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Rapid response of fish and aquatic habitat to removal of a tidal barrier

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Abstract

1. River barrier removal is used increasingly as a conservation tool to restore lotic habitat and river connectivity, but evidence of its efficacy is incomplete. This study used a before–after methodology to determine the effects of removing a tidal-limit barrier on the fishes, macroinvertebrates, and habitats of an English coastal stream.
2. Following barrier removal, habitat diversity increased immediately upstream and remained similar downstream. Mobilized silt altered the substrate composition immediately downstream, but this was temporary as silt was flushed out the following winter. Changes to macroinvertebrate communities occurred upstream and downstream of the former barrier but these were transient.
3. A dramatic and sustained increase in fish density occurred immediately upstream of the barrier after its removal, but effects downstream were minor. The fish community upstream changed, largely due to rapid recruitment and dispersal of endangered European eel (*Anguilla anguilla*). Eel density in the formerly impounded zone increased from 0.5 per 100 m^2 before barrier removal to 32.5 per 100 m^2 5 months after removal. By 17 months after barrier removal there was no difference in eel density across the six sections sampled.
4. Although resident stream fishes such as bullhead (*Cottus gobio* species complex, protected under the European Habitats Directive) were abundant in middle and upper-stream sections, brown trout (*Salmo trutta*, a listed species for biodiversity conservation in England and Wales) density remained low during the study and recruitment was poor. This suggests that although colonization access for anadromous trout was available, habitat upstream may have been unsuitable for reproduction, indicating that wider catchment management is required to complement the restoration of connectivity.
5. These findings suggest that tidal barrier removal is an effective method of restoring lotic habitats and connectivity, and can be beneficial for resident and migratory fishes including those of conservation importance (e.g. European eel) in coastal streams.

KEYWORDS
Anguilla anguilla, barrier removal, connectivity, dam, habitat restoration, recolonization

1 | INTRODUCTION

Instream obstacles such as dams, weirs, and culverts fragment rivers by interrupting longitudinal connectivity and altering habitat (Nilsson et al., 2005; Sun, Galib & Lucas, 2020), having major effects on the biodiversity and functioning of river ecosystems (Bunn & Arthington, 2002; Pringle, 2003; Galib et al., 2018). These obstacles frequently affect the dispersal and migration of fish species, and can result in population decline and biodiversity reduction (Lucas & Baras, 2001; Gehrke, Gilligan & Barwick, 2002; Katano et al., 2006; Mueller, Pander & Geist, 2011). The flow-impounding effects of river barriers result in alteration to slower, deeper, fine-sediment dominated habitat immediately upstream, especially in low-gradient reaches, with resultant effects on the biota (Boon, 1988; Mueller, Pander & Geist, 2011; Birnie-Gauvin et al., 2017a). Barriers close to the sea can have disproportionate effects on the distribution of diadromous fish species in rivers by limiting access to suitable habitat upstream (Kemp & O'Hanley, 2010; Nunn & Cowx, 2012; Harris, 2016).

One such species is the European eel (*Anguilla anguilla*), the abundance of which has decreased greatly since the early 1980s (Dekker, 2003; Henderson et al., 2012; Jacoby et al., 2015). Recruitment of glass eel (the transparent juvenile stage that enters fresh water) has reduced by more than 90% and the population of silver eel (migrating to sea) has reduced by more than 50% (Piper et al., 2013; Jacoby & Gollock, 2014). Owing to its rate of decline, this species has been classified as 'Critically Endangered' in the International Union for Conservation of Nature (IUCN) global Red List (Jacoby & Gollock, 2014; Pike, Crook & Gollock, 2020). Under the Water Framework Directive (WFD), European Union (EU) countries are required to provide free migration of fishes (Council of the European Communities, 2000), which is a particularly relevant policy tool for supporting the recovery of European eel, as well as for other migratory fish species such as brown trout (*Salmo trutta*). The European Commission also initiated an Eel Recovery Plan (Council Regulation No 1100/2007) to ensure sustainable levels of adult eel abundance and glass eel recruitment across the European Union (Council of the European Communities, 2007). Through this, EU states are required to develop Eel Management Plans across 'river basin districts'. Also in 2007 (ratified in 2009), European eel was listed in Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), allowing export only without detriment to the species' survival. As a result, since December 2010 all commercial trade of European eel to and from the EU has been banned (Musing et al., 2018).

The reasons for the decline in recruitment of European eel are still not fully understood, with various threats ranging from over-exploitation to climate change, but are mirrored by several other *Anguilla* species (Jacoby et al., 2015). However, the occurrence of instream barriers restricting access to juvenile habitat is considered to be one of the major threats to the European eel population (Dekker, 2003; Piper et al., 2013; Tamario et al., 2019). It is also a threat that can be responded to, through river restoration.

The upstream migration of juvenile European eels can last several years, during which time they may migrate hundreds of kilometres and grow to ~40 cm, although a proportion never enter fresh water (Lucas & Baras, 2001). Barriers such as weirs, dams, and sluices limit their upstream migration, restricting access to suitable nursery habitat upstream (Mouton et al., 2011; Tamario et al., 2019). Although juvenile eels, especially those smaller than 10 cm, can climb and crawl on wet and rough surfaces (Porcher, 2002; Watz et al., 2019), only a small proportion may manage to pass barriers (White & Knights, 1997; Tamario et al., 2019). Instream barriers and associated engineering infrastructure can reduce survival and delay the downstream migration of the maturing silver eel stage (Behrmann-Godel & Eckmann, 2003; Calles et al., 2010; Piper et al., 2013) before migration to oceanic spawning grounds. For all diadromous species, enabling their bidirectional migration in rivers is crucial (Calles & Greenberg, 2009).

Although a variety of fishway designs exist to facilitate upstream or downstream migration (Silva et al., 2018), their efficacy for many species can be low (Bunt, Castro-Santos & Haro, 2012). Eel-specific fishways pass a proportion of juvenile eel (Environment Agency, 2011; Watz et al., 2019) but are unsuitable for most other species. Tide flaps and management of sluices can also be used to support the passage of eels in tidal reaches (Environment Agency, 2011; Wright, Wright & Kemp, 2015; Guiot et al., 2020). Unlike these mitigation measures, barrier removal reinstates hydrological connectivity, more natural habitat, sediment transport, and free movement of aquatic biota (Roni, Hanson & Beechie, 2008; Kemp & O'Hanley, 2010; O'Hanley, 2011). Removal of redundant barriers is increasingly used as a river management and conservation tool in many countries (Birnie-Gauvin et al., 2017b; Silva et al., 2018). Several studies have measured the effects of barrier removal on geomorphological and ecological responses in rivers (Pizzuto, 2002; Doyle et al., 2005; Chang et al., 2017; Clark et al., 2020). For barriers that occur in tidal reaches, however, the recovery of fish communities in response to barrier removal is still poorly known (but see Souder et al., 2018). The tidal sections of rivers are characterized by large fluxes of nutrients, sediment, and organisms between marine and freshwater environments (Levin et al., 2001) and barriers that interrupt tidal reaches can dramatically alter these. Free-flowing rivers provide a range of physical habitats that are important for supporting the fish populations (Brink et al., 2018). Therefore, removal of tidal barriers may be hypothesized to have a rapid effect on changes in local habitat and the fish community through reinstating sediment transport, bidirectional flow, and facilitating fish dispersal and migration. In particular, removal of such barriers is predicted to benefit the migration and production of species such as European eel. Moreover, aquatic invertebrates are important food sources for many fish species (e.g. European eel, brown trout, and bullhead *Cottus gobio* species complex) and changes in aquatic habitats resulting from impounding effects may alter invertebrate assemblages (Vinson, 2001), which could affect the diversity and abundance of fishes.

