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Short-term growth, movement and response of European eel *Anguilla anguilla* to re-meandering of a small English chalk stream

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Abstract – In recent decades, the population of European eel *Anguilla anguilla* has strongly declined and the stock is outside safe biological limits. Freshwater habitat degradation has been cited as a key causal factor in the European eel decline, but there are limited studies assessing the responses of this species to river habitat restoration efforts. This study utilized mark-and-recapture data from annual electrofishing surveys conducted between 2009 and 2014 to describe European eel population density and size structure (length, weight) in the River Glaven – a chalk stream in eastern England. Short-term effects of river restoration on European eel were assessed via a Before-After-Control-Impact experimental design. Of the recaptured individuals, 73% were sedentary and the rest mobile. Despite re-meandering work increasing habitat heterogeneity in the restoration reach relative to the control reach, no change in European eel density or size structure was detected across treatments and time. While length and weight increased in the downstream control reach over the study period, density declined. This can be attributed to various local stressors such as barriers to European eel migration, as well as broader range-scale causes including climatic and oceanic factors. Although further research is ideally necessary to ensure adequate sample sizes, as well as to provide long-term monitoring of eel responses to river restoration, this study emphasizes the need for whole-catchment efforts in European eel conservation that combine river–floodplain restoration with greatly improved fish passage.

Keywords: River Glaven / restoration / mark-and-recapture / fish passage / Before-After-Control-Impact

1 Introduction

In recent decades, in response to widespread river degradation, restoration initiatives involving in-stream habitat modifications as well as channel re-profiling and repositioning have become widespread in European and North American rivers (Brun, 2015; Friberg *et al.*, 2016). River restoration initiatives have sought to increase the hydrological connectivity, geomorphological complexity and biological richness of aquatic ecosystems, in turn aiming to ameliorate the effects of past river regulation (Brun, 2015; Deffner and Haase, 2018). In Europe, river restoration has been widely recognized as an integral tool (Schmitt *et al.*, 2018; Deffner and Haase, 2018) in the European Union (EU) Water Framework Directive (WFD). This directive has the aim of returning rivers and streams to

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'Good Ecological Status' (European Commission, 2015a), which more than half of the surface waters in the EU failed to reach in 2012 and 2018. As implemented in the WFD, fishes are often used as indicators of ecological status (Solimini *et al.*, 2006). Consequently, several studies have assessed the response of fishes to a variety of measures implemented to restore both river systems (*e.g.* Haase *et al.*, 2013; Lorenz *et al.*, 2013; Smith, 2013) and adjacent floodplain habitats (Stoltefaut *et al.*, 2024). However, evidence for improvements in fish communities following such measures is variable and inconsistent, with some studies reporting positive responses and others minimal beneficial change (*e.g.* Lorenz *et al.*, 2013; Thompson *et al.*, 2018; Sinclair *et al.*, 2023).

A fish species for which population uplift is urgently needed and river restoration may have an important role for conservation purposes is the critically endangered European eel *Anguilla anguilla* – a catadromous fish of prominent ecological and economic value (Pike *et al.*, 2020). European eels represent important prey for a range of piscivorous birds and mammals (Knights, 2003; Almeida *et al.*, 2012). The European eel has also been exploited by humans as a food source for centuries, forming the foundation of large commercial fisheries (Feunteun, 2002; Bevacqua *et al.*, 2007; Dekker, 2019) and an aquaculture industry of global significance (Nielsen and Prouzet, 1998). However, the status of the European eel stock is critical, with recruitment undergoing a strong decline since the 1980s, after which it has remained at a very low level (ICES, 2023). This decline has likely had ecological consequences for other species at both lower (prey) and higher (predator) trophic levels. Moreover, there are important economic implications of European eel decline since more than 25,000 people in Europe depend upon eel fisheries and aquaculture for a substantial proportion of their income (Dekker, 2003, 2004). Therefore, a Council Regulation (EU 1100/2007) established a framework for the recovery of European eel stocks and the species was added to CITES Annex II (Ciccotti *et al.*, 2012). Since 2008, the European eel has also been classified globally as critically endangered by the IUCN Red List of Threatened Species (Pike *et al.*, 2020), and more recently, using IUCN criteria, as threatened with extinction in the UK at both regional (Britain) and national (England, Scotland and Wales) levels (Nunn *et al.*, 2023).

Partly due to the complex life cycle of the European eel (Wright *et al.*, 2022), there are several different factors attributed to its decline (Feunteun, 2002; van Ginneken and Maes, 2005; Friedland *et al.*, 2007). These include oceanographic changes (Westerberg, 1998; Kettle *et al.*, 2011), such as declines in Atlantic Ocean productivity (Desaunay and Guerault, 1997; Dekker, 1998) and changes in the Gulf Stream current, which threaten the transport of larvae to the European continent (White and Knights, 1994; Knights *et al.*, 1996). Additionally, several continental human-related factors may have also contributed to the species' decline, particularly artificial barriers (*e.g.* sea defences, weirs, sluices, watermills and hydroelectric dams: Solomon and Beach, 2004; McCarthy *et al.*, 2008). These may prevent both upstream and downstream migration (Moriarty and Dekker, 1997; Acou *et al.*, 2008) and in some cases cause high mortality (Winter *et al.*, 2006; Brown *et al.*, 2007). Further, human-induced degradation of freshwater habitats including channelization, water abstraction, eutrophication and pollution also negatively affect the European eel (Feunteun, 2002; Starkie, 2003). Therefore, the International Council for the Exploration of the Seas (ICES, 2023) has recently added a strong conservation element in its advice on fishing opportunities for the European eel, stating that all species' habitats should be restored, including connectivity but also chemical, physical and biological features.

To ameliorate the European eel decline, member states of the EU have implemented national Eel Management Plans (EMPs: Aprahamian *et al.*, 2007; Bilotta *et al.*, 2011) aimed at facilitating increased escapement of adults to the Sargasso Sea (European Commission, 2014). Conservation work has centred on mitigating the impacts of barriers to the upstream migration of juveniles through the implementation of eel passes (Knights and White, 1998; Solomon and Beach 2004; Piper *et al.*, 2023). However, several EMPs have also included initiatives to restock freshwater systems with juveniles (Moriarty and Dekker, 1997; Feunteun, 2002; Bevacqua *et al.*, 2015), although the effectiveness of this measure remains unknown (*e.g.* Haubrock *et al.*, 2019; Rohtla *et al.*, 2021). While river restoration does feature in several regional EMPs (Couldrick *et al.*, 2011), assessments of the effects of habitat improvement strategies on European eel populations are still widely lacking, despite habitat degradation being cited as one of the primary causes of the species' decline (Feunteun, 2002). It is of great importance, therefore, that river restoration implications for the European eel are more widely assessed.

