to consider global warming issues: An approach using biogeographical models. *Biological Conservation* **141**: 1105–1118.

Lassalle G, Crouzet P, Rochard E. 2009. Modelling the current distribution of European diadromous fishes: an approach integrating regional anthropogenic pressures. *Freshwater Biology* **54**: 587–606.

de Leaniz CG. 2008. Weir removal in salmonid streams: implications, challenges and practicalities. *Hydrobiologia* **609**: 83–96.

Lejon AGC, Renofalt BM, Nilsson C. 2009. Conflicts associated with dam removal in Sweden. *Ecology and Society* **14**. http://www.ecologyandsociety.org/vol14/iss2/art4/

Liermann CR, Nilsson C, Robertson J, Ng RY. 2012. Implications of dam obstruction for global freshwater fish diversity. *Bioscience* **62**: 539–548.

Limburg KE, Waldman JR. 2009. Dramatic declines in North Atlantic diadromous fishes. *Bioscience* **59**: 955–965.

Lucas M, Baras E. 2001. Migration of Freshwater Fishes. Blackwell Science: Oxford, United Kingdom.

Lucas MC, Bubb DH, Jang MH, Ha K, Masters JEG. 2009. Availability of and access to critical habitats in regulated rivers: effects of low-head barriers on threatened lampreys. *Freshwater Biology* **54**: 621–634.

Maloney KO, Dodd HR, Butler SE, Wahl DH. 2008. Changes in macroinvertebrate and fish assemblages in a medium-sized river following a breach of a low-head dam. *Freshwater Biology* **53**: 1055–1068.

McDowall RM. 1998. Fighting the flow: downstream-upstream linkages in the ecology of diadromous fish faunas in West Coast New Zealand rivers. *Freshwater Biology* **40**: 111–122.

Meckley TD, Wagner CM, Luehring MA. 2012. Field evaluation of larval odor and mixtures of synthetic pheromone components for attracting migrating sea lampreys in rivers. *Journal of Chemical Ecology* **38**: 1062–1069.

Morman RH, Cuddy DW, Rugen PC. 1980. Factors Influencing the distribution of sea lamprey (Petromyzon marinus) in the Great Lakes. *Canadian Journal of Fisheries and Aquatic Sciences* **37**: 1811–1826.

Moser ML, Butzerin JM, Dey DB. 2007. Capture and collection of lampreys: the state of the science. *Reviews in Fish Biology and Fisheries* **17**: 45–56.

Murdoch SP, Docker MF, Beamish FWH. 1992. Effect of density and individual variation on growth of sea lamprey (*Petromyzon marinus*) larvae in the laboratory. *Canadian Journal of Zoology* **70**: 184–188.

Neeson TM, Wiley MJ, Adlerstein SA, Riolo RL. 2011. River network structure shapes interannual feedbacks between adult sea lamprey migration and larval habitation. *Ecological Modelling* **222**: 3181–3192.

Neeson TM, Wiley MJ, Adlerstein SA, Riolo RL. 2012. How river network structure and habitat availability shape the spatial dynamics of larval sea lampreys. *Ecological Modelling* **226**: 62–70.

Nilsson C, Reidy CA, Dynesius M, Revenga C. 2005. Fragmentation and flow regulation of the world's large river systems. *Science* **308**: 405–408.

Nislow KH, Hudy M, Letcher BH, Smith EP. 2011. Variation in local abundance and species richness of stream fishes in relation to dispersal barriers: implications for management and conservation. *Freshwater Biology* **56**: 2135–2144.

Noonan MJ, Grant JWA, Jackson CD. 2012. A quantitative assessment of fish passage efficiency. *Fish and Fisheries* **13**: 450–464.

Nunn AD, Cowx IG. 2012. Restoring river connectivity: prioritizing passage improvements for diadromous fishes and lampreys. *Ambio* **41**: 402–409.

