Refining monitoring practices and applying novel enhancement strategies to populations of threatened diadromous species

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Copyright statement

Abstract

Diadromous species are those which migrate between marine and freshwater environments. These can be sub-divided into anadromous (breed in freshwater but migrate to the sea to attain maturity, such as Atlantic salmon, *Salmo salar*) and catadromous species (breed in the sea but mature in freshwater, such as European eel, *Anguilla anguilla*). High socioeconomic importance has led to both species listed being subject to widespread and often large-scale commercial and recreational fisheries, with this driving extensive population monitoring and management. However, overexploitation and other anthropogenic impacts mean both species are threatened and/or declining throughout their range.

Population monitoring for salmonids generally consists of electrofishing surveys to determine juvenile abundance, where accurate population estimates are critical for conservation target-setting. However, the accuracy of some current population monitoring practices remains untested, with many studies also showing current management techniques to be unproductive, especially enhancing salmonid populations with hatchery reared fish. These two issues are addressed in this research.

To evaluate the accuracy of current population monitoring methods, a common population monitoring technique for juvenile salmonids, time-delineated single-pass electrofishing surveys, was tested against a more precise monitoring method (area-delineated single-pass electrofishing surveys), using Atlantic salmon as the focal species. Comparison of these two methods showed a high degree of density-dependent error in abundance estimates from time-delineated surveys. Further analysis showed that the area covered during time-delineated electrofishing surveys is highly variable, leading to

imprecision around abundance estimates. The application of time-delineated single-pass electrofishing was then reviewed by analysis of an electrofishing dataset with over 11,000 observations, used to monitor Atlantic salmon fry (age 0+) abundances. Currently these surveys are carried out over a three month summer sampling period. Linear models revealed this is leading to substantial under- or overestimation of salmonid abundances by not accounting for high mortality experienced by salmonid populations during this time, with model predictions showing a decline in fry numbers of 35 % across this sampling window.

With mounting scientific evidence showing salmonid stocking is ineffective at enhancing existing populations, alternative approaches are needed. This research tested the application of a novel management tool (intra-catchment translocation) on salmonids, using Atlantic salmon as the model species. Additionally, given the potential broader applicability of this management technique and need to conserve other diadromous species, this research also demonstrated the efficacy of a similar technique (inter-catchment translocation) on European eels. Using an existing dataset from a translocation experiment, the effectiveness of translocations in enabling critically endangered European eels to colonise headwater stream habitats was tested. Juvenile elvers were released into 13 streams in Wales under two treatments: (1) streams populated by brown trout (*Salmo trutta*), and; (2) brown trout-free streams. Electrofishing surveys conducted three months post-release showed that elvers successfully colonised all streams but that trout presence reduced eel recapture rates by approximately 70 % and predicted eel survival from 4 to 2 %, with this primarily related to the density of 2+ age class trout, most likely via predation.

To test the efficacy of intra-catchment translocations on Atlantic salmon, a series of large-scale field experiments were conducted across three years within the River Erriff catchment, Ireland. Atlantic salmon undergo a period of density-dependent mortality immediately following their larval emergence, leading to high mortality rates at sites with an abundance of spawning gravel. These experiments tested whether freshwater production of Atlantic salmon may be increased by removing surplus fry from such sites and releasing these fish into areas of lower fry density, hence reducing the level of density-dependent mortality. The methods employed for these experiments underwent significant refinements throughout the study period, with the results of the first two experiments considered together and the third experiment considered separately. During years 1 and 2, post-emergent fry densities were recorded through area-delineated single pass electrofishing surveys. Fish were then captured from high fry density sites, adipose fin clipped to enable identification, and released at low density sites. These two treatments were compared to high- and low density control sites where no salmon fry were removed or added. Electrofishing surveys were carried out at all sites in autumn to determine autumn fry densities, with habitat variables recorded and accounted for within analyses. Testing of the efficacy of the translocations revealed no significant effect on autumn fry densities at sites where fry were removed or released. However, as sites which received additional fry were relatively small (20 m instream length), the study design was highly vulnerable to the effects of fry dispersal, with electrofishing surveys of suitable habitats upstream and downstream of fry release sites confirming the presence of translocated fish.

Substantial refinements to the experimental design were made for year 3. To account for dispersal, fry were released at the centre of two larger stream reaches, approximately 500 m long, with approximately 1500 fry released per reach. These were compared against two stream reaches which received no salmon fry. Post-emergent fry densities were

recorded through electrofishing surveys at all high- and low density sites prior to translocations, with low density stream reaches split into individual sites based on habitat units (i.e. pools and riffles). Electrofishing surveys were conducted at all sites in September to determine the effect of translocations on the two treatments versus their controls, with habitat variables used to account for additional variation in fry densities. Testing revealed that removal of post-emergent fry from high density sites had no significant effect on autumn fry densities. Additionally, translocated fry densities were significantly and positively correlated with total density of autumn salmon fry. Translocated fry had a small negative impact on population depletion of native salmon, which was offset by the increase in fry densities from translocations. Moreover, translocated fry densities had no effect on native fry lengths in autumn. Thus, translocation shows promise as a management tool to increase freshwater production of Atlantic salmon.

Considered together, these findings highlight the need to refine current monitoring practices for salmonids and to further test novel management strategies on salmonids and other diadromous species, ensuring that viable management techniques are available to policy makers and fisheries managers, and can be applied based on robust abundance data.

Contents

Preface

This thesis is based on a combination of analysis of existing datasets and the experimental data of three field experiments conducted in the Republic of Ireland, which were the subjects of collaboration between Bournemouth University (BU) and Inland Fisheries Ireland (IFI). None of the text of the thesis is taken directly from previously published or collaborative articles. This work was supported by funding from IFI, and from the Fisheries Society of the British Isles.

The designs of the experiments reported in Chapters 2, 5 and 6 were my own work, with assistance from my supervisory team. The experimental data reported in Chapters 2, 5 and 6 were collected by me, with the assistance of several IFI and BU staff. The analyses and text presented in the above chapters represent my original work.

The dataset used in Chapter 3 was collected by IFI, with the analysis presented in this thesis designed by myself, with the assistance of my supervisory team. The dataset used in Chapter 4 was initially collected by my supervisor, Kyle Young and Lewis Naisbett-Jones, who designed the methodology for the experiment. The analyses and text presented in Chapter 4 of this thesis represent my original work.