The River Glaven in England (UK) was the subject of an extensive two-phase river restoration initiative involving embankment removal to reconnect the river with its flood plain, followed by re-meandering (Champkin *et al.*, 2018). A previous study evaluated the impact of restoration on general fish communities at Hunworth (Champkin *et al.*, 2018), whereas the current study focuses, in more detail, on European eel density, size structure (length, weight), movement and growth (Objective 1), as well as on the consequences of restoration for the species (Objective 2). To address Objective 1, changes in European eel density and size structure were assessed over the study period in the control reach, with spring and annual growth as well as movement between reaches described. To address Objective 2, a Before-After-Control-Impact (BACI) study was undertaken, comprising one survey prior to embankment removal (pre-restoration: 2009), two surveys following embankment removal but prior to re-meandering (post-embankment removal: 2009–2010) and four surveys subsequently (2011–2014: post-re-meandering). We hypothesized that physical changes in substrata, channel character and meso-habitat resulting from the restoration would have affected European eel growth rates and demographic variables.

2 Methods

2.1 Study area

The River Glaven is a small chalk stream in North Norfolk, eastern England, UK. It rises from headwaters in the Bodham area (52.90° N, 1.13° E) and is 17 km long. It initially flows in a south-westerly direction prior to a sharp turn at Hunworth, after which it continues northwards, discharging into the North Sea at Blakeney Point (Fig. 1). The Glaven River flows over

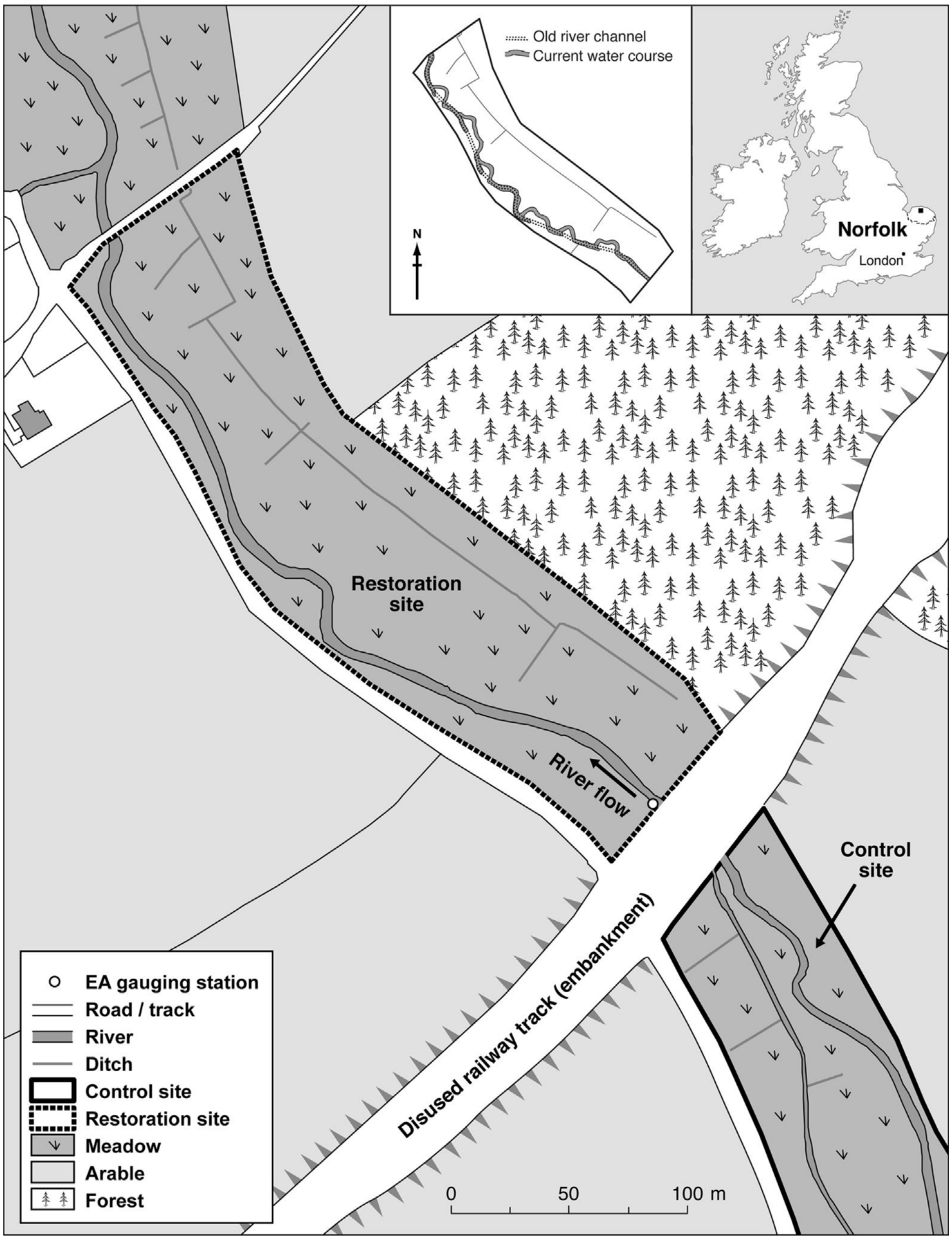

Fig. 1. The River Glaven at Hunworth (North Norfolk, eastern England, UK). Both study reaches are shown as is Thornage Mill, downstream of the restoration reach, and the Environment Agency gauging station between the two study reaches. The geographical extent of the River Glaven catchment and its position in the UK are shown in the inset. Image courtesy of H. Clilverd (UCL).

Upper Cretaceous chalk bedrock in turn overlain by chalk-rich sandy till and glaciogenic sand and gravels (Clilverd *et al.*, 2013, 2016). Accordingly, much of the river is classified as chalk stream (Pawley, 2008) – a river type of high conservation importance that is highly vulnerable to human-induced degradation (Bowes *et al.*, 2005). The River Glaven catchment area covers 115 km^2 and consists of diverse land use, predominantly arable land, ancient and other deciduous woodland, coniferous plantations (upper river) and grazing meadows (middle and lower reaches).

The River Glaven catchment is of high conservation interest because it supports several species listed under Annex II of the EU Habitats Directive (92/43/EEC). These include white-clawed crayfish *Austropotamobius pallipes*, European bullhead *Cottus gobio*, brook lamprey *Lampetra planeri* and European otter *Lutra lutra* (European Commission 2015b), in addition to brown trout *Salmo trutta* and the European eel, which are UK priority species (Joint Nature Conservation Committee, 2014). Nevertheless, many reaches of the River Glaven have suffered a long history of human-induced alteration. These include straightening and relocation of the channel, interruption of longitudinal connectivity through the introduction of mills and weirs, and removal of bankside trees and large in-channel wood pieces (Clilverd *et al.*, 2013; Harwood *et al.*, 2022). Further, as for many lowland European rivers, the River Glaven is degraded by nutrient and finesediment pollution associated with upper catchment farmland and the influence of sewage treatment facilities.