Polkinghorne CN, Olson JM, Gallaher DG, Sorensen PW. 2001. Larval sea lamprey release two unique bile acids to the water at a rate sufficient to produce detectable riverine pheromone plumes. *Fish Physiology and Biochemistry* **24**: 15–30.

Prato EP, Comoglio C, Calles O. 2011. A simple management tool for planning the restoration of river longitudinal connectivity at watershed level: priority indices for fish passes. *Journal of Applied Ichthyology* **27**: 73–79.

Pringle CM. 2001. Hydrologic connectivity and the management of biological reserves: A global perspective. *Ecological Applications* **11**: 981–998.

Pringle C. 2003. What is hydrologic connectivity and why is it ecologically important? *Hydrological Processes* **17**: 2685–2689.

Pringle CM, Freeman MC, Freeman BJ. 2000. Regional effects of hydrologic alterations on riverine macrobiota in the New World: Tropical-temperate comparisons. *Bioscience* **50**: 807–823.

R Core Team. 2012. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org/. Accessed 12 January 2014

Renofalt BM, Lejon AGC, Jonsson M, Nilsson C. 2013. Long-term taxon-specific responses of macroinvertebrates to dam removal in a mid-sized Swedish stream. *River Research and Applications* **29**: 1082–1089.

Rolls RJ. 2011. The role of life-history and location of barriers to migration in the spatial distribution and conservation of fish assemblages in a coastal river system. *Biological Conservation* **144**: 339–349.

Rolls RJ, Ellison T, Faggotter S, Roberts DT. 2013. Consequences of connectivity alteration on riverine fish assemblages: potential opportunities to overcome constraints in applying conventional monitoring designs. *Aquatic Conservation: Marine and Freshwater Ecosystems* **23**: 624–640.

Roni P, Hanson K, Beechie T. 2008. Global review of the physical and biological effectiveness of stream habitat rehabilitation techniques. *North American Journal of Fisheries Management* **28**: 856–890.

Sabatié MR, Lasne E, Baglinière JL. 2011. La lamproie marine. In Les poissons d'eau douce de France, Keith P, Persat H, Feunteun E, Allardi J (eds). Biotope, Mèze; Muséum National d'histoire Naturelle: Paris; pp. 245–246.

Silva S, Servia MJ, Vieira-Lanero R, Barca S, Cobo F. 2013. Life cycle of the sea lamprey *Petromyzon marinus*: duration of and growth in the marine life stage. *Aquatic Biology* **18**: 59–62.

Sorensen PW, Vrieze LA, Fine JM. 2003. A multi-component migratory pheromone in the sea lamprey. *Fish Physiology and Biochemistry* **28**: 253–257.

Sousa R, Araujo MJ, Antunes C. 2012. Habitat modifications by sea lampreys (Petromyzon marinus) during the spawning season: effects on sediments. *Journal of Applied Ichthyology* **28**: 766–771.

Stanley EH, Catalano MJ, Mercado-Silva N, Orra CH. 2007. Effects of dam removal on brook trout in a Wisconsin stream. *River Research and Applications* **23**: 792–798.

Vrieze LA, Sorensen PW. 2001. Laboratory assessment of the role of a larval pheromone and natural stream odor in spawning stream localization by migratory sea lamprey (*Petromyzon marinus*). *Canadian Journal of Fisheries and Aquatic Sciences* **58**: 2374–2385.

Vrieze LA, Bjerselius R, Sorensen PW. 2010. Importance of the olfactory sense to migratory sea lampreys *Petromyzon marinus* seeking riverine spawning habitat. *Journal of Fish Biology* **76**: 949–964.

Wagner CM, Twohey MB, Fine JM. 2009. Conspecific cueing in the sea lamprey: do reproductive migrations consistently follow the most intense larval odour? *Animal Behaviour* **78**: 593–599.

Waldman J, Grunwald C, Wirgin I. 2008. Sea lamprey *Petromyzon marinus*: an exception to the rule of homing in anadromous fishes. *Biology Letters* **4**: 659–662.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web site.