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Chapter 1: Introduction

1.1 Current status of diadromous species: population decline, anthropogenic impacts, and ineffective management

1.1.1 Impact of anthropogenic activities on diadromous species

In the current 'Anthropocene' epoch, anthropogenic activities represent the dominant factor in determining global environmental change, including the decline of most flora and fauna worldwide (Lewis and Maslin, 2015). Anthropogenic activities, such as carbon emissions, land use changes, species introductions, river impoundments and abstracting ground and surface water, all contribute to altering ecosystems and their functioning, leading to deleterious effects in the biota (Opdam and Wascher, 2004; Urban, 2015; Birk *et al.*, 2020; Orr *et al.*, 2020). These effects are clearly demonstrated in populations of diadromous fish species. These fishes, which migrate between the marine environment and freshwater as part of their life history strategy (Myers, 1951), have been heavily impacted by these anthropogenic activities, with population declines across their ranges (McDowall, 1999; McIntyre *et al.*, 2016; Verhelst *et al.*, 2021).

Diadromous fishes can be further sub-divided into two main groups. Anadromous species are those which reproduce in freshwater but migrate to the marine environment at some stage of their life, generally to take advantage of superior feeding opportunities (Allendorf and Utter, 1979; Quinn and Myers, 2004). A wide variety of species utilise this life history strategy, including a number of sturgeon species, some clupeids and several species of the family Salmonidae (primarily salmon, trout and char). Catadromous species employ a mirror image of this life history strategy, reproducing in the marine environment but migrating to freshwater at some stage of their life to feed (Allendorf and Utter, 1979), such as species of genus Anguilla, including the European (*Anguilla anguilla*) American (*A. rostrata*) and Japanese (*A. japonica*) eels.

1.1.2 Conservation issues for diadromous species

The life history strategies of diadromous species make them particularly vulnerable to a number of anthropogenic activities, with their movements between freshwater and marine habitats requiring high connectivity between these, leading to the phrase 'triple jeopardy' being applied to their plight (McIntyre *et al.*, 2016). Diadromous species might be especially vulnerable during critical periods of movement in their lifecycle, particularly their transition(s) between marine and freshwater environments (McIntyre *et al.*, 2016). Movement of these species to and from freshwater habitats is often inhibited and, in some cases, prevented by the ever-increasing number of anthropogenic obstructions, and particularly dams (McDowall, 1999; McIntyre *et al.*, 2016; Verhelst *et al.*, 2021). Of the world's large rivers (> 1000 km in length), only 23 % flow uninterrupted to the ocean (Grill *et al.*, 2019). Within Europe alone there are now at least 1.2 million barriers within river catchments, including dams, weirs, fords and other man-made structures (Belletti *et al.*, 2020). Globally, there are there are over 16 million dams, with more than 50,000 large dams exceeding 15 m high (Lehner *et al.,* 2011). Dams and other obstructions have been shown to severely reduce the connectivity of river catchments (Morita and Yamamoto, 2002; Poff and Hart, 2002; Santos *et al.,* 2006). Populations of sturgeon, clupeids, salmonids and anguillids have all been shown to be negatively impacted by such anthropogenic obstructions (Auer, 1996; Boubée *et al.*, 2001; Jonsson and Jonsson, 2004; Raabe and Hightower, 2014). Additionally, the installation of various structures to aid fish passage over these obstructions, commonly known as 'fish passes', has had mixed results, with many found to be ineffective (Jungwirth, Schmutz and Weiss, 1998; Travade *et al.*, 1998; Bunt, Castro-Santos and Haro, 2012). For example, a meta-analysis of studies into the efficiency of these structures for a range of fish species has revealed that, on average, only 42 % of upstream-migrating fish individuals, and 69 % of downstream migrating individuals, were able to successfully use these structures to clear obstructions (Noonan, Grant and Jackson, 2012). The efficiency of these structures for enabling movement of non-salmonid species specifically was even lower, at just 21 % of upstream-migrating individuals and 40 % of downstream migrating individuals respectively (Noonan, Grant and Jackson, 2012). Furthermore, even when considered successful in enabling migration, fish passage structures can still lead to migratory delay, and thus increased energy expenditure and potentially higher mortality (Caudill *et al.*, 2007; Nyqvist *et al.*, 2017).

In addition to physical obstructions, artificial structures and anthropogenic activities can also affect riverine flow regimes, with hydropower dams, reservoirs, water abstraction and other activities all serving to create regulated flow regimes, such as through reductions or increases in natural flow variability and/or decreased minimum flow levels, in addition to reducing substrate mobility (Strevens, 1999; Murchie *et al.*, 2008; Smolar-Žvanut and Mikoš, 2014; Peterson *et al.*, 2022). These impacts may in turn affect both freshwater and migratory phases of the lifecycles of diadromous species. For example, groundwater abstraction has been shown to reduce freshwater rearing habitat for juvenile salmonids by as much as 77% (Strevens, 1999), with such flow-related reductions in habitat potentially leading to increased juvenile mortality (Nislow and Armstrong, 2012). Additionally, migration patterns of many diadromous species are linked to flow levels (Fox, Hightower and Parauka, 2000; Acolas *et al.*, 2006; Cullen and McCarthy, 2006; Thorstad *et al.*, 2008), with artificial flow regimes shown to affect both the timing and success of such migrations (Verhelst, Baeyens, *et al.*, 2018; Vine *et al.*, 2019; Peterson *et al.*, 2022).

Furthermore, the relatively predictable inter-annual movements of these species and their congregation within specific habitats, such as estuaries, river mouths and rivers, during these migrations also leads to specific targeting of fish at these locations (McIntyre *et al.*, 2016), and may increase the risk of over-exploitation where commercial and/or recreational fisheries are not effectively managed. Indeed, it is estimated that global landings of diadromous fish species were in excess of 1.6 million metric tonnes in 2019, with the vast majority of this being either anadromous salmonid (≈ 996,000 tonnes) or clupeid (≈ 601,000 tonnes) species (FAO, 2021).

Diadromous species are also affected by more general anthropogenic activities, including introductions of alien species, habitat degradation, the release of pollutants into the environment and the activities that are driving contemporary climate change (Arthington *et al.*, 2016; Merg *et al.*, 2020; Nyboer *et al.*, 2021). Salmonids are particularly vulnerable to the effects of pollution as these species tend to require high water quality, as characterised by low pollutant loadings, high dissolved oxygen content and specific temperature ranges (Richter and Kolmes, 2005; Finn, 2007; Kroglund *et al.*, 2007; Woelfle-Erskine, Larsen and Carlson, 2017). Hence, they are often considered to act as indicator species for freshwater ecosystems (Lee *et al.*, 1998; Ainerua *et al.*, 2020). A number of European salmonid populations have also been severely affected by the spread of parasites associated with aquaculture, including the monogenean *Gyrodactylus salaris* and copepod *Lepeoptheirus salmonis*, with the former resulting in catastrophic decline of many populations of Atlantic salmon (*Salmo salar*) in Norway (Johnsen, 1978; Johnsen and Jensen, 1986; Shephard and Gargan, 2017; Mo, 2020). Meanwhile, populations of European and American eels have been severely impacted by the spread of the invasive nematode parasite *Anguillicola crassus* (Jacoby and Gollock, 2017; Pike, Crook and Gollock, 2020), where the introduction and spread of this parasite was directly facilitated by aquaculture activities (Fries, Williams and Johnson, 1996; Gollock *et al.*, 2004).