The study area comprised the Hunworth meadow river restoration reach immediately downstream of Hunworth Bridge (52.882152° N, 1.0658938° E) and an unmodified control reach just above the bridge (boundary: from 52.882035° N, 1.0661432° E to 52.880925° N, 1.0673284° E) (Fig. 1). The two study reaches are situated around 8 km upstream of the Glaven's tidal limit at Cley at an altitude of around 20 m. Four major barriers (three water mills and one tidal sluice) are present below the study reaches which are in themselves separated by a small Environment Agency gauging weir (Harwood et al., 2022). This isolates the fish populations of either reach to some extent, although not during periods of elevated discharge.

2.2 The Hunworth Meadow restoration

Prior to restoration, the River Glaven was constrained by embankments along the entire length of the Hunworth meadow, which ranged from 0.4 to 1.1 m above the meadow surface (Clilverd *et al.*, 2016). These embankments entirely eliminated flooding at the site. The restoration reach is a 400 × 100 m grazed grassland bordered by a minor road to the south and coniferous woodland and arable land to the north. The river at the site is both alkaline (pH 7.7–8.0) and eutrophic, with phosphate and nitrate nitrogen concentrations of <0.05 mg l^{-1} and 5.8–7.5 mg l^{-1} respectively (Clilverd *et al.*, 2013).

The restoration was undertaken in two phases. The first phase was conducted during March 2009 and involved the removal of embankments to reconnect the river with the flood plain (Fig. S1). Then, in August 2010, the river was re-meandered to create a more sinuous channel, with pools and riffles incorporated into the design (Fig. S1). During this process, six backwaters (ranging in length from 3 to 18 m) were also created from remnants of the old river channel and were not in-filled (Sayer, 2014). For the most part, river banks were left to natural plant colonization, although limited planting was undertaken with small patches of locally sourced manna grass *Glyceria maxima* (from the study reach) used to assist bank stabilization.

The re-meandering increased channel length of the restoration reach from 370 to 430 m and decreased mean channel width by approximately 0.5 m (from ≈3.2 ± 0.4 to ≈ 2.7 ± 0.5 m). This resulted in an overall increase in channel surface area of 407 m^2 (from 1549 to 1956 m). Mean water depth did not change significantly following restoration, but the dominant substrate changed from silt/sand to gravel, which increased by >13% between 2009 and 2012. Restoration also increased meso-habitat diversity, with a greater number of deeper pools present at the restoration reach. In the control stretch, mean depth declined by ≈ 23% (from 24.1 ± 2.2 cm in 2009 to 18.4 ± 1.5 cm in 2012) likely as result of reduced discharge, but no change occurred in substrate composition. In addition, the incidence of riffle meso-habitats declined, while runs increased. The prevalence of glides or pools remained unchanged in the control stretch between 2009 and 2012 (Champkin *et al.*, 2018).

2.3 Eel sampling and tagging

The eel population was sampled along the restoration and control reaches of the River Glaven over the course of seven successive sampling events to encompass geomorphological and hydrological conditions prior to and following the two-phase re-naturation scheme. Both reaches were initially sampled in February or March 2009 (pre-restoration) and then subsequently in June of the same year, following embankment removal. Both reaches were sampled again in June 2010, prior to re-meandering works (post-embankment removal), and then over consecutive days in each subsequent May or June for four years after the restoration was completed, most recently in June 2014 (post-re-meandering). The restoration (downstream) reach was always sampled first to avoid disturbance-induced turbid water (due to sediment resuspension while electro-fishing) from the control (upstream) reach making downstream fishing more challenging.

On each sampling date, the reach to be sampled was isolated using upstream and downstream stop nets (8 mm mesh). Each reach was then electro-fished using a 230 V Electracatch control box, 50 Hz Pulsed Direct Current, 2 m twin-tailed cathode and two persons fishing, each with a 300 mm ringed anode and hand net. This was performed in successive removals style (DeLury, 1951), based on three complete runs through the 370 and 160 m restoration and control reaches, respectively, with approximately the same fishing effort (in terms of time and people involved) put into each. All captured fishes were quickly transferred to large, aerated tanks adjacent to the river, identified to species level, with their abundance recorded (Champkin *et al.*, 2018). European eel density was calculated as abundance, estimated using the general weighted *k*-pass estimator (Carle and Strub, 1978) in the *removal* function of package *FSA* (Ogle, 2017) for R v. 4.3.3 (R Core Team, 2024), divided by the area surveyed.

All captured fish were anaesthetized on the bankside in a solution of 2-phenoxyethanol (2 ml l^{-1}), measured for total length (TL, nearest mm) and then weighed (precision 0.1 g). To allow recapture inferences and calculations of growth rate, fish captured from both reaches during the pre-restoration (March 2009) and post-embankment removal sampling (June 2009) were tagged utilizing two distinct tagging methods, depending on body length. Fish larger than 250 mm TL had a passive integrated transponder (PIT) tag inserted into the peritoneal cavity, specifically to lie in the posterior third of this region. Fish < 250 mm TL were injected with visible implant elastomer (VIE) tags, with different colours and bodily locations used to allow for distinctive identification. Following the completion of three electrofishing runs, and once they had fully recovered from the effects of the anaesthesia, all fish were returned to the reach from which they were captured. During successive sampling events, all fish were anaesthetized and scanned with a PIT reader to identify recaptured individuals; if no PIT tag could be detected, then a VI light was used to illuminate the VIE tag. Any untagged fish captured post-embankment removal were also tagged using the methods described above. The numbers of fish caught, tagged and recaptured per each time period are shown in Table 1. All work was carried out under a UK Home Office Project Licence (PPL 80/2302).

Table 1. Numbers of European eels *Anguilla anguilla* in the River Glaven at Hunworth (north Norfolk, eastern England, UK) caught, tagged and recaptured during the study. n.a. = not applicable.

				Number of individuals		
Reach	Time period	Year	Treatment	Caught	Tagged	Recaptured
Control	1	2009	Pre-restoration	38	34	n.a.
Control	2	2009	Post-embankment removal	30	17	10
Control	3	2010	Post-embankment removal	38	n.a.	17
Control	4	2011	Post-re-meandering	17	n.a.	6
Control	5	2012	Post-re-meandering	15	n.a.	5
Control	6	2013	Post-re-meandering	10	n.a.	0
Control	7	2014	Post-re-meandering	6	n.a.	0
Restoration	1	2009	Pre-restoration	81	35	n.a.
Restoration	2	2009	Post-embankment removal	87	58	18
Restoration	3	2010	Post-embankment removal	42	n.a.	15
Restoration	n.a.	2010	Fish rescue	14	n.a.	3
Restoration	4	2011	Post-re-meandering	18	n.a.	4
Restoration	5	2012	Post-re-meandering	26	n.a.	7
Restoration	6	2013	Post-re-meandering	34	n.a.	0
Restoration	7	2014	Post-re-meandering	32	n.a.	0

During the re-meandering works in August 2010 and prior to the old river channel being backfilled, a ‘fish rescue’ was carried out by a private contract team using the aforementioned sampling approach in order to temporarily remove and relocate fishes. However, these data are derived from short reaches of the existing channel only; as such, they are not representative and were excluded from all population demography analyses. However, tagged fish recorded during this operation were opportunistically used for growth rate calculations (Tab. 1).