In this study, the changes in aquatic habitat, fish abundance, and fish and benthic invertebrate communities were measured in response to the removal of a tidal weir in a small stream of the River Tees, north-east England. A before–after methodology was used, and particularly focused on the recolonization of European eel in the stream. Although the primary action was removal of a tidal weir, the study operated over multiple sites along the entire stream catchment to determine wider-scale as well as local effects. It was hypothesized that the tidal barrier removal would result in the change of habitat from impounded, lentic water to more diverse habitat, with associated rapid change in the fish community in the formerly impounded zone and benefit the recruitment of diadromous fishes in the stream.

2 | STUDY SITE

Claxton Beck, north-east England, is a low-gradient stream that joins Greatham Creek within the intertidal zone of the River Tees (Figure 1) downstream of the Tees Barrage. Claxton Beck is a small watercourse (1–4 m wide at the natural tidal limit, after barrier removal) that rises at an altitude of 126 m. Claxton Beck and its upstream reach, North Burn, drain an area of 41 km^2 before joining Greatham Creek. The latter is located in an area surrounded by wet pasture and mudflats. Cloff Bridge weir, a barrier located at the head of tide (54°37′39.2″N 1°15′14.5″W) was built around 1910 to prevent tidal intrusion and so enable abstraction of fresh water, from above the weir, to a nearby brickworks (now defunct). The weir was a 2.4-m high concrete structure (Figure 2) that was impassable to most fish species under most conditions, and a major obstruction to eel. Throughout much of the 20th century, the Tees estuary was heavily polluted by industrial and urban waste, with an impoverished fish community, but the estuary became cleaner from the 1980s onwards, enabling progressive recovery of the fish community and recolonization of suitable habitat.

Prior to the agricultural and industrial revolutions, small streams entering northern English estuaries, such as Claxton Beck entering the Tees estuary, are likely to have been populated by a fish community comprising diadromous migratory fishes, especially brown trout, European eel, European flounder (*Platichthys flesus*), euryhaline species and small, resident species such as stone loach (*Barbatula barbatula*) (Wheeler, 1969). In small, lowland Danish coastal streams, similar in climate and natural hydromorphology to Claxton Beck, anadromous brown trout are often the dominant species (Birnie-Gauvin et al., 2018). However, agricultural intensification, land drainage, stream straightening and pollution has degraded the habitat of many lowland streams across England, including Claxton Beck, so although Claxton Beck probably once contained a substantial brown trout population, it was almost extirpated. The Environment Agency (EA) stocked North Burn with brown trout fry in 1997 but they did not perpetuate at the sites stocked (R. Jenkins, EA, personal communication). In recent years, small numbers of adult sea trout (*S. trutta*) have been observed in the reach downstream of Cloff Bridge weir

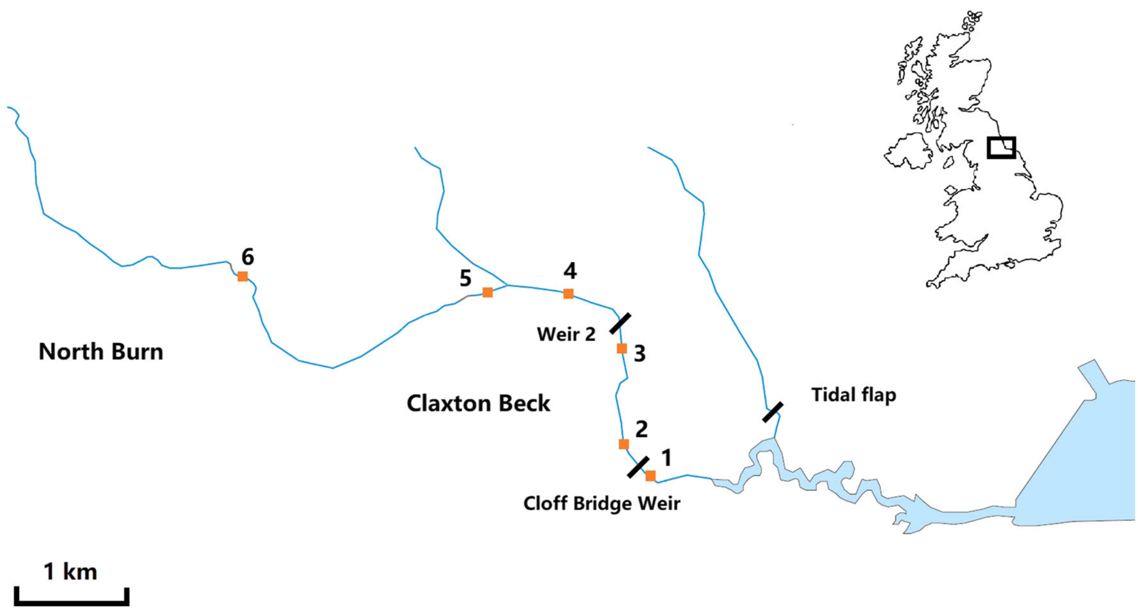

FIGURE 1 Claxton Beck catchment and the midpoint of each fish sampling section. Sampling only occurred on Claxton Beck/North Burn

FIGURE 2 Cloff Bridge weir on Claxton Beck before removal (a), immediately after removal on 30 April 2018 (b), five months after the weir removal (c), and 17 months after the weir removal (d). Photographs were taken under base flow conditions

during the autumn breeding season (B. Lamb, Tees Rivers Trust, personal communication).

Owing to Cloff Bridge weir's impounding effects, the upstream reach was dominated by a 480-m long, uniformly deep (~1 m), slow glide, with fine sediment on the bed. A small scour pool with industrial rubble and gravel had developed immediately downstream of the weir. The weir formed an artificial tidal limit and, within a few hundred metres downstream of the weir, the channel became progressively more characteristic of a tidal creek, dominated by tidally transported soft sediment, with exposed mud banks and marginal reeds (*Phragmites australis*). From WFD monitoring in the upstream freshwater reach, the ecological status of the fish community at Claxton Beck was classified as 'bad' between 2013 and 2016 by the EA (Environment Agency, 2020). Cloff Bridge weir was considered to be the main reason of WFD failure for fish. Another 1-m high weir is located 1.5 km upstream of Cloff Bridge weir and 0.2 km downstream of a major road bridge that crosses Claxton Beck.

To provide free passage for fish and help restore the upstream river habitat, by reinstating flow and sediment connectivity, Cloff Bridge weir was removed by the Tees Rivers Trust on 30 April 2018 (Figure 2). The unnamed weir 1.5 km upstream of Cloff Bridge could not be removed because of concerns over potential stream bed erosion actions on the road bridge upstream. Therefore, a wooden pool fish pass was installed on the middle of the second weir in June 2018. The slope of the fish pass is 30°, it has nine 0.1-m high pools and a width of 0.5 m. In addition, a bristle elver pass was installed on the left side of the pool fish pass in September 2018.

3 | METHODS

3.1 | Experimental approach

Because environmental conditions, especially flow, vary seasonally and could be expected to alter habitats, especially after weir removal, sampling of habitat (especially around Cloff Bridge weir) and biota was carried out twice per year, in autumn and spring. Samples were taken on five occasions: in autumn 2017 and spring 2018, before the removal of Cloff Bridge weir, and in autumn 2018, spring 2019, and autumn 2019 after barrier removal. Spring samples were collected in April and autumn samples in late September and early October.