This broad range of anthropogenic impacts means populations of many diadromous species are in decline, with 40 diadromous species within the aforementioned families currently listed as near-threatened or higher by the IUCN as of November 2021, including the majority of sturgeon (93 %) and anguillid (63 %) species assessed. Although many salmonid species are not currently considered threatened, many have also experienced significant declines across their ranges (Irvine and Fukuwaka, 2011; Mills *et al.*, 2013; Almodóvar *et al.*, 2019). Within Europe, Council Directive 92/43/EEC (1992), commonly known as the Habitats directive, lists 15 salmonid species or sub-species under annex II, including Atlantic salmon. Under this legislation core areas of these species' habitat are protected by assignation as sites of community importance (SCIs) or special areas of conservation (SACs) within the Natura 2000 network. These sites must be managed in accordance with the ecological needs of the relevant species to prevent further decline and/or restore natural populations. Furthermore, Council Directive 2000/60/EC (2000), commonly known as the Water Framework Directive, necessitates the implementation of river basin management plans, which must include specific protections for water-dependent Natura 2000 sites, and thus Habitats Directive annex II species. Such management plans must additionally involve monitoring and management of diadromous fish species, with these used as indicators to assess overall ecological status, with the aim of ensuring all river basins reach 'good ecological status' and are not subject to further ecological deterioration.

These declines are of great concern given the high ecological importance of many of these species. As already noted, salmonids act as indicator species for ecosystem health (Lee *et al.*, 1998; Ainerua *et al.*, 2020). Additionally, Pacific salmon species (*Oncorhynchus spp.*) are often considered ecosystem engineers due to the nutrient enrichment from their migrations into freshwater and their subsequent post-spawning mortality (Janetski *et al.*, 2009). While comparable studies on Atlantic salmon are lacking, it is likely that larger populations of this species may perform a similar role, given post-spawning survival may be as low as 11% in some populations (Fleming, 1998). Furthermore, many of these species are also of substantial socioeconomic importance, including most salmonids and a number of anguillids. Approximately 1 million tonnes of Pacific salmon species were landed in 2019 (FAO, 2021), while the commercial landings from the US wild Pacific salmon fishery alone in 2020 were valued at $478 million USD (National Marine Fisheries Service, 2022). Recreational angling also represents a key socioeconomic contribution of many salmonid species. For example, globally it has been estimated that approximately 300,000 Atlantic salmon anglers fished for around 2 million total fishing days, to catch approximately 380,000 salmon in 2017 (Myrvold *et al.*, 2019). Within a single river catchment in the UK (River Spey, Scotland), the total value of recreational angling for atlantic salmon and anadromous brown trout (*Salmo trutta*) was estimated at £11.6 million GBP per annum in 2003, with these fisheries supporting 401 full-time employees and with each individual adult salmon caught contributing an estimated £970 GBP to local household incomes (Butler *et al.*, 2009).

1.1.3 Ineffective management of diadromous species

The socioeconomic importance of these species has, in some cases, lead to considerable conservation effort, with these often extending to fisheries restrictions, partial or complete removal of barriers to migration, installation of fish passes, supplemental stocking of hatchery-reared fish, and freshwater habitat restoration (McDowall, 1999; McIntyre *et al.*, 2016; Verhelst *et al.*, 2021). However, in many cases this has done little to halt the continued decline of these species (Arthington *et al.*, 2016; McIntyre *et al.*, 2016). As noted above, fish passes are often ineffective (Jungwirth, Schmutz and Weiss, 1998; Travade *et al.*, 1998; Bunt, Castro-Santos and Haro, 2012; Noonan, Grant and Jackson, 2012), and may still affect fish survival, even where passage is possible (Caudill *et al.*, 2007; Nyqvist *et al.*, 2017).

Given the extent of anthropogenic impacts on diadromous fish populations, population enhancement schemes that involve supplemental stocking of hatchery-reared fish appear to makes intuitive sense, yet there are numerous examples of the potential deleterious effects of this management practice (Araki *et al.*, 2007; Araki, Cooper and Blouin, 2009; Aas *et al.*, 2018). Indeed, captive breeding programmes have been shown by multiple studies to reduce the fitness of hatchery-reared anadromous fish under natural conditions (Reisenbichler and Rubin, 1999; Araki *et al.*, 2008; Kitada, 2019). In part, this likely results from the combination of relaxation of natural selection and imposed selection for traits which are beneficial under hatchery conditions but may have negative consequences in the wild (Araki *et al.*, 2008; Roberts, Taylor and Garcia de Leaniz, 2011; Stringwell *et al.*, 2014). Additionally, further genetic consequences of captive breeding, such as genetic diversity loss due to founder effects (Cross and King, 1983; Winkler, Bartley and Díaz, 1999; Vasemägi *et al.*, 2001), and inbreeding depression (Cross and King, 1983; Wang, Hard and Utter, 2002) may serve to further reduce fitness of hatchery-reared fish in the wild. These issues are particularly important where hatchery-reared fish interbreed with wild fish, and can result in reduced fitness of the wild population (Säisä, Koljonen and Tähtinen, 2003; Berejikian and Ford, 2004; Araki, Cooper and Blouin, 2009; Kostow, 2009). This has been demonstrated for Chinook salmon (*Oncorhynchus tshawytscha*), where hybrid offspring of mixed hatchery and wild parents have been shown to differ phenotypically from both parent groups after both a single (hatchery x wild) and second (hybrid x wild) generation (Wessel, Smoker and Joyce, 2006).

Stream habitat restoration techniques have shown promise in restoring fish populations in some studies (van Zyll De Jong, Cowx and Scruton, 1997; Hendry *et al.*, 2003; Floyd, MacInnis and Taylor, 2009). However, the results are equivocal, with other studies indicating these techniques often fail to meet their primary objectives (Stewart *et al.*, 2009; Jähnig *et al.*, 2011; van Zyll De Jong and Cowx, 2016). Additionally, the long-term effects of stream habitat restorations are poorly studied, with the limited studies available suggesting that the benefits accrued are often short-lived (van Zyll De Jong and Cowx, 2016). Most habitat restoration techniques will ultimately be ineffective if the root cause of habitat degradation is not addressed (Hendry *et al.*, 2003). Given the ever-increasing level of urbanisation (Pugh, 2014; Wan and Wang, 2014), and the intensification of agricultural practices (Garnett *et al.*, 2013), this is likely to become increasingly difficult.