2.4 Data analysis

Annual growth rates were based upon a fish individual's increase in length between June 2009 and its most recent capture, divided by the duration of the time interval between capture in days. The resulting values for daily growth rate (mm day^{-1}) were then multiplied by 365 to calculate annual (mm year^{-1}) growth rates. For fish not captured in June 2009, calculations of annual growth rates were based upon their original length in February or March 2009 and their most recent capture. Growth increments for a spring period (the approximate three-month period between the initial two sampling events in February or March 2009 and in June 2009) were also calculated, where recaptures allowed.

Several tagged fish had ascended the small weir separating the upstream and downstream reaches. Consequently, the data were separated into three classes: individuals tagged and subsequently always recaptured in the restoration reach (sedentary group 1); individuals tagged and always recaptured in the control reach (sedentary group 2); and individuals captured at least once in each reach (mobile group). Growth rates of all individuals recaptured prior to major restoration work were included when describing mean annual and spring growth rates in the Glaven, but for comparison between reaches, growth rates of all individuals that were captured consecutively in the same reach at least twice were considered.

Changes in European eel density (per 100 m^2), length and weight over time were assessed only at the control reach using linear models given potential effects of restoration on observed trends at the restoration reach, with Time period (1–7; see Tab. 1) used as a continuous explanatory variable (Objective 1). Length and weight were log-transformed prior to being fitted as response variables to comply with the linear regression assumptions of normality and homoscedasticity of model residuals. ANOVA was used to compare annual and spring growth rates of individuals between the restoration and control reaches. Annual growth rates were also compared between mobile and sedentary individuals as well as VIE-tagged and PIT-tagged individuals using ANOVA to see if there were any differences in growth between different groups.

Impact of restoration on European eel density (per 100 m^2), length and weight were assessed using a BACI design, with one sampling event pre-restoration, two post-embankment removal, and four following re-meandering (Objective 2). Due to the lack of tagged fish captured at least twice following the re-naturation ($n = 3$ over both reaches: Table 1), it was not possible to assess impact of restoration on eel growth rates. In the BACI design, a statistically significant effect is identified if a change in any of the response variables is detected at the restoration reach following intervention relative to the control reach (Schwarz, 2014), so that the parameter of interest is the Reach × Treatment period interaction. Given small sample sizes and lack of replicates, a randomization approach was used to test for impact of restoration on European eel density. Abundance data were bootstrapped from the normal distribution using mean and standard deviation values from the Carle and Strub model, within the stratification Reach, Treatment and Time period (10,000 iterations). These bootstrapped values were then transformed into densities and averaged per Treatment and Reach. Differences between the restoration and control reaches was calculated for each Treatment, and resulting boxplots were compared for overlap to determine if there was any statistically significant difference ($\alpha = 0.05$)

between different treatments. To test for impact of restoration on European eel length and weight, linear models were fitted, with log-transformed eel length and weight used as response variables and Reach (restoration vs control reach), Treatment (pre-restoration vs post-embankment removal vs post-re-meandering) and their interaction used as fixed effects.

Linear models were fitted using package *lme4* (Bates *et al.*, 2015) of R and evaluated by an *F*-test with the *Anova* function in the *car* package (Fox and Weisberg, 2011). When testing for effect of Time period, as well as restoration (Reach × Treatment) on European eel length and weight, fish ID was not fitted as a random effect on the intercept given the small overall proportion of tagged and recaptured eel individuals (Tab. 1) and thus any effect of autocorrelation was considered negligible. Marginal effect plots were constructed in R package *ggplot2* (Wickham, 2009). Model residuals were tested against the assumptions of normality, homogeneity, and independence using standard graphical validations (Figs. S2–S6; Zuur *et al.*, 2009).

3 Results

The density of European eel showed a pronounced decrease between 2009 and 2014 in the control reach ($F_{1,5} = 44.31$, $P < 0.05$), with mean density decreasing by 1.5 individuals 100 m^{-2} (Fig. 2). The size structure of the population in the control reach also changed, with both the length ($F_{1,152} = 11.65$, $P < 0.05$) and weight of individual fish ($F_{1,152} = 16.46$, $P < 0.05$) showing increases of 11.5 mm $year^{-1}$ and 6.2 g $year^{-1}$, on average, respectively between 2009 and 2014 (Fig. 2).

Of the 59 recaptured individuals, the majority (73%) showed high site fidelity and were classified as sedentary, with some individuals being captured at the same reach three to four times during the study period. Sixteen individuals were observed to move from one reach to another and were thus classified as mobile. Most of these mobile individuals (75%) moved upstream. Two mobile individuals undertook multiple trips over the weir from one reach to another and back to the initial reach.

Spring and annual growth rates of all individuals recaptured prior to restoration ranged from −5 to 36 mm $year^{-1}$ (mean ± SE = 7.2 ± 2.0 mm $year^{-1}$) and −5 to 104 mm $year^{-1}$ (mean ± SE = 35.8 ± 2.5 mm $year^{-1}$), respectively. One individual exhibited a negative annual growth rate, three individuals had negative spring growth rates, and three individuals did not grow over the spring period. When comparing all VIE-tagged and PIT-tagged individuals, no difference was found in annual growth rates ($F_{1,55} = 2.98$, $P = 0.09$). Similarly, mobile (mean ± SE = 34.9 ± 3.8 mm $year^{-1}$) and sedentary individuals (mean ± SE = 34.1 ± 2.3 mm $year^{-1}$) exhibited similar growth rates ($F_{1,55} = 0.47$, $P = 0.50$). Mean annual growth of sedentary eels was 35% greater in individuals residing at the restoration reach (37.56 ± 3.00 mm $year^{-1}$) than at the control reach (27.90 ± 3.68 mm $year^{-1}$), albeit marginally not statistically significant ($F_{1,33} = 3.60$, $P = 0.06$; Fig. 3). There was no difference in the spring growth rate of eels between the two reaches ($F_{1,24} = 0.48$, $P > 0.05$; Fig. 3). Both spring and annual growth rates of individuals at either reach varied widely, and several individuals resident in the restoration reach increased in length by over 30 mm between March and June 2009, while others showed very little or no change in length over the same period.