3.2 | Habitat measurements

To assess river habitat close to Cloff Bridge weir before and after barrier removal, a habitat survey was performed during seasonal base-flow conditions. Hydromorphological characteristics comprising wetted width, depth (at 25%, 50% and 75% of wetted width) and flow velocity (at 50% depth and 25%, 50% and 75% of wetted width) were measured every 12 m in the upstream impounded section (length, 480 m) and downstream tidal section (length, 204 m). These measurements were made 7 months before (September 2017) and 5 months (September 2018), 12 months (April 2019), and 17 months (September 2019) after weir removal. Sampling could not be carried out in April 2018 owing to prioritization of biotic sampling during the only period of low flows that month. Sampling in the tidal section was carried out close to low tide. Dominant habitat types (riffle, glide, pool) and substrate types (sand, silt, gravel, etc.) in each 12-m section were recorded. The river-bed substrate composition in each 12-m section was visually and manually assessed, using an approximation to the Wentworth scale: boulder (>256 mm), cobble (64–256 mm), gravel (2–64 mm), sand (0.06–2 mm) and silt (<0.06 mm) (Wentworth, 1922; Environment Agency, 2003). An additional substrate category, 'earth', was used to describe compacted soil (inorganic and organic materials) that formed submerged banks and, in some areas, part of the stream bed, particularly within the inundated impounded reach.

A more detailed survey grid of water depth and flow velocity was carried out in zones stretching 20 m upstream and 40 m downstream of the weir's midpoint. These data were used for generating 2D graphs, to visualize habitat changes after weir removal. Both characteristics were measured on a 1-m mesh. If the wetted width was less than 3 m, then measurements were taken at positions of 25, 50, and 75% width. An electromagnetic flow meter (Valeport 801) was used to take flow velocity measurements except in a 10-m long section affected by electromagnetic interference from high voltage electricity transmission pylons, where an analogue Hydro-prop Impeller flow meter was used.

3.3 | Sample sections for biota surveys

Six sampling sections, each 300-m long, were chosen in which to sample biota (Figure 1). It was feasible to sample only one section downstream of Cloff Bridge weir because of the deep, soft mud further downstream. In Section 1, located immediately downstream of the weir (Figure 1), the tide mark was approximately 1 m high on the banks. The riparian zone of Section 1 is mostly semi-improved grassland. Land use adjacent to Section 1 is pasture and arable land on the left bank and semi-natural parkland on the right bank. Downstream of Section 1, the riparian zone is dominated by common reed. Section 2 was located immediately upstream of the weir, within the impounded zone, and Section 3 was located nearly 700 m upstream of Section 2, downstream of the second weir. Sections 4–6 were located upstream of the second weir (Figure 1). The riparian zone of Sections 2–6 mostly consists of broadleaf trees such as sycamore (*Acer pseudoplatanus*) and common alder (*Alnus glutinosa*) together with some tall herbs such as nettle (*Urtica dioica*) and butterbur (*Petasites hybridus*). The predominant land use adjacent to Sections 2–5 is mixed agricultural land. For Section 6, the land use is semi-improved grassland on the left side and broadleaf woodland on the right side. Apart from Section 2, which, prior to weir removal, was an impounded area, the remaining sampling sections contained multiple habitat types (riffle, glide, and pool). Because the second weir has not been removed, the removal of Cloff Bridge weir is unlikely to have had any impacts on river habitat upstream of the second weir. Initially, Section 3 was positioned 700 m upstream of Section 2, but owing to difficulties with land access permission after summer 2018, the sampling section was moved 500 m further upstream until the end of the study. The new Section 3 had similar river habitat compared with the original location, and the fish population surveys after weir removal were all conducted in the new Section 3.

3.4 | Fish community sampling

Fish were sampled by electrofishing using wading with a single anode, operated with a bankside generator and control box (Honda EU10i, Electracatch WFC1, ∼200 V). For Section 1 in the tidal reach (Figure 1), sampling was carried out close to low tide, when depth and conductivity were lowest (always <1 ppt salinity). Although single-funnel, 5-mm mesh, baited traps were trialled as another method of sampling fish, these were ineffective and their use was discontinued. Six 20-m long, full channel-width sample replicates, targeting a mixture of habitat types, approximately proportionately to their availability, were spread along each 300-m sample section.

The three-pass electrofishing 'depletion' method (Reynolds & Kolz, 2013) was carried out for each 20-m sample length, using 4-mm mesh stopnets to delimit the fished section. Fish removed from each pass were kept in separate aerated containers, after which the catches were processed separately. Fish were identified and their total length measured. If more than 50 fish of a species were caught at a site, then 50 per species were randomly selected and measured, and the remainder counted. Processed fish were released back to the capture location. Fish capture and handling complied with UK legislation and guidelines.

3.5 | Invertebrate sampling

Sections 1–4 were chosen for conducting benthic macroinvertebrate sampling. Sections 5 and 6 were not sampled because we did not expect rapid changes in invertebrate communities in the sections located furthest upstream, as none of the Tees brackish-water invertebrates are capable of colonizing fresh water. Three sites were sampled in each section, and each site was surveyed twice per year, once in spring and once in autumn. All instream habitats were kick-sampled in proportion to their occurrence for a total of 3 min using a handnet with 1-mm mesh, plus 1 min of hand searching. At sites with little flow, material suspended by kick-sampling was washed into the net by generating flow with a hand or foot. After sampling, all invertebrates were stored in 70% ethanol and identified to family level in the laboratory using a binocular microscope and standard literature (e.g. Pawley, 2011). The taxonomic resolution for Oligochaeta and Mysidacea was not to family level.

3.6 | Data analysis

For habitat metrics, pairwise permutational multivariate analysis of variance (PERMANOVA) from the 'RVAideMemoire' package (Hervé, 2020) was applied to analyse whether the habitat types, substrate types and hydromorphology (water depth, flow velocity, and wetted width) differed between the downstream section (Section 1) and upstream impounded section (Section 2) (Chang et al., 2017). All habitat data were log(x + 1) transformed before conducting analyses. Before and after changes in water depth and flow velocity immediately upstream and downstream of the weir were visualized using Iric (version. 2.3) (Nelson et al., 2016).

Fish densities per site were calculated according to Carle and Strub's K-pass removal method, by using the R (version 3.6.1) package 'FSA' (Ogle, 2020). Fish densities and relative abundance data for invertebrates were fourth-root transformed before conducting the following analysis (Boys et al., 2012; McDonald, 2014). PERMANOVA was used to determine changes in the fish and invertebrate communities after weir removal, using the R 'Vegan' package (Oksanen et al., 2019). In order to create a balanced design to perform PERMANOVA, the surveys were split into three periods, each comprising a spring survey and an autumn survey (Period 1: autumn 2017, spring 2018; Period 2: autumn 2018, spring 2019; Period 3: spring 2019, autumn 2019). Similarity percentage (SIMPER) analysis, based on the decomposition of the Bray–Curtis dissimilarity index (Clarke, 1993), was used to identify the contribution of individual species to the overall fish community in each section. Linear mixed-effects models (LMMs) were constructed to analyse the changes in fish abundance using the 'lme4' and 'lmerTest' package (Kuznetsova, Brockhoff & Christensen, 2017). Tukey's multiple comparison test was performed to analyse the differences in total fish abundance (all fish species combined) and eel abundance between study sections, using the 'multcomp' package (Hothor et al., 2020). Sites (nested within sections) and seasons (nested within sampling years) were used as random factors when performing both analyses. To visualize the spatial and temporal differences in fish communities, a non-metric multidimensional scaling (Kruskal & Wish, 1978) ordination plot was generated using the 'metaMDS' function of the 'vegan' package.