1.2 Atlantic salmon and the European eel

The research in this thesis primarily focusses on the issues faced by one key diadromous species, Atlantic salmon, with a secondary focus on the European eel. However, the findings here also have much broader implications for the conservation of diadromous species generally, and species of the Salmonidae and Anguillidae specifically, given these species share very similar life history traits, population dynamics and anthropogenic threats to the model species used here.

1.2.1 Atlantic salmon

The Atlantic salmon is an iteroparous salmonid native to the temperature and arctic regions of the North Atlantic (Rochard and Elie, 1994; Kottelat and Freyhof, 2007; Webb *et al.*, 2007). Mature adult salmon breed within shallow, moderate to fast flowing, and well oxygenated riffle areas of rivers (Kottelat and Freyhof, 2007), with breeding generally occurring where suitable spawning gravels are present (generally 2 to 64 mm diameter; Louhi et al., 2008), and where eggs are deposited in depressions or ‘redds’ constructed by the female (Drummond, 1982; Webb *et al.*, 2007). Upon hatching from the eggs, early larval stages, known as alevins, remain within the gravels until the egg yolk sac is fully absorbed (Webb *et al.*, 2007). Following yolk absorption, these fish, now generally referred to as ‘fry’, emerge from the gravel (Fig. 1.1), and begin feeding exogenously (Webb *et al.*, 2007). These juveniles are generally referred to as fry until the end of their first calendar year, after which they are most commonly referred to as ‘parr’. These juveniles generally remain in freshwater for anywhere between 2 and 6 years before migrating to sea as ‘smolts’ (Fig. 1.1), with smolt age linked to growth rates which are influenced by water temperatures and food availability, and with older smoltification more common at higher latitudes (Metcalfe and Thorpe, 1990; Marschall *et al.*, 1998; Strothotte, Chaput and Rosenthal, 2005). Smolts undergo a number of physiological changes (including changes in colouration and osmoregulation) prior to and during the transition between freshwater and marine environments (Saunders and Schom, 1985; Rochard and Elie, 1994; Webb *et al.*, 2007). These fish generally remain in the marine environment for between 1 and 4 years, before returning to their natal river to spawn at the onset of maturity (Saunders and Schom, 1985; Rochard and Elie, 1994; Webb *et al.*, 2007), with the length of this marine stage denoted by the number of sea winters (SW; e.g. 1SW, 2SW), and where 1SW fish are often referred to as grilse and ≥ 2SW fish as multi sea-winter (MSW) fish. Migration into and within freshwater is triggered by a number of environmental cues, such as discharge and water temperature, with specific water levels aiding in freshwater passage, for example over obstructions such as waterfalls (Jonsson, 1991; Thorstad *et al.*, 2008). At the point of migration from the marine environment to freshwater adult salmon undergo further physiological changes, which are more pronounced in males than females, including colouration changes, and the development of a hooked jaw or 'kype' in males (Drummond, 1982; Webb *et al.*, 2007). Adults then typically spawn in late autumn and early winter, with the eggs hatching in the spring of the following year (Kottelat and Freyhof, 2007; Webb et al., 2007; Fig. 1.1). Adults are iteroparous and may spawn on multiple occasions, although most die post-spawning, with extremely high post-spawning mortality seen in males (Kottelat and Freyhof, 2007). It should also be noted that a proportion of male salmon may mature and breed as parr (i.e. prior to smoltification and migration to seas), with these responsible for as much as 60% of the total progeny (Saura *et al.*, 2008).

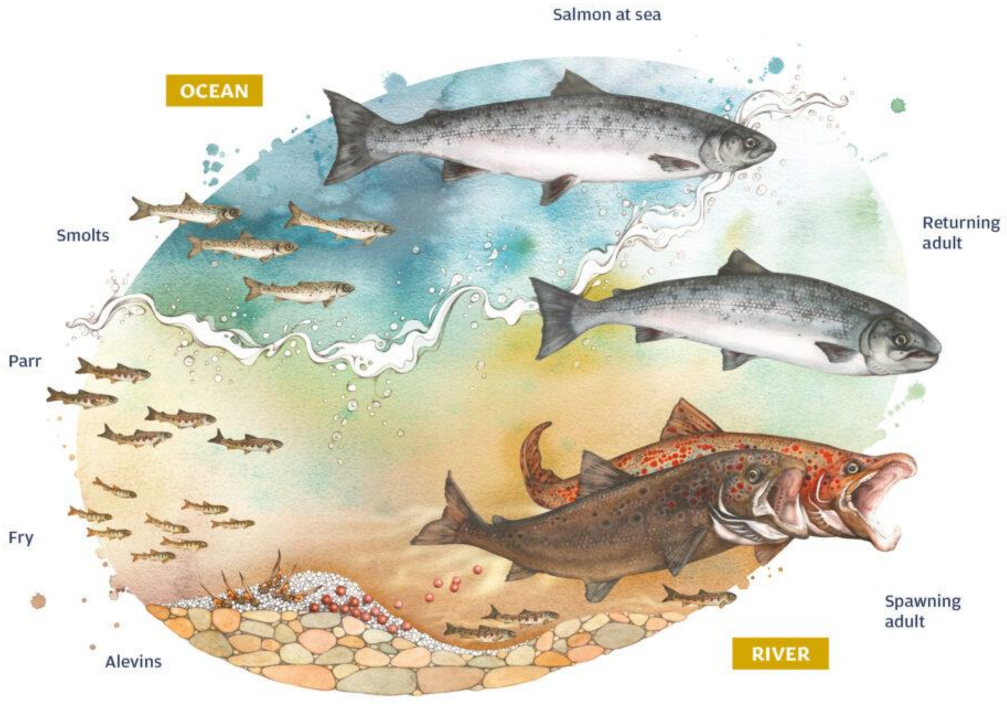

Figure 1.1: Life cycle of the Atlantic salmon, showing the different life-stages from eggs, through alevins, fry, parr, smolts, and marine, migratory and spawning adult life stages (NASCO, 2019)

Fisheries for Atlantic salmon have existed for millennia, with cave art in France indicating that these date back at least 25,000 years (Cleyet-Merle, 1987). Atlantic salmon is both currently, and has historically been, a key food fish species within countries bordering the northern Atlantic, with approximately 2,000 tonnes of wild salmon landed in 2019, and over 2.6 million tonnes produced from aquaculture, while wild salmon landings peaked at over 15,000 tonnes in 1974 (FAO, 2021). Additionally, this species represents a prized catch for recreational anglers, and is often referred to as the ‘king of fish’ (Walton, 1653; Montgomery, 2003). Given their high socioeconomic importance, populations of this species have been subject to conservation effort since before the advent of conservation biology, with ‘The Salmon Preservation Act’ within the Statute of

Westminster (1285) representing the first example of a close season for fisheries within the United Kingdom, and perhaps worldwide.