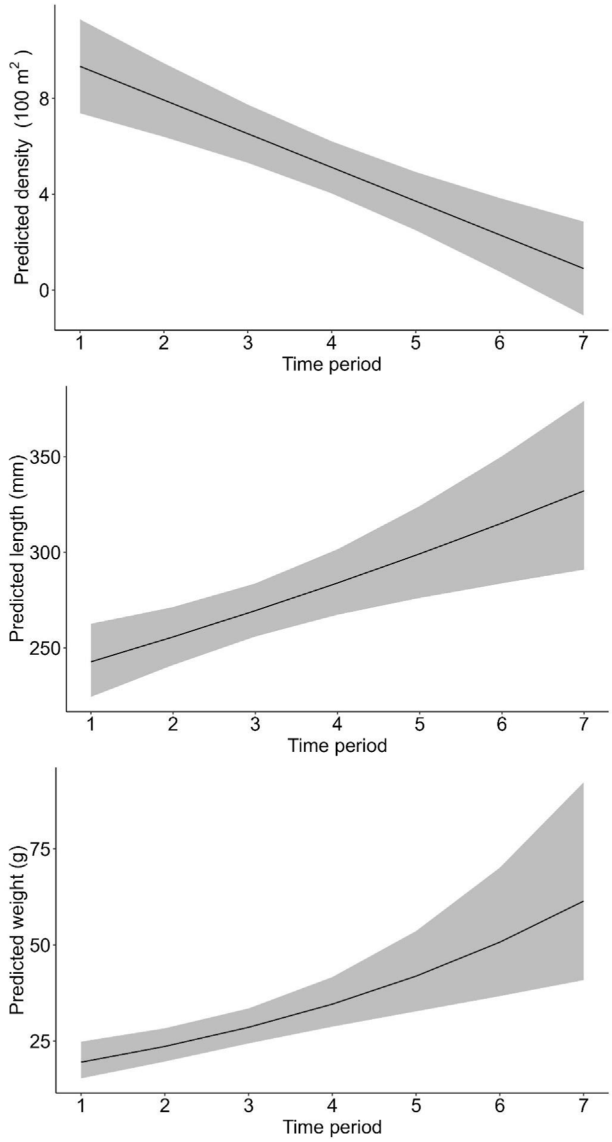

Fig. 2. Marginal effects from linear models showing significant changes in density, length, and weight of European eel *Anguilla anguilla* during the study period in the control reach. Error bars represent 95% confidence intervals of the estimated effects.

There was no difference in European eel density between the control and restoration reaches post-embankment removal, but density had slightly increased in the restoration reach compared to the control reach following re-meandering, although was not statistically significant when compared to the pre-restoration phase (Fig. 4). Habitat improvement also had no effect on European eel length or weight as indicated by a lack of significant BACI interaction term, *i.e.* Reach × Treatment (Tab. 2; Figs 5 and 6).

4 Discussion

Habitat improvement measures have been identified as important to European eel conservation in many catchments

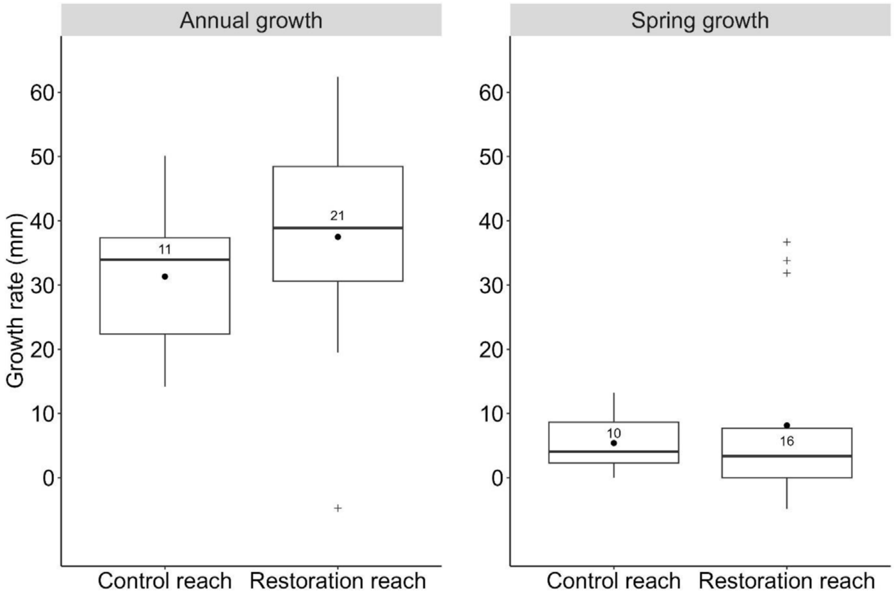

Fig. 3. Spring growth (March–June 2009) and annual growth rate of two populations of European eel resident in the two adjacent reaches of the Hunworth restoration reach, calculated using length data of tagged and recaptured individuals between 2009 and 2012. Boxes represent all values between the 25th and 75th quartiles and show the median (—) and mean (•) for each category. Box plot whiskers represent minimum and maximum calculated growth increments for each population. Outliers (+) are also shown. *n* = number of individuals from which growth rate was calculated.

under regional EMPs (Couldrick *et al.*, 2011). Despite this, our study is one of the first to assess the local effects of a typical river restoration initiative on the European eel population in detail (see Champkin *et al.*, 2018).

The European eel population in the control reach of the River Glaven declined over the study period, with a concurrent increase in the length and weight of individuals. This likely relates to more general trends in European eel escapement and recruitment over the study period. Specifically, decreasing European eel density in the River Glaven can be linked to the overall decline in recruitment observed across the species' distribution range. A northward shift in the position of the Gulf Stream was associated with reductions in elver catches in most European catchments throughout the 1980s and early 1990s (White and Knights, 1994). Therefore, climate change-induced oceanographic changes with consequent shortages of available food resources (Bonhommeau *et al.*, 2008) may have decreased recruitment of European eel larvae to the East Anglian coast (Chang *et al.*, 2019) and hence the River Glaven. At a local river scale, barriers to upstream migration can represent one of the main factors determining the demography and density of European eel populations (White and Knights, 1997). Very few man-made barriers in British rivers are completely impassable by the European eel, and consequently the proportion of freshwater habitat rendered inaccessible by such structures (<5%) is much less than in other European countries where hydropower stations and large dams prevail (Moriarty and Dekker, 1997). Nevertheless, river flows for most lowland British rivers are interrupted by numerous mills, weirs, sluices and tidal gates, which can prevent the complete colonization of habitats by European eel (Moriarty and Dekker, 1997; Lasne and Laffaille, 2008).

European eels tend to migrate progressively further upstream throughout their development, such that their mean age and size are generally greater in upper catchment areas, while abundance is accordingly lower (Feunteun *et al.*, 2003; Couldrick *et al.*, 2011). Evidence from recaptured individuals in this study suggests that many eels lead a relatively sedentary lifestyle and show high site fidelity in the River Glaven prior to maturation, with some individuals being recaptured in the same short reach up to three years after initially being tagged. Other tagging and telemetry studies that have tracked movements in the freshwater stage of catadromous Anguillidae species in small streams and marsh ecosystems have demonstrated similar behaviour (Baras *et al.*, 1998; Laffaille *et al.*, 2005; Ovidio *et al.*, 2013). Many tagged individuals recaptured in this study exceeded 350 mm at which size a proportion of an eel population (*i.e.* males) is known to mature and begin seaward migration (Tesch, 2003). This suggests that eels could have vacated the river system over the survey period, but did not.