Invertebrate communities are good indicators of watercourse pressures (e.g. pollution), and they are frequently used in assessing the level of general degradation (Water Framework Directive – United Kingdom Technical Advisory Group, 2014). The WHPT ASPT (Whalley, Hawkes, Paisley & Trigg – Average Score Per Taxon) was applied as an abundance weighted metric (Water Framework Directive – United Kingdom Technical Advisory Group, 2014) for assessing responses of the invertebrate community across stream sections before and after barrier removal. The ASPT at each section was also analysed by using LMM.

4 | RESULTS

4.1 | Aquatic habitat before and after barrier removal

Before barrier removal, Section 2 was impounded and dominated by a deep, very slow glide (Table S1). Substrate in the impounded section was mostly composed of sand (68.7 ± 33.7%), together with some exposed earth (12.6 ± 28.2%) close to the water's edge, and silt (11.4 ± 23.3%) accumulated on the upstream side of the weir (Table S1). Downstream, and before removal of the weir, the stream was shallower (28.2 ± 9.0 cm) and narrower (4.22 ± 1.62 m). The tidal stream section exhibited a more natural form with faster flow (0.08 ± 0.04 m s^{-1}) and glide, riffle, and pool habitats at low tide (Table S1). Mud (46.7 ± 25.3%) and sand (23.6 ± 13.5%) formed the majority of the bottom substrates, but gravel and boulder occurred intermittently (Table S1).

Although the whole weir was removed, a steep riffle remained at its former position (Figure 2) and the tidal limit remained in the vicinity of the former weir's position for the duration of the study. The riparian vegetation and river bank canopy in the former impounded zone and downstream tidal zone were not affected by barrier removal. Bed substrates, habitat types, and hydromorphology exhibited dramatic changes in Section 2 within the first 5 months after barrier removal (PERMANOVA, $P < 0.05$ in all cases; Table S2). Section 2 became shallower and narrower, with faster flow (Figure 3). Large volumes of fine sediment were washed to the downstream section; the proportion of bed in Section 2, covered by sand decreased from 68.7 to 20.4% 5 months after barrier removal, then slightly increased to 31.4%, after 12 months (Table S1). After the sand was washed away, it exposed underlying compacted earth of the channel bed, and this became the dominant substrate in Section 2, increasing to 60.7% cover 5 months after barrier removal, then slightly decreasing to 44.5% 17 months after barrier removal (Table S1). The overall upstream substrate composition appeared stable at 17 months after removal of the barrier (Table S3; PERMANOVA pairwise post hoc, $P > 0.05$). A few riffles and pools were formed in the previously impounded section (Table S1) and caused significant changes in habitat type 5 months after removal (PERMANOVA pairwise post hoc, $P < 0.01$) with no further changes at 12 and 17 months post-removal (PERMANOVA pairwise post hoc, $P > 0.05$ in both cases). Similar to the habitat attributes, water depth, wet width and flow velocity all changed within 5 months following removal (PERMANOVA pairwise post hoc, $P < 0.01$); these variables then became stable and showed no further significant changes (Table S3).

In the downstream reach, Section 1, the bed substrate composition changed after weir removal (PERMANOVA pairwise post hoc,

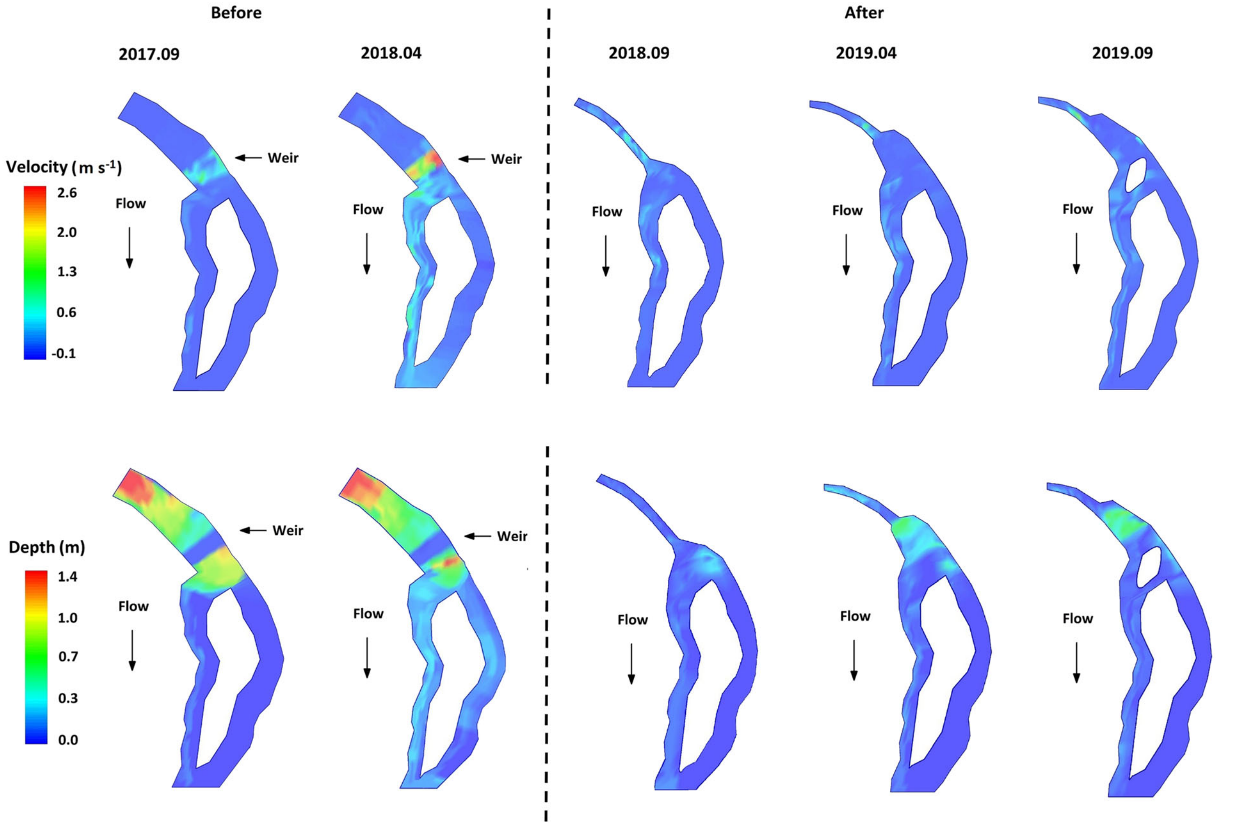

FIGURE 3 Flow velocity and water depth before and after the weir removal (upper panel: Velocity; lower panel: Depth)

P < 0.01), with much of the bed covered by 10-cm thick silt. The proportion of substrate classed as silt increased from 46.7 to 72.3% at 5 months post-removal (Table S1). Most surface silt was washed further downstream after several winter high-flow events by 12 months post-removal, and the silt proportion in Section 1 reduced to 27.2% (Table S1). Meanwhile, the proportion of sand increased from 5.8 to 34.7%. The overall bottom substrates showed no further change by 17 months post-removal (PERMANOVA pairwise post hoc, *P* > 0.05). The habitat factors were not affected by the barrier removal in the downstream reach through the study periods (PERMANOVA pairwise post hoc, *P* > 0.05 in both cases).