Given their socioeconomic importance, the decline of Atlantic salmon populations throughout most of the 1900s and 2000s has been subject to extensive research (Windsor and Hutchinson, 1994; Gibson, 2017; ICES, 2018), with major inter-government agencies, such as the North Atlantic Salmon Conservation Organisation (NASCO) set up to prevent further decline. This extensive research has identified a number of key issues with the sustainability of their populations, including over-exploitation, water pollution, parasites related to aquaculture, climate change, river regulation and barriers to migration (Parrish *et al.*, 1998; Costello, 2009; Mills *et al.*, 2013; Gibson, 2017). One of the key findings of these studies has been that conservation methods have largely been ineffectual, especially the supplementation of natural salmon populations with hatchery-reared individuals, commonly known as ‘stocking’, which has historically been one of the primary conservation techniques for this species (Aas *et al.*, 2018; Harrison, Hauer, *et al.*, 2019).

Stocking of hatchery reared salmon has been widely used as a conservation method to either halt declines in salmon stocks or to mitigate the damaging effects of river regulation schemes (Milner *et al.*, 2008). The driver for this has often been recreational angling, where hatchery reared fish are released to bolster the number of returning adults for angling exploitation (Aas *et al.*, 2018). However, extensive research has pointed to a number of significant issues with these stocking schemes that can minimise their effectiveness. Numerous studies have shown that the survival of hatchery reared fish in the wild is relatively low (Jonsson, Jonsson and Hansen, 2003; Araki *et al.*, 2008;

Thorstad *et al.*, 2011). These impacts likely arise from hatchery reared salmonids differing genetically from wild fish, even where first generation fry from wild broodstock are used (Araki, Cooper and Blouin, 2007; Christie *et al.*, 2012). This effect is exacerbated where fish are raised for several generations under hatchery conditions, due to adaptation to captivity (Araki, Cooper and Blouin, 2007; Kostow, 2009). The mechanisms behind this reduced fitness include the removal of normal mate selection under hatchery conditions, and the artificial selection for traits which are beneficial in hatcheries but may have negative consequences in the wild, such as increased boldness and reduced predator response (Araki *et al.*, 2008; Roberts, Taylor and Garcia de Leaniz, 2011; Stringwell *et al.*, 2014). Consequently, the number of returning adults produced from these hatcheries relative to the level of investment can be low (Jonsson, Jonsson and Hansen, 2003; Araki *et al.*, 2008). Where interbreeding of hatchery and wild fish occurs, this might also have detrimental impacts on the fitness of wild salmonid populations (Säisä, Koljonen and Tähtinen, 2003; Berejikian and Ford, 2004; Araki, Cooper and Blouin, 2009; Kostow, 2009). Thus, while hatchery stocking may provide an increase of salmon abundances, the cost benefit ratio is highly skewed and the long-term effects on wild populations, in terms of genetic diversity and fitness, may be negative (Aas *et al.*, 2018; Harrison, Hauer, *et al.*, 2019).

As a consequence of the negative impacts of hatchery reared salmon, there has been an increasing shift towards the decommissioning of hatcheries (Harrison, Rybråten and Aas, 2018; Harrison, Hauer, *et al.*, 2019; Harrison, Kochalski, *et al.*, 2019). However, while this shift avoids the potential negative consequences of this conservation method, it potentially means that the continued decline of many Atlantic salmon populations is not being addressed. Additionally, salmon populations in many rivers are composed mainly or entirely of hatchery-reared fish or their offspring, and thus their continued existence may be wholly reliant on this method (Granek *et al.*, 2008; Harrison *et al.*, 2018). Consequently, the phasing out of stocking programmes could be viewed as the loss of a flawed tool for the management of this species, rather than any significant progress in ensuring sustainability of salmon populations. Thus, there is a salient need to consider alternative enhancement methods that are based on sound science and promote population sustainability.

It is thus concerning that this shift away from stocking of hatchery-reared fish has not been accompanied by any substantial developments in terms of new conservation methods to replace stocking. Alternative established conservation strategies, such as habitat improvement schemes and the imposition of stricter regulations on commercial and/or recreational fishing, are now increasingly becoming the preferred method of conservation for this species (Harrison, Rybråten and Aas, 2018; Harrison, Hauer, *et al.*, 2019; Harrison, Kochalski, *et al.*, 2019). However, there is evidence to suggest that the impact of these may be limited. No kill, or 'catch-and-release', policies have become an increasingly common conservation technique designed to preserve the socioeconomic benefits of recreational fisheries for this species, while reducing or eliminating negative population impacts. However, the theroetical conservation benefit of these may be limited by post-release mortality, particularly where fish handling is not according to best-practice guidelines, or during periods of higher water temperatures (Lennox *et al.*, 2017; Van Leeuwen *et al.*, 2020). Furthermore, as noted previously, habitat improvements schemes have shown mixed results (Floyd, MacInnis and Taylor, 2009; Stewart *et al.*, 2009; Jähnig *et al.*, 2011; van Zyll De Jong and Cowx, 2016). The few long-term studies on these methods also indicate that the effects of some techniques may be temporary (van Zyll De Jong and Cowx, 2016), or limited by a failure to address the root cause of degradation (Hvidsten and Johnsen, 1992; Hendry *et al.*, 2003). These schemes often require cooperation from local landowners, such as voluntary cessation of detrimental agricultural practices or addition of livestock exclusion fencing (Hendry *et al.*, 2003). This is likely to become increasingly dificult, given the increasing prevalence of intensive agriculture practices (Garnett *et al.*, 2013), and current extent of urban areas, with Western Europe in particular representing one of the most urbanised regions worldwide (Liu *et al.*, 2020).

In addition to the above, both the removal of fish hatcheries and enforcement of alternative conservation measures, particularly catch-and-release fishing regulations, have created a socio-political problem. These measures are often contentious with some recreational anglers and riparian owners. Controversy amongst stakeholders has frequently surrounded the closure of salmon hatcheries (Harrison, Rybråten and Aas, 2018; Harrison, Hauer, *et al.*, 2019; Harrison, Kochalski, *et al.*, 2019). Furthermore, although qualitative data are limited, previous studies on other species have indicated that imposition of mandatory catch-and-release fishing regulations may be unpopular with some anglers and can lead to decreased angling participation in fisheries (Arlinghaus *et al.*, 2007), as demonstrated in fisheries for both Atlantic salmon and other salmonid species (Johnston *et al.*, 2011; Olaussen, 2016). Abundant anecdotal evidence provides further support for this, with angling magazines and forums littered with testimonials from anglers bemoaning the closure of salmonid hatcheries and imposition of ever stricter fishing regulations. These latter points are important, as these stakeholders are numerous (circa 300,000; Myrvold *et al.*, 2019), often vocal and politically active (Harrison *et al.*, 2018; Harrison, Kochalski, *et al.*, 2019), and fund conservation activities directly or indirectly, for example through angling licence sales, angling clubs, and fishing permit sales, the values of which are likely considerable (Pitcher and Hollingworth, 2008; Butler *et al.*, 2009; Liu, Bailey and Davidsen, 2019). In entirety, these issues indicate a salient need to explore novel conservation strategies for this species, through which alternative enhancement methods can be developed to more effectively sustain declining salmon populations, while allaying concerns of stakeholders over the perceived reduction in conservation effort.