The growth rates of yellow-stage European eels are typically highly variable between individuals and among different water bodies (Moriarty, 2003), being dependent on factors such as habitat characteristics, water temperature, population density and food availability (Tesch, 2003). This concurs with the present findings in which calculated annual growth rates varied extensively between individuals. Nevertheless, the mean annual growth rate of 36 mm year^{-1} was consistent with values calculated for European eel populations in other British river systems: *e.g.* 38 mm year^{-1} in the upper River Thames (Naismith and Knights, 1993), 31 mm year^{-1} in the River Frome, southern England (Mann and Blackburn, 1991), 33 mm year^{-1} in the Barrow River, Northern Ireland (Moriarty, 1983), and 16–28 mm year^{-1} in the lower River Severn, western England (Aprahamian, 2000). Higher annual and spring growth rates were observed for European eels at the restoration reach, although this was not statistically significant.

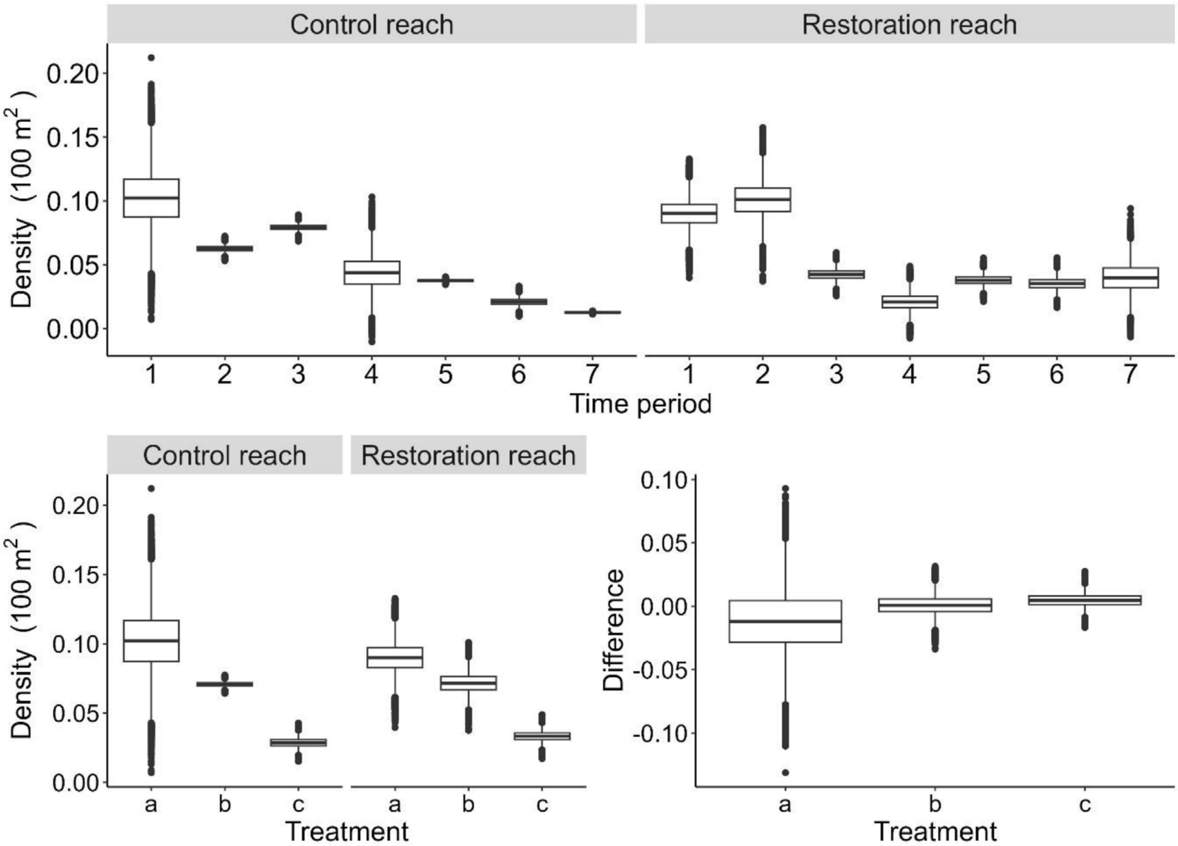

Fig. 4. Boxplots showing changes in density of European eel in the restoration and control reaches of the River Glaven during the study period following a randomization approach. Top plot: boxplot showing bootstrapped density values during pre-restoration (1), post-embankment removal (2–3) and post-re-meandering (4–7). Bottom left plot: boxplot showing averaged bootstrapped densities per Treatment and Reach, where a = pre-restoration, b = post-embankment removal, and c = post-re-meandering. Bottom right plot: boxplot showing difference in bootstrapped densities between restoration and control reach per Treatment. Dark black horizontal line represents 50% of the data, light black horizonal lines represent 25% and 75% of the data (Interquartile Range – IQR) and light black vertical lines minimun and maximum data values in comparison to IQR. Dark black dots represent outliers.

Table 2. Statistical results of ANOVA applied to linear model testing for changes in European eel length and weight in the two reaches of the River Glaven pre-restoration, post-embankment removal, and post-re-meandering (Treatment). * Denotes significant effect at $\alpha = 0.05$.

	Length		Weight	
	F	*P*	*F*	*P*
Reach	0.13	0.72	0.35	0.55
Treatment	20.1	<0.01*	28.2	<0.01*
Reach × Treatment	0.17	0.85	0.25	0.78

In this study, no significant response of the European eel population to habitat restoration was detected during the study period. This could suggest that increases in meso-habitat heterogeneity were not sufficient to initiate a change in the size structure or density of the European eel population, that other factors may be more important, or that the period monitored after the restoration measure was not sufficiently long (Didham *et al.*, 2020). Although European eels inhabit a great diversity of freshwater meso-habitats (Ovidio *et al.*, 2013), they are typically closely associated with cryptic areas comprising soft (silt) substrate, high aquatic macrophyte cover and crevices between boulders, roots or beneath undercut banks in which they seek refuge from predators and bright light (Ovidio *et al.*, 2013). Recently, in a study of European eel distribution and habitat preferences in Swedish coastal rivers and streams, it was concluded that restoration efforts aimed at enhancing European eel populations should focus on the lower reaches of larger rivers (where European eels are more abundant) with stony substrates (Degerman *et al.*, 2019). However, in the River Glaven itself, Harwood *et al.* (2022) did not find a strong positive relationship between European eel occurrence and coarse substrates, instead showing that presence of eels was