4.2 | Fish abundance and fish community before and after barrier removal

Before barrier removal, eight fish species were captured during the electrofishing surveys (Figure 4). European flounder, nine-spined stickleback (*Pungitius pungitius*) and common goby (*Pomatoschistus microps*) were only captured in Section 1. Section 1 was dominated by flounder in spring and by European eel in autumn. The predominant species in Section 2 was three-spined stickleback (*Gasterosteus aculeatus*), and sites further upstream (Sections 3–6) were dominated by bullhead (*Cottus perifretum*, part of the *Cottus gobio* species complex *sensu* Freyhof, Kottelat & Nolte, 2005). Before barrier removal, among all sampled sections, total fish density in Section 1 was significantly higher than in all upstream sections in autumn (Figure S1; Table S4; LMM pairwise post hoc, *P* < 0.05 in all cases) and fish density in Section 2 was significantly lower than in all other sections in spring (Figure S1; Table S4; LMM pairwise post hoc, *P* < 0.05 in all cases).

After barrier removal, the predominant species of Sections 1–6 remained similar, but eel became relatively more abundant further upstream than previously (Figure 4). The overall fish densities across all sections exhibited a significant increase in density after barrier removal (Figure S1, Table S5; LMM, $F_{1,143}$ = 14.154, *P* < 0.001). Five months after barrier removal, fish abundance in Section 2 had greatly increased, and there was no significant difference in total fish density between Section 2 and all other sections (LMM, *P* > 0.05 in all cases).

The fish communities differed significantly between Sections 1, 2, and 3 before the barrier removal (PERMANOVA, *P* < 0.05 in all cases; Table S6). The fish communities in Sections 1, 2, and 3 changed after barrier removal (Figure 5, Table 1; PERMANOVA, *P* < 0.05 in all cases) and remained different from each other after barrier removal in both P2 (autumn 2018–spring 2019) and P3 (spring 2019–autumn 2019) (PERMANOVA, *P* < 0.05 in all cases). For Section 1, SIMPER showed that eel and flounder contributed more than 80% of the change in fish assemblages after barrier removal, in both P2 and P3. For Section 2, both three-spined stickleback and eel abundance increased

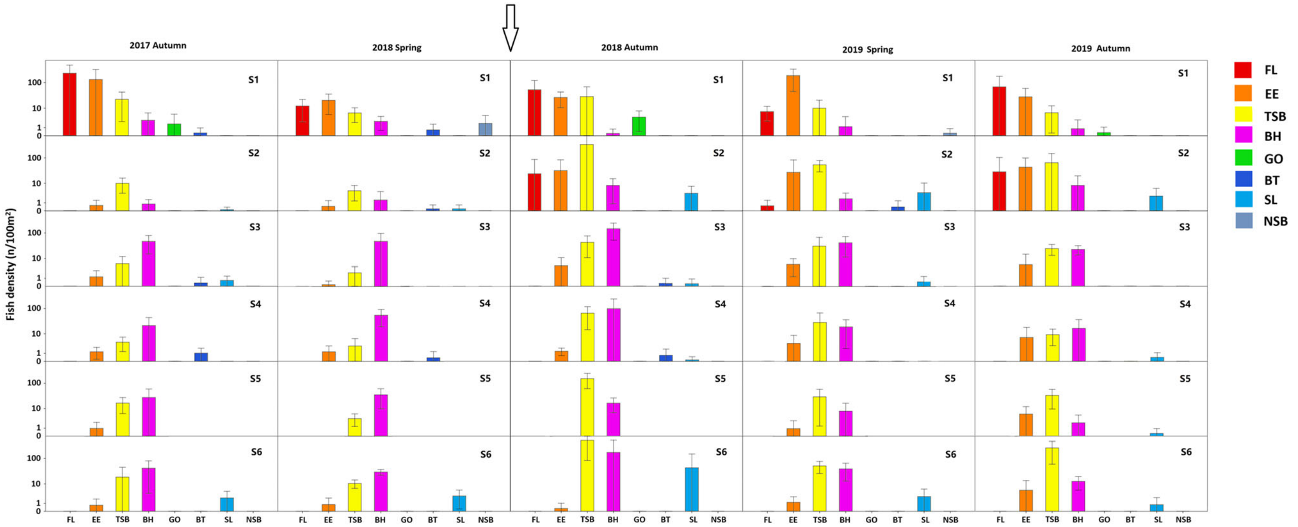

FIGURE 4 Mean fish densities (per 100 m^2) of each species in each section before and after the barrier removal. Error bar: 95% confidence interval. FL: European flounder, EE: European eel, TSB: three-spined stickleback, BH: bullhead, GO: common goby, BT: brown trout, SL: stone loach, NSB: nine-spined stickleback. The arrow signifies when the barrier was removed. Section numbers are ordered from downstream to upstream, with Section 1 being downstream of the barrier location and Section 2 the impounded zone prior to barrier removal

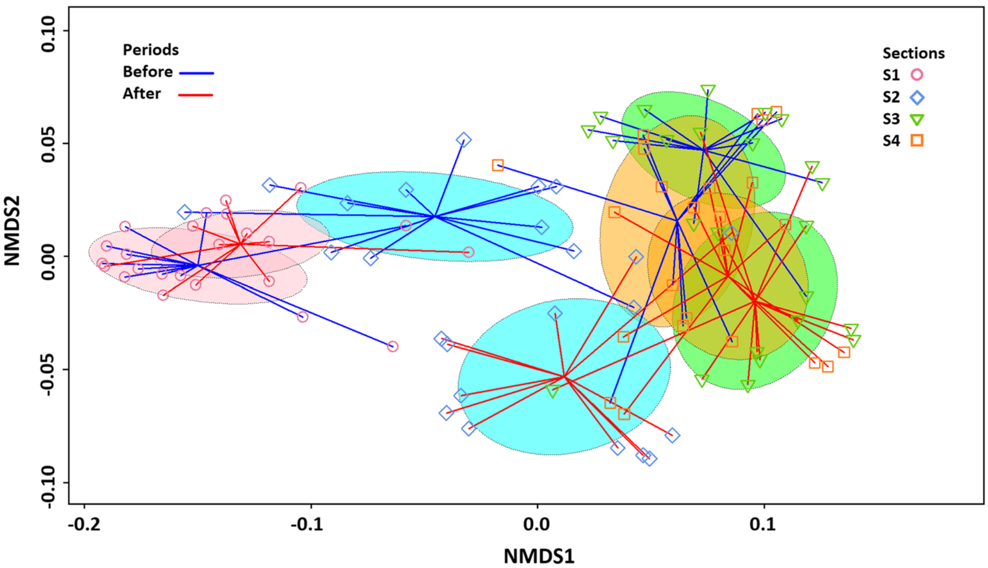

FIGURE 5 Non-metric multidimensional scaling (NMDS) ordination plot (centroids and 95% confidence ellipses) of fish communities in Sections 1–4 before (autumn 2017 and spring 2018) and after (spring 2019 and autumn 2019) tidal weir removal. Data for Sections 5 and 6 are not shown because they overlapped greatly with Section 4 and obscured the pattern

significantly after barrier removal (LMM, stickleback: $F_{1,28}$ = 21.599, P < 0.001; eel: $F_{1,23}$ = 16.782, P < 0.001), and these two species contributed more than 80% of the dissimilarity in fish assemblages after barrier removal. There was little change further upstream. Eels contributed less to fish community change at S3–S6.