1.2.2 The European eel

The current status of the European eel is more severe than for Atlantic salmon, with this species listed as critically endangered on the IUCN Red List since 2008 (Pike, Crook and Gollock, 2020), having experienced a decline of approximately 99 % in recruitment between the early 1960s and early 2000s (Dekker, 2003). As with many diadromous species, the causes for this decline are partially linked to this species' life history traits.

The European eel is a semelparous and facultatively catadromous anguillid species commonly found within marine, estuarine and freshwater environments of the Eastern North Atlantic, as far south as Mauritania and as far north as Iceland, the Scandinavian peninsula and Russia (Rochard and Elie, 1994; van Ginneken and Maes, 2005; Pike, Crook and Gollock, 2020). Mature adult eels spawn within the Sargasso sea in the Western Atlantic (van Ginneken and Maes, 2005), with the leptocephalan larvae carried by the gulf stream and North Atlantic drift to the coasts of Europe and north Africa over a period of approximately 7 to 11 months (Tesch, 1977; Rochard and Elie, 1994; Aarestrup *et al.*, 2009). Upon reaching the Eastern North Atlantic the eel larvae are known as 'glass eels' (Fig. 1.2). Many of these juveniles then migrate into freshwater habitats, at which point they are generally referred to as 'elvers', although some may remain in estuarine or coastal areas until maturity (Rochard and Elie, 1994; Moriarty and Dekker, 1997). This is then followed by a freshwater growth phase which may last between 5 and

20 years, during which time the juvenile eels are referred to as ‘yellow eels’ due to their yellowish-brown colouration (Miller *et al.*, 1986). Upon nearing maturity, European eels undergo a number of physiological changes, with their pigmentation changing to silver, hence the name ‘silver eels’, with a darker dorsal surface, and their eyes becoming enlarged (Miller *et al.*, 1986). At this point adult eels then migrate back to the Sargasso sea (≈ 5000-7000 km) to spawn, reaching sexual maturity during this migration (Aarestrup *et al.*, 2009; Miller *et al.*, 2019; Fig. 1.2).

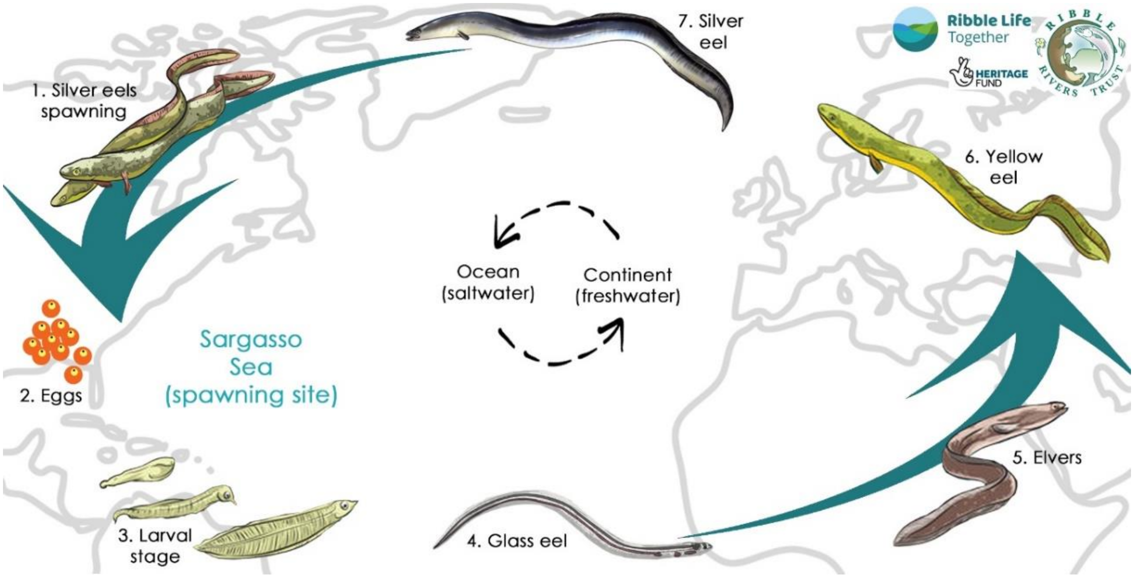

Figure 1.2: Life cycle of the European eel, showing the different life stages from eggs, through leptocephalan larvae, glass eels, elvers and yellow eels, to adults (Ribble Life Catchment Partnership, 2020)

As with Atlantic salmon, the decline of this species has been subject to extensive research, with this pointing to a combination of effects, including barriers to migration, over-exploitation, and the effect of the invasive parasite *A. crassus* (Feunteun, 2002; Kirk, 2003; Pike, Crook and Gollock, 2020). Habitat fragmentation has become a particular issue in many river systems, where anthropogenic obstructions render large river sections inaccessible to juvenile eels, thus reducing the available freshwater habitat for this species, as well as potentially causing escapement issues for migrating silver eels (Laffaille *et al.*, 2005; Acou *et al.*, 2008). In response to the severe and prolonged decline in eel numbers, European Union (EU) legislation was drawn up which established a target of 40 % escapement of silver (migratory adult) eel biomass relative to the best estimate of escapement without anthropogenic influences (European Commission, 2007). Under this legislation EU member states must draw up eel management plans outlining the conservation measures to be taken in order to achieve this target. Within the UK, 14 separate eel management plans have been formed, corresponding to the 14 river basin districts, while the UK and the Republic of Ireland (RoI) additionally share a transboundary eel management plan, known as the north west international eel management plan (CEFAS *et al.*, 2021). Conservation measures under these include restrictions on fisheries, such as landings quotas, closed seasons and fishing bans, stocking of glass eels, removal of barriers to upstream migration and installation of fish passes (CEFAS *et al.*, 2021)

Currently, European eel management plans also advise that 60 % of commercially caught juvenile eels must be released, with a proportion needing to be stocked into river catchments other than those from which they were caught (European Commission, 2007). This does not impact their populations genetically, given that they are generally considered as panmictic (Pujolar *et al.*, 2014). This is considered to represent an example of inter-catchment translocations, defined here as the capture of fish from one river catchment and their subsequent release within a different river catchment, or catchments. The fundamental rationale behind this method is similar to that for many translocations (often referred to as managed relocations, assisted colonisations, reintroductions, or any other term to which the movement of individual animals from one location to another is applied). Their general aim is to establish additional populations which lower the overall extinction risk for a given species (Griffith *et al.*, 1989; George *et al.*, 2009), re-establish extirpated populations (Seddon, 2010), or to facilitate species range shifts or colonisation of new habitats where habitat fragmentation is an issue (Seddon, 2010; Lawler and Olden, 2011).