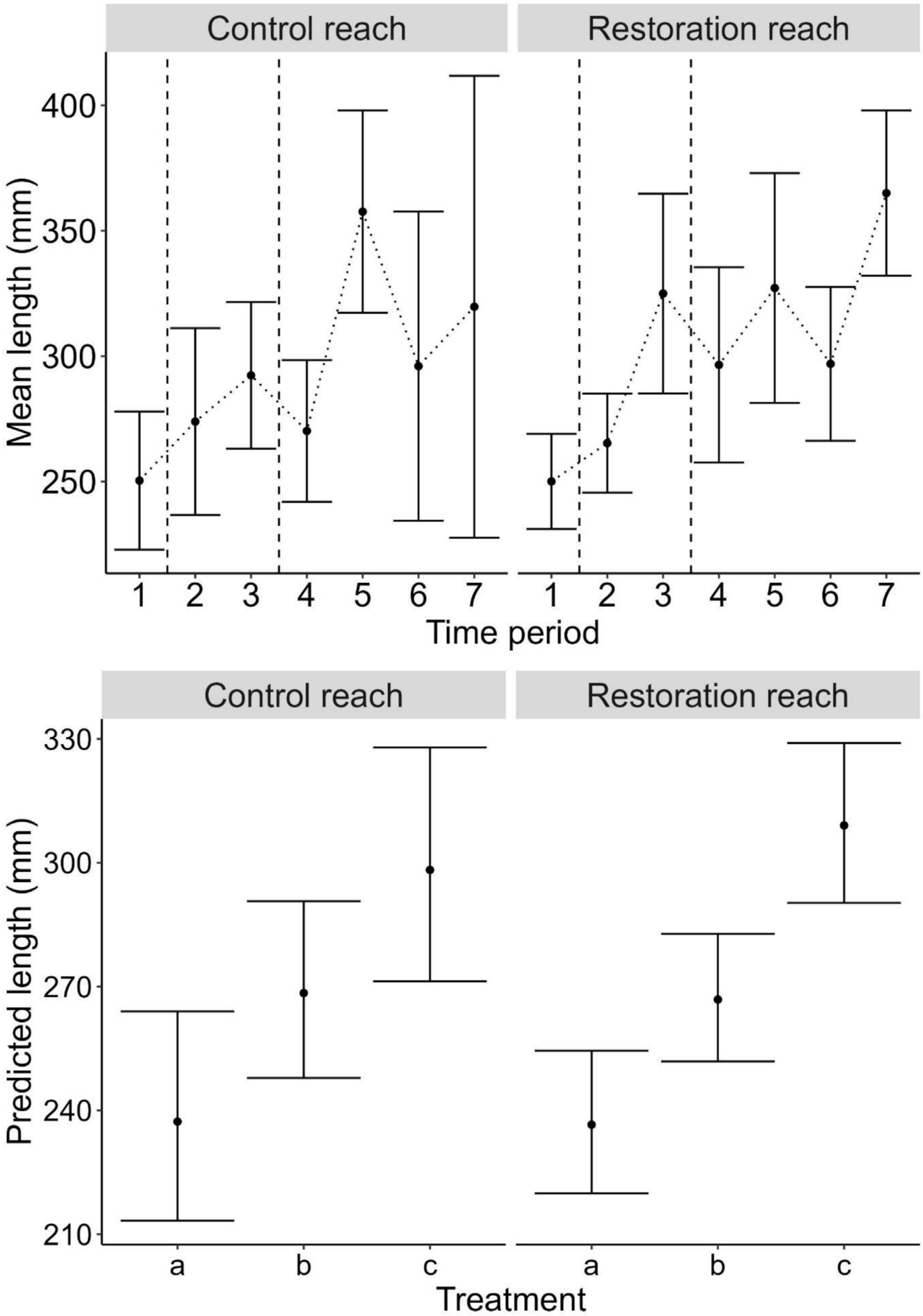

Fig. 5. Plots showing changes in the length of European eel in the restoration and control reaches of the River Glaven during the study period. Top plot: line plot showing mean length with 95% confidence intervals in restoration and control reaches during pre-restoration (1), post-embankment removal (2–3) and post-re-meandering (4–7). Emanating vertical dotted lines denote embankment removal and re-meandering. Bottom plot: marginal effects plot from the linear model showing no significant impact of interaction of Reach and Treatment on eel length, where a = pre-restoration, b = post-embankment removal, and c = post-re-meandering. The error bars represent 95% confidence intervals of the estimated effects.

significantly benefited by overhanging branches and in-stream large wood. This may be due to the vastly different bed structure of the Glaven compared to a typical rocky Swedish stream, where large boulders are present. Given the association between large wood habitat and European eel occurrence in the wider River Glaven catchment, it is possible that habitat modifications were not beneficial for European eel because they failed to provide suitable refuge habitat. Both before and after restoration, overhanging trees were rare and the restoration section entirely lacks tree root and in-stream large