4.3 | Upstream recolonization by eel and flounder

Although eels were present upstream of the barrier before its removal, they occurred at very low densities (Figure 6). Eel densities before barrier removal differed significantly among sampling sections (LMM, $F_{5,60}$ = 29.54, P < 0.001); eel abundance was higher in Section 1 than other upstream sections in both seasons (Figure 6, Table S7; LMM pairwise post hoc, P < 0.001 in all cases). Before barrier removal, there was no significant difference in eel density between upstream sampling sections (Sections 2–6; LMM pairwise post hoc, P > 0.05 in all cases).

Eels were divided into three length classes: class 1 (40–109 mm; recently recruited glass eels and elvers), class 2 (110–219 mm; those that had spent less than 2 years in fresh water) and class 3 (≥ 220 mm; those that had spent more than 2 years in fresh water) (Domingos, Costa & Costa, 2006). Before weir removal, 47.2% of eels in Section 1 were glass eels/elvers, but, in the remaining upstream

TABLE 1 PERMANOVA comparisons of fish and invertebrate communities in each section between periods P1 (autumn 2017 and spring 2018, before barrier removal), P2 (autumn 2018 and spring 2019), and P3 (spring 2019 and autumn 2019)

Community	Section	Periods	Mean square	*df*	*F*	*P*
Fish	1	P1 vs. P2	0.190	1,22	4.259	**<0.05**
		P1 vs. P3	0.212	1,22	2.656	**<0.05**
	2	P1 vs. P2	0.460	1,22	6.077	**<0.01**
		P1 vs. P3	0.420	1,22	5.683	**<0.01**
	3	P1 vs. P2	0.195	1,22	3.337	**<0.05**
		P1 vs. P3	0.255	1,22	5.098	**<0.05**
	4	P1 vs. P2	0.040	1,22	1.186	>0.05
		P1 vs. P3	0.061	1,22	1.434	>0.05
	5	P1 vs. P2	−0.002	1,22	−0.119	>0.05
		P1 vs. P3	0.239	1,22	5.401	**=0.05**
	6	P1 vs. P2	0.003	1,22	0.109	>0.05
		P1 vs. P3	0.059	1,22	1.794	>0.05
Invertebrate	1	P1 vs. P2	0.537	1,10	2.180	<0.05
		P1 vs. P3	0.424	1,10	1.850	>0.05
	2	P1 vs. P2	0.177	1,10	0.821	>0.05
		P1 vs. P3	0.167	1,10	0.819	>0.05
	3	P1 vs. P2	0.249	1,10	2.182	**<0.05**
		P1 vs. P3	0.168	1,10	1.647	>0.05
	4	P1 vs. P2	0.102	1,10	0.672	>0.05
		P1 vs. P3	0.219	1,10	1.631	>0.05

Note: Significant values are in bold.

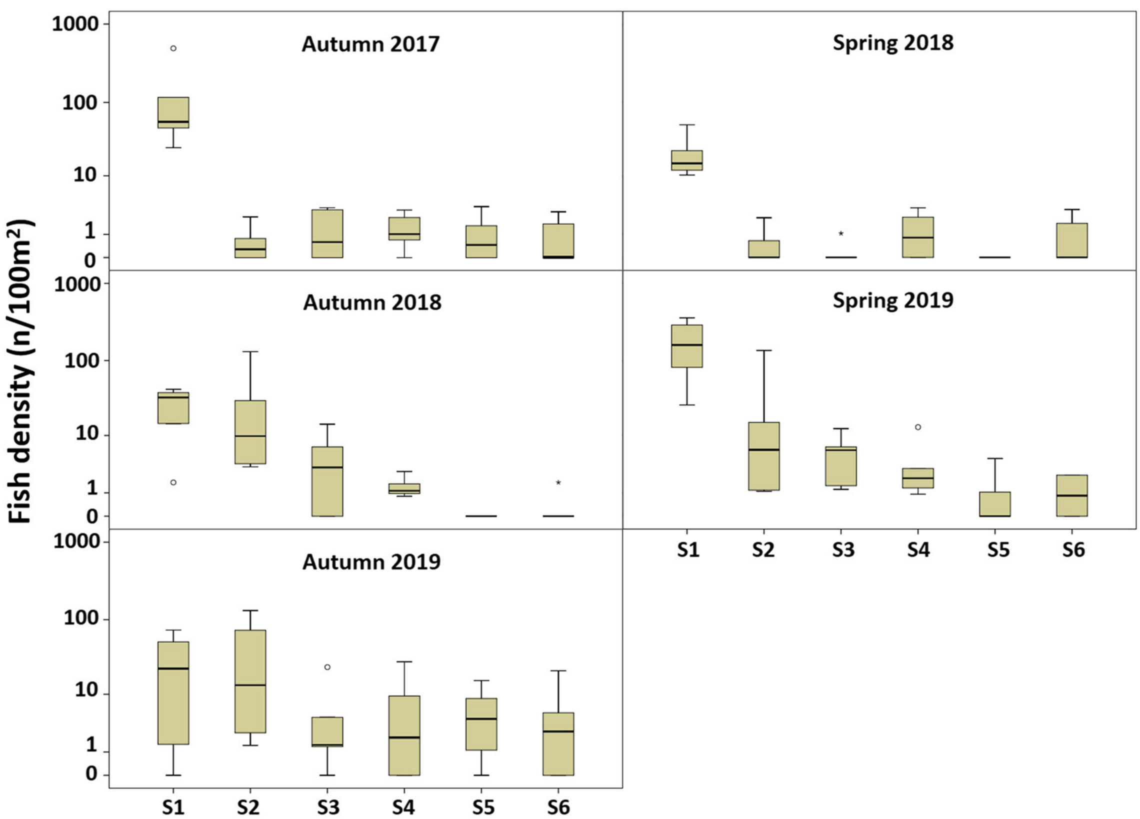

FIGURE 6 Box plots showing median (with quartiles, ranges, and outliers) European eel densities (per 100 m^2) in each section before and after tidal barrier removal (removed, after spring 2018 sampling). Section 1 is in the tidal zone, downstream of the barrier, Section 2 is the impounded zone, while Section 6 is the furthest site upstream