The European eel management plan means that inter-catchment translocations are already occurring in many catchments throughout Europe, with juvenile glass eels or elvers collected from coastal areas or large river catchments (Shiao *et al.*, 2006; Matondo *et al.*, 2021). These are then stocked into other catchments, often to supplement natural recruitment, hence sustaining commercial fisheries (Rosell, Evans and Allen, 2005; Shiao *et al.*, 2006), to maintain or increase small or declining populations, or to re-establish populations following extirpation (Shiao *et al.*, 2006; Matondo *et al.*, 2021). The term ‘population’ is used loosely here, given European eel represent a single reproductive unit due to their panmixia. Within the UK, the great majority of eel stocking occurs into the Lough Neagh and River Bann catchment, with approximately 4.5 metric tonnes of glass eels stocked into this catchment between 2017 and 2020 (CEFAS *et al.*, 2021). Studies into this method indicate that it has some merit in providing some sustainability to local populations (Rosell, Evans and Allen, 2005; Shiao *et al.*, 2006; Psuty and Draganik, 2008; Matondo *et al.*, 2021). However, despite the potential benefit of such inter-catchment translocations, and the recommendation within EU legislation to carry these out on a large-scale, the number of such assessment studies is severely limited, and there is currently little information available on the criteria for success relating to this technique.

1.3 Novel population enhancement tools for conservation

The increasing use of translocation as a management tool to support European eel populations means there is pressing need to further evaluate the effectiveness of inter-catchment translocations as a conservation strategy, especially as the findings will be highly relevant to the conservation of other anguillid species globally. It was also outlined in Section 1.2.1 that there is a pressing need for the development and testing of novel Atlantic salmon population enhancement tools in order to overcome the issues associated with hatchery rearing and release. Given that translocations have been a feature of eel conservation programmes for some time, albeit their effectiveness has some uncertainty (Section 1.2.2), then this potentially provides a novel management tool for Atlantic salmon. Although the overarching goals (supplementation of threatened or declining natural populations) and methods (translocations) would thus be the same for both species, the differences in their life history strategies means that the application of translocation would need to differ between them. In the case of Atlantic salmon, inter-catchment translocations would be ill-advised, given the genetic differences between salmon populations from separate river catchments (Nielsen, 1998; Garcia de Leaniz *et al.*, 2007). Indeed, the failure of many inter-catchment translocations for this species has been theorised to be a result of local adaptation (Garcia de Leaniz *et al.*, 2007), while genetic differentiation between wild and hatchery-reared fish is considered a primary reason for the poor survival of hatchery-reared fish in the wild (Jonsson, Jonsson and Hansen, 2003; Araki *et al.*, 2008; Thorstad *et al.*, 2011). Similarly, genetic introgression between wild and hatchery-reared salmon represents another serious issue with this method (Säisä, Koljonen and Tähtinen, 2003; Berejikian and Ford, 2004; Araki, Cooper and Blouin, 2009; Kostow, 2009). Thus, these points illustrate the counterproductivity in introducing genetically distinct individuals from a secondary population.

Correspondingly, to avoid the potential negative consequences of mixing salmon from different river catchments, it was considered here that their translocations should only be intra-catchment. Thus, intra-catchment translocations are defined here as the capture of fish from one or more areas within a single river catchment, and their subsequent release at a secondary location, or locations, within that same catchment. This method therefore avoids the introduction of genetically distinct individuals, and does not interfere with natural mate-selection or selective pressures on translocated fish, as with hatchery-rearing techniques.

The theoretical basis for the use of intra-catchment translocations as a management tool lies in the life history and population dynamics of Atlantic salmon. Atlantic salmon spawn in gravel areas within rivers, which may be unevenly distributed, resulting in patchy distribution of salmon eggs and, subsequently, fry (Webb *et al.*, 2001; Moir *et al.*, 2004; Armstrong, 2005; Finstad *et al.*, 2010; Foldvik, Finstad and Einum, 2010). As dispersal of these fry is limited during the first summer, large numbers of salmon fry are often concentrated near favourable spawning areas (Bujold *et al.*, 2004; Armstrong, 2005; Armstrong and Nislow, 2006; Foldvik, Finstad and Einum, 2010). This often results in extremely high density-dependent mortality in the initial weeks and months following fry emergence, a phenomenon which has been widely documented (Einum and Nislow, 2005; Einum, Sundt-Hansen and Nislow, 2006; Einum, Nislow, Mckelvey, *et al.*, 2008; Honkanen, Boylan, *et al.*, 2018). This has also been demonstrated quantitatively through studies determining salmon stock-recruitment relationships, which are often found to best fit dome-shaped curves, such as that described by the Ricker model (Schnute and Kronlund, 2002; Honkanen, Boylan, *et al.*, 2018), or flat-topped curves (Buck and Hay, 1984; Jonsson, Jonsson and Hansen, 1998b; Fig. 1.3). This period is thus often considered to represent a population bottleneck for this species, with mortality during later life stages considered to be mainly density-independent (Jonsson and Jonsson, 2004; Armstrong, 2005; Einum, Sundt-Hansen and Nislow, 2006).