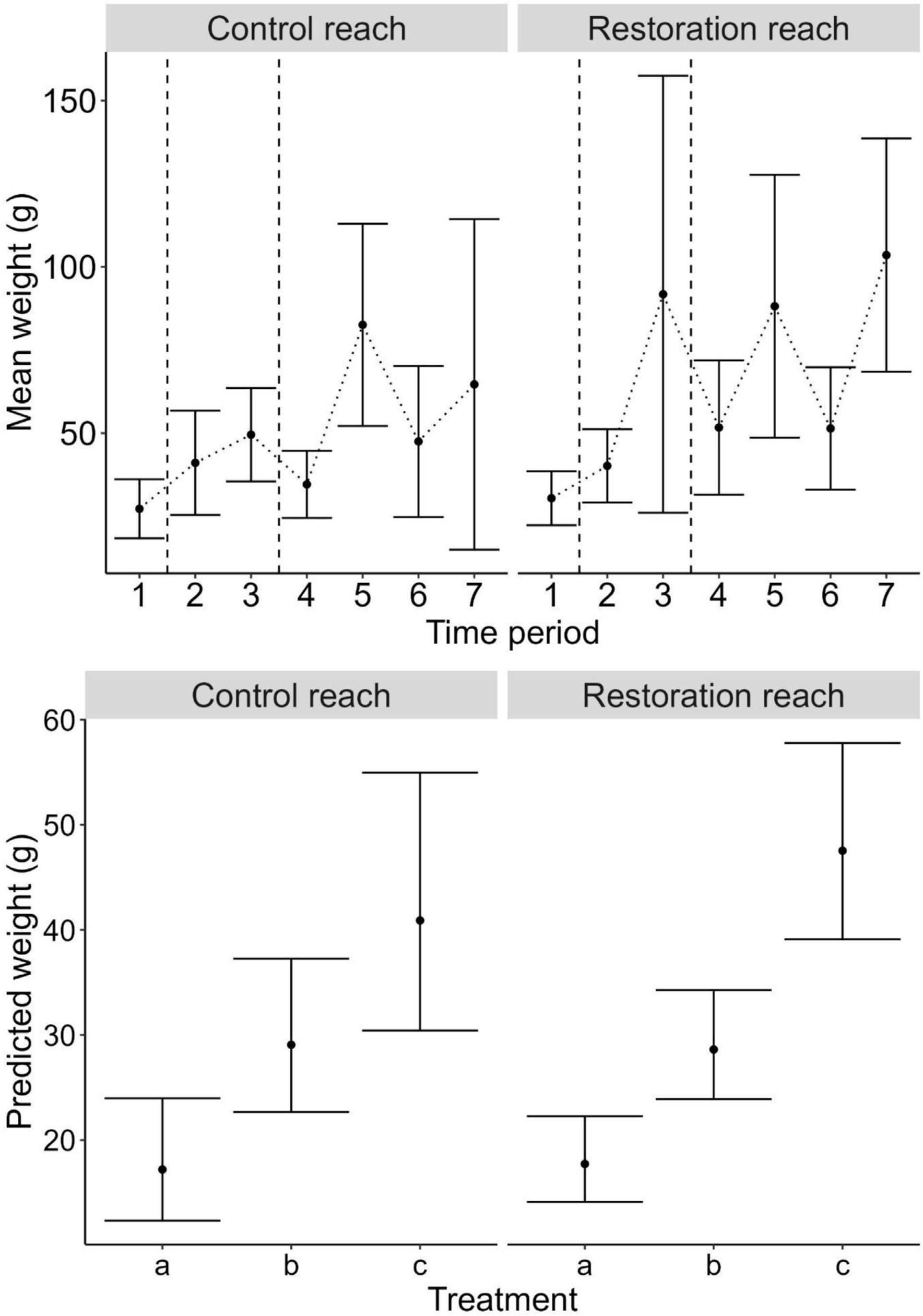

Fig. 6. Plots showing changes in the weight of European eel in the restoration and control reaches of the River Glaven during the study period. Top plot: line plot showing the mean weight with 95% confidence intervals in restoration and control reaches during pre-restoration (1), post-embankment removal (2–3) and post-re-meandering (4–7). Emanating vertical dotted lines denote embankment removal and re-meandering. Bottom plot: marginal effects plot from the linear model showing no significant impact of interaction of Reach and Treatment on eel weight, where a = pre-restoration, b = post-embankment removal, and c = post-re-meandering. The error bars represent 95% confidence intervals of the estimated effects.

wood habitat. In the context of Eurasian otter recovery in the catchment for which European eel is a key diet item (Almeida *et al.*, 2012), absence of sufficient predation-refuges in fallen trees and associated debris dams may be of critical importance.

As they grow, European eels demonstrate ontogenetic shifts in meso-habitat preference in fresh water (Laffaile *et al.*, 2003, 2004). Smaller individuals (<300 mm) typically inhabit shallower regions with a greater density of aquatic macrophytes and deeper silt substrate, whereas larger individuals are most commonly associated with slow-flowing, deeper water courses (Lafaille *et al.*, 2004; Couldrick *et al.*, 2011) that have less macrophyte cover (Lafaille *et al.*, 2003, 2004). These findings suggest that, to preserve and promote freshwater habitats for European eel, a heterogeneous patchwork of habitats must be maintained throughout a catchment. Thus, it cannot be concluded that the Hunworth restoration will not be beneficial for European eel when considered at the whole-catchment scale. In addition, the lack of significant changes in eel density and size structure could be an artefact of small sample size, lack of replicates and unbalanced design, which could have hampered the detection of positive effects on the eel population. Future studies are therefore required that incorporate an adequate experimental design to see if the patterns observed immediately following restoration are upheld in the longer term. This is especially pertinent given the return of trees to the banks of the restoration reach in the present day (C. Sayer, pers. obs).

5 Conclusion

Whilst river restoration initiatives can be beneficial to fish assemblages (Hohausová and Jurajda, 2005; Summers *et al.*, 2008; Lorenz *et al.*, 2013), many studies show that positive responses of fish populations to such approaches are not assured (*e.g.* Smith, 2013; Sinclair *et al.*, 2023). Previous studies recommend larger-scale rehabilitation efforts to boost fish density and diversity, advising a focus on catchment-scale improvements such as barrier removal and enhanced connectivity, and addressing water quality issues including eutrophication, sedimentation and pollution for ecosystem recovery (Champkin *et al.*, 2018). This includes small coastal streams, which may have an important, but overlooked, role in conservation strategies for European eel (Copp *et al.*, 2021). Given its small size, the River Glaven could be more important as a conduit for eel upstream and downstream passage, rather than as permanent habitat (Harwood *et al.*, 2022). Other studies have also concluded that the restoration and protection of wider wetland ecosystems, which are among the most important freshwater macro-habitats for European eels (Laffaille *et al.*, 2004), would be more beneficial than river restoration (Eybert *et al.*, 1998). In the River Glaven, it is known that outfall sluices from old artificial lakes act as considerable barriers for European eels, with substantial aggregations observed for elvers downstream of these structures (Harwood *et al.*, 2022). Thus, future eel conservation work might be best focused on addressing wider-scale river-to-lake European eel passage issues. Due to its complex life cycle, the European eel is threatened by different factors, from the global to the local scale, and these interactions make it difficult to assess the effectiveness of small-scale conservation projects (Bevacqua *et al.*, 2015). Reducing fishing pressure (Lyach, 2022), tackling the illegal trade in glass eels (Richards *et al.*, 2020) and implementing habitat restoration plans (as here), may not yield significant contributions to the restoration of fish stocks if they are not integrated into a cohesive management strategy (Ciccotti *et al.*, 2012). In this case of the Hunworth restoration reach, further investigation is required to establish whether European eel and other fishes will derive benefits from the river restoration initiative described herein over the longer term.

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Supplementary material

Fig. S1. Restoration reach of the River Glaven at Hunworth (north Norfolk, UK): (a) in January 2009, prior to the renaturation project; (b) after removal of embankments in March 2009; and (c) in December 2010, after recreation of meanders in August.

Fig. S2. Diagnostic plots suggesting that the assumptions of normally distributed, homoscedastic and independent residuals of linear model testing for effect of Time period on eel density at the control reach were not severely violated.

Fig. S3. Diagnostic plots suggesting that the assumptions of normally distributed, homoscedastic and independent residuals of linear model testing for effect of Time period on eel length at the control reach were not severely violated.

Fig. S4. Diagnostic plots suggesting that the assumptions of normally distributed, homoscedastic and independent residuals of linear model testing for effect of Time period on eel weight at the control reach were not severely violated.

Fig. S5. Diagnostic plots suggesting that the assumptions of normally distributed, homoscedastic and independent residuals of linear model testing for effect of interaction of Reach and Treatment on eel length were not severely violated.

Fig. S6. Diagnostic plots suggesting that the assumptions of normally distributed, homoscedastic and independent residuals of linear model testing for effect of interaction of Reach and Treatment on eel weight were not severely violated.

The Supplementary Material is available at https://www.kmae.org/10.1051/kmae/2024021/olm.

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