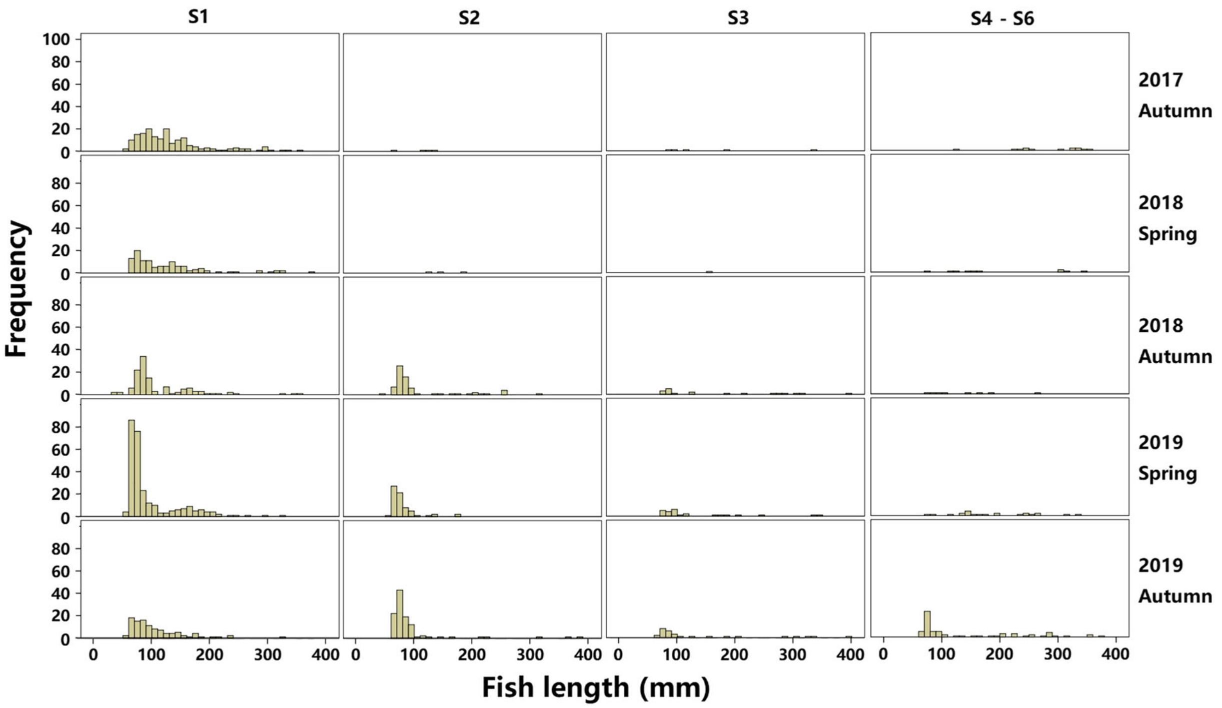

FIGURE 7 Length frequency distribution of European eel in each section before and after weir removal (removed after spring 2018 sampling). Section 1 is the furthest downstream site in the tidal zone, Sections 2–6 are non-tidal, with Section 6 the furthest upstream. Samples in Sections 4–6 have been combined

TABLE 2 Linear mixed-effects model output showing changes in European eel abundance in each stream section before, compared with after, barrier removal (Before: autumn 2017 and spring 2018; After: autumn 2018, spring 2019 and autumn 2019)

Section	Mean square	*df*	*F*	*P*	*Trend*
All combined	11.874	1,143	24.992	**<0.001**	↑↑↑
1	0.008	1,23	0.011	>0.05	-
2	16.782	1,23	48.895	**<0.001**	↑↑↑
3	4.90	1,23	14.591	**<0.001**	↑↑↑
4	0.999	1,23	4.673	**<0.05**	↑↑
5	0.393	1,22	0.920	>0.05	↑
6	0.317	1,23	0.996	>0.05	↑

Note: Season and site were used as random factors in the analysis. Significant values are in bold.

sections, only 10.3% of those caught were glass eels/elvers (Figure 7). Five months after weir removal, mean eel density in Section 2 increased from 0.5 to 32.5 per 100-m^2, significantly higher than sections further upstream (LMM pairwise post hoc, $P < 0.005$ in all cases, Table S7), and 79.2% were glass eels/elvers. In Section 2, eels contributed 15.6% of the dissimilarity in fish assemblages in P2 and it increased to 22.6% in P3 (SIMPER). However, eel density in Section 1 remained unchanged following removal of the weir (Table 2; LMM, $F_{1,23} = 0.008$, $P > 0.05$).

For Sections 4–6, eel abundance did not change markedly until autumn 2019, 17 months after weir removal. In spring 2019, strong eel recruitment was recorded in the tidal zone and 77.9% of the total eel catch comprised the class 1 group. By autumn 2019, it was evident that this year class had colonized the whole stream (Figure 7). Even in Section 6, 68.8% of captured eels were class 1. For all upstream sections combined (Sections 2–6), mean eel length in autumn 2019 (114 ± 82 mm) was shorter than in autumn 2017 (247 ± 121 mm; independent *t*-test, $t_{226} = -7.176$, $P < 0.001$). No difference in eel density was found among stream sections in autumn 2019 (LMM, $F_{5,25} = 6.10$, $P > 0.05$). Overall, eel density across all sections increased significantly after barrier removal (Table 2; LMM, $F_{1,143} = 11.874$, $P < 0.001$).

Flounder were divided into two length-age classes: 10–80 mm, Age-0 group; 81–140 mm, Age-1 group (Summers, 1979; Summers, 1980). Before weir removal, flounder occurred only in the downstream tidal section (Section 1, Figure 4), of which 95.7% were Age-0

(Figure S2). After barrier removal, flounder started colonizing upstream (Figure 4, Figure S2); mean flounder density at Section 2 increased from zero to 14.9 per 100 m^2 (P1 vs. P3). Over the same time period, mean flounder density in Section 1 decreased from 119.9 to 37.6 per 100 m^2 (LMM, $F_{1,27} = 4.62$, $P < 0.05$). Flounder were not recorded upstream of Section 2.

4.4 | Invertebrate community changes after barrier removal

The benthic invertebrate communities in Sections 1 and 3 differed in P2 compared with the pre-removal period (P1; Figure S3, PERMANOVA, $P < 0.05$ in both cases; Table 1), but no differences were evident for any sections between P1 and P3. For Section 1, SIMPER outputs showed that the contribution of three invertebrate taxa (Oligochaeta, Asellidae and Dixidae) changed significantly after weir removal (SIMPER, all $P < 0.05$; Table S8). For Section 3, SIMPER revealed that the contribution of three invertebrate families (Baetidae, Hydropsychidae, and Heptageniidae) changed significantly after weir removal (SIMPER, all $P < 0.05$, Table S8). No difference in ASPT was found in each section before and after the weir removal (LMM, $P > 0.05$ in all cases).

5 | DISCUSSION

To our knowledge, this is the first study to report on the effects of removal of a small tidal barrier on adjacent aquatic habitat, and on the fish and invertebrate communities. The results of this study show that although the small tidal barrier did not fully prevent eel passage, it dramatically reduced upstream eel abundances and altered eel size structure within the upstream reach. The study provides evidence that removal of the barrier reinstated longitudinal connectivity effectively, and without unforeseen consequences. Increased habitat diversity was created immediately upstream, and although large amounts of silt were mobilized, most was transported through the system within a year. Effects on the benthic invertebrate community appear to have been minor and transient. Strong benefits of the barrier removal were evident for the fish community. The density of European eel, particularly new recruits, increased in all five upstream sections, and the total fish density in the previously impounded zone also increased after barrier removal. Before barrier removal, three-spined stickleback dominated the impounded zone. Following the weir removal, resident fishes such as bullhead and stone loach benefitted from the lotic habitat (Tomlinson & Perrow, 2003; Freyhof, 2013), and their abundance increased. Bullhead (*Cottus gobio* species complex) is protected under the European Habitats Directive (Council of the European Communities, 1992) through its inclusion on Annex II, which requires Member States to designate 'special areas of conservation' for the species listed. Bullhead is also a Biodiversity Action Plan species in the UK, so the return of lotic conditions by barrier removal can provide a tool to support the recovery of this species in degraded lowland streams, especially as it has poor dispersal abilities (Tummers, Hudson & Lucas, 2016).

This study suggests that: (i) the removal of the tidal barrier restored more suitable habitat for migratory and resident fishes; (ii) free passage to upstream nursery habitat was restored; and (iii) after weir removal, the upstream recolonization and recruitment of eel was greatly increased within 2 years. Evidence is growing rapidly that stream barrier removal can be very effective for aquatic conservation (Catalano, Bozek & Pellett, 2007; Burroughs et al., 2010; Birnie-Gauvin et al., 2018; Ding et al., 2018). Where possible, barrier removal should be one of the first tools in the conservationist's 'toolbox' to be used for stream connectivity restoration (Garcia De Leaniz, 2008; Tummers, Hudson & Lucas, 2016; Birnie-Gauvin et al., 2017b; Birnie-Gauvin et al., 2018). Earlier debate over the tradeoff of risks and benefits of barrier removal concentrated particularly upon medium- and large-sized dams, where the removal costs are relatively high and especially centred on the risks of contaminated and uncontaminated fine sediment release from the impoundment (Bednarek, 2001; Poff & Hart, 2002). That risk applies much less to small barriers, which do not retain large amounts of fine-sediment deposits behind them. The vast majority of artificial river barriers are small (Januchowski-Hartley et al., 2013; Jones et al., 2019; Sun, Galib & Lucas, 2020). Nevertheless, although removal of redundant barriers is a preferred restoration tool, in many cases barriers cannot be removed owing to societal needs or because of constraints such as erosion risks on nearby infrastructure (Birnie-Gauvin et al., 2017b). On the River Tees, only two out of 20 barriers where connectivity has been restored have been removed, with the remainder installed with fish passes (Sun, Galib & Lucas, 2020). This proportion is probably typical of European and North American rivers. As evidence of the benefit to cost ratio of stream barrier removal increases and confidence grows, it is hoped that efforts will increasingly be concentrated on achieving barrier removal.

5.1 | Response of the fish and invertebrate communities

The single most important indicator of the success of tidal barrier removal in this study was the rapid recolonization of most of the stream by juvenile eels, suggesting it can have similar benefits elsewhere. Tamario et al. (2019) provided evidence that fishway types, other than nature-like bypasses, have no better effect on eel distribution upstream of dams than dams with no fishways. Their study was unable to evaluate the benefits of barrier removal owing to small sample size. We recommend that eel conservation measures are likely to benefit disproportionately from investment in removing redundant barriers and providing nature-like bypasses in the lower reaches of rivers. The importance of unimpeded passage of diadromous fishes, especially in the lower reaches of catchments, is widely acknowledged (Kemp & O'Hanley, 2010; Nunn & Cowx, 2012).

Tidal barrier removal allowed rapid upstream immigration of juvenile eels from the tidal reach. Although a 1-m barrier, approximately

1.5 km upstream, remained, it is evident that its size, form and possibly the addition of a pool fishway and bristle-type eel pass, did not impede the passage of eels smaller than 110 mm. After the previously impounded reach was restored to shallower lotic habitat, it may also have become more suitable for eels to colonize. Recent research has shown that European eel in lotic waters prefer to use shallow and rocky habitat such as riffles and runs rather than deep pool habitat (Acou et al., 2011). Use of shallow habitat can also potentially reduce the chance of small eels being preyed upon (Degerman et al., 2019). Mean eel length in autumn 2019 was less than in autumn 2017, suggesting that young recruits (glass eels and elvers) were primarily responsible for the increase in the upstream eel population. In Section 6, the furthest upstream site, more than 60% of the eels captured were below 110 mm in length in autumn 2019. A dam removal study in America found that dam removal significantly increased American eel (*Anguilla rostrata*) abundance in headwater streams, and the immigration of small individuals (<300 mm) was primarily responsible for the observed increases in eel numbers (Hitt, Eyler & Wofford, 2012).

The study stream, Claxton Beck, flows into the Tees estuary downstream of the Tees Barrage, which opened in 1995, and was built as part of an urban economic redevelopment plan. That tidal barrage has a salmon ladder, navigation lock and a bristle pass for eels but represents a major barrier for upstream eel migration to most of the Tees catchment. The rapid increase in eel density and distribution through Claxton Beck shows how such restorative actions can contribute towards eel management plans for individual catchments such as the Tees, part of the Northumbria river basin district.

In autumn 2018, after the weir removal, flounder decreased in abundance although there was no significant difference in total fish density in Section 1, downstream of the barrier's former position, compared with before removal. This is probably because a large amount of silt was released to the downstream section after barrier removal and covered the previously suitable sandy habitat. Juvenile flounder have been observed to use sandy and gravelly substrate (Le Pichon et al., 2014), so it is likely that after weir removal some flounder in Section 1, especially in those patches most affected, moved upstream or further downstream to more suitable habitat. Indeed, flounder rapidly colonized the previously impounded reach soon after barrier removal. In contrast, the downstream invertebrate community only showed differences in the first period, and the invertebrate community changes in Section 3 may have been caused by moving the sampling location after weir removal. Any change in invertebrate communities seems to have been transient, perhaps resulting from initial sediment mobilization soon after weir removal. This suggests that downstream river habitat recovered within 17 months. In addition, there was no significant change in the ASPT, suggesting that downstream water quality was not degraded by weir removal. In contrast to flounder, the eel population in the tidal reach was not affected by the temporary increase in fine sediment, probably because eels are more tolerant to muddy substrate and elvers often use soft substrates as shelter in which to hide (J. Sun, personal observation). In addition, eels may hibernate in soft, muddy substrate when the water temperatures drop to below 8–9 °C (Degerman et al., 2019).

In contrast to eel, and to the study of Birnie-Gauvin et al. (2018), the population of brown trout in Claxton Beck has not yet benefitted from barrier removal. Brown trout is a species of 'principal importance' for biodiversity conservation in England and Wales under Section 41 of the Natural Environment and Communities Act 2006. In 1997, the Environment Agency stocked approximately 10,000 brown trout fry upstream of Section 6, but fish surveys close to the release site in 1998, 2000 and 2004, caught only small numbers of trout (R. Jenkins, unpublished data). During the present study, a few juvenile and adult brown trout were caught before weir removal. No significant changes were found in the trout population in the surveys following weir removal, and no Age-0 trout were caught in 2019. Although adult sea trout can easily immigrate from the Tees estuary it is possible that few were doing so during the study. The philopatric nature of sea trout would also tend to result in slow recolonization if the existing population is small. It is also the case that, although the previously impounded reach became shallower and more diverse in habitat types, the bed comprised mainly sand and compacted earth, which is unsuitable spawning and sub-optimal juvenile habitat for trout (Louhi, Mäki-Petäys & Erkinaro, 2008). In the upper reach (Section 6), although riffles with gravel occurred and lotic specialists such as bullhead were common, it is possible that interstitial fine sediment might be too abundant, and interstitial oxygen supply too poor, to enable trout egg survival and development (Kemp et al., 2011). Indeed, three-spined stickleback, a species typically associated with degraded water quality and habitat were also abundant at this site. Enhanced connectivity, without sufficient improvement in habitat quality and water quality cannot achieve desired restoration outcomes (Roni, Hanson & Beechie, 2008; Tummers, Hudson & Lucas, 2016) and needs to be a focus in this intensively farmed sub-catchment in the future. It is also possible, however, that unlike the observations of Birnie-Gauvin et al. (2018), recovery of trout populations in Claxton Beck will take much longer than the short duration of this study.

6 | CONCLUSIONS

This study suggests that for small tidal barriers in temperate climates barrier removal is an appropriate method by which to restore aquatic habitat and increase the abundance of both resident and migratory fish species, especially benefitting eels. Our findings support the recent emphasis on barrier removal as a very powerful tool for river restoration, and have important implications for environmental agencies engaged in river and estuary management. In addition, this study also showed that barrier removal can be an effective method in the management of priority conservation species such as the threatened European eel. The apparent success of barrier removal for reconnecting habitats for European eel, albeit at the small scale of this study, and American eel (Hitt, Eyler & Wofford, 2012), suggests that it should be trialled for other eel species. This is, perhaps, especially so for 'tropical' eel species (Jacoby et al., 2015), including those in Africa which, although poorly studied, are urgently in need of further research and conservation actions (Hanzen et al., 2019).

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Raw data are available from the lead author upon request.

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