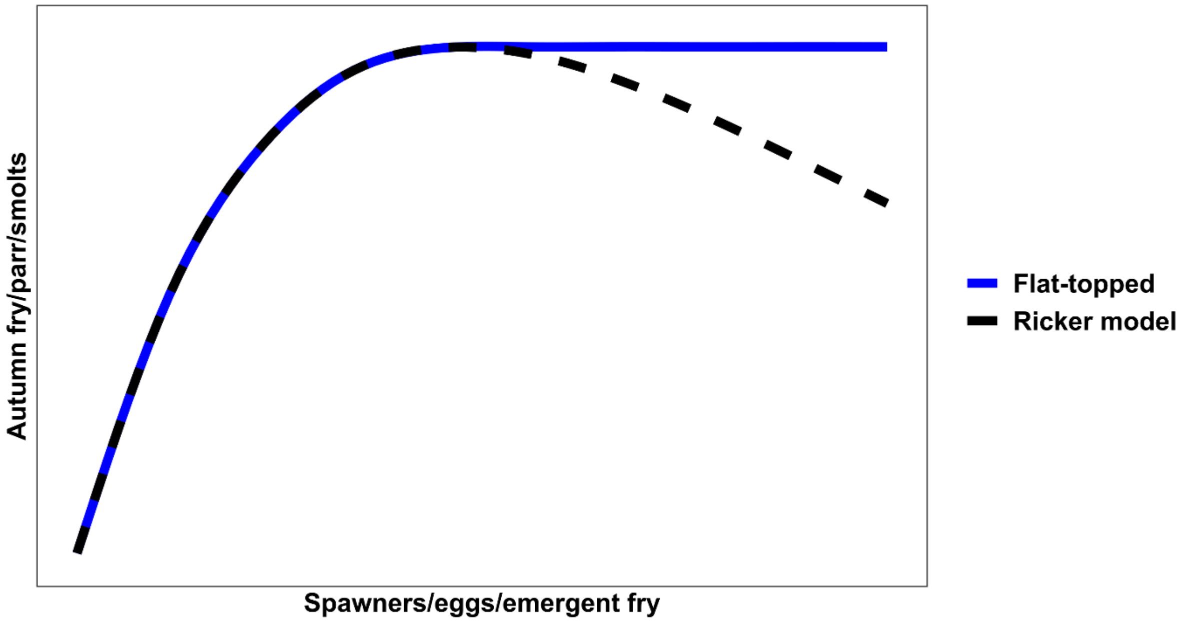

Figure 1.3: Hypothetical stock recruitment curves for Atlantic salmon, corresponding to either the Ricker model (Schnute and Kronlund, 2002; Honkanen, Boylan, *et al.*, 2018), or a flat-topped curve (Buck and Hay, 1984; Jonsson, Jonsson and Hansen, 1998b).

Correspondingly, a novel way in which the freshwater production of Atlantic salmon could be increased is by increasing fry survival by working with this density-dependence (Fig. 1.3). Where sites have high larval production, theory suggests their density-dependent mortality will be relatively high, whereas lower fry densities would be expected to result in reduced mortality rates. Hence, a small reduction in initially high fry numbers should theoretically not negatively impact recruitment to the smolt stage due to this ‘doomed surplus’. Reducing the number of fry at the beginning of the post-emergence period would reduce the effects of density-dependence on fry mortality in high density areas (so releasing the density-dependent pressure), and subsequently releasing these surplus fish into areas of the same catchment of lower fry density (i.e. areas with suitable fry habitat but poor spawning habitat). Provided these recipient sites have sufficient fry and parr habitat, then it would be expected that translocation into these sites would enhance smolt production which, in turn, should theoretically increase the number of returning adults (Jonsson and Jonsson, 2004; Armstrong, 2005). Furthermore, given that a stage of high density-dependent mortality is considered to be a shared trait of many salmonid species (Biro, Post and Parkinson, 2003; Johnston and Post, 2009; Grossman and Simon, 2020), then testing the efficacy of larval translocations could have benefits for multiple species.

1.4 Evaluating population monitoring techniques for salmonids

Population data form the fundamental basis upon which conservation techniques are applied (Radinger *et al.*, 2019). This is particularly relevant given the declining status of populations of Atlantic salmon and many other salmonids, and thus the need for effective application of management practices (Reisenbichler, 1997; Parrish *et al.*, 1998). Hence, there is a critical need to ensure that these data are accurate to avoid mismanagement of conservation efforts. Salmonids represent one of the most extensively monitored fish taxa, with numerous techniques used to determine abundances of salmonids at various life-stages. These include, but are not limited to, redd counts at spawning areas, trapping of juvenile smolts during their migration to sea, trapping of adults upon their return to freshwater, and electric fishing (‘electrofishing’ hereafter) surveys of the juvenile freshwater life stages. (Volkhardt *et al.*, 1964; Bohlin *et al.*, 1989; Jonsson, Jonsson and Hansen, 1990; Gallagher, Hahn and Johnson, 2007). The high sampling effort of redd counts (Gallagher, Hahn and Johnson, 2007), and the need for large and expensive fish traps to sample smolts and upstream-migrating adults, have likely contributed to the relative popularity of summer fry electrofishing surveys among many government agencies around the world.

Electrofishing surveys targeted at salmonids typically involve one of three methods: area-delineated multiple pass electrofishing, area-delineated single pass electrofishing, and timed, or ‘time-delineated’, single pass electrofishing. Area-delineated multiple pass electrofishing involves performing multiple upstream electrofishing passes within a defined river area, with upstream and downstream stop nets generally used to prevent movement of fish outside of the specified area (Peterson, Thurow and Guzevich, 2004). As the name suggests, both single pass methods involve a single upstream pass, usually without stop nets, with these differentiated by whether this pass covers a set area (area-delineated: Arnason, Antonsson and Einarsson, 2005; Matson *et al.*, 2018), or is conducted within a set time period (time-delineated; Crozier and Kennedy, 1994).

The primary aim of all the above methods is to obtain robust abundance data on both spatial and temporal scales, i.e. between river catchments and within catchments between years (Cowx and Fraser, 2003; Radinger *et al.*, 2019). These data provide the framework for management action, for example where rivers do not meet their conservation limits for salmonid abundance (Cowx and Fraser, 2003). Thus, the accuracy of these data is of paramount importance to the conservation outcomes for many salmonid populations and species. It is therefore concerning to note that, of the above methods, time-delineated single pass electrofishing remains relatively untested, both in terms of its fundamental accuracy and current application. Currently, the only independent (i.e. not authored by the original proponents of this method) published study evaluating this method, in terms of abundance estimation for salmonids, has indicated that it may lead to high density-dependent and species-dependent errors in abundance estimates (Honkanen, Dodd, *et al.*, 2018). These result from fish handling time at higher fish densities affecting the time spent fishing, with these also likely to differ between species (Honkanen, Dodd, *et al.*, 2018).

For the monitoring for Atlantic salmon, time-delineated surveys, as well as both area-delineated methods, are generally completed over an approximately three-month summer sampling period (e.g. July-September). This is generally to ensure that salmon fry emergence has been completed prior to the commencement of electrofishing surveys (Gargan *et al.*, 2008). Additionally, the cessation of these surveys at or around the end of September avoids disturbance of spawning salmonids, as well as avoiding the main periods of inclement weather and poor river conditions for sampling (Gargan *et al.*, 2008), while the broad three month sampling period allows a large number of surveys to be completed using the time-delineated method. It is generally the case that the specific date on which a particular survey is recorded is not accounted for in the abundance estimates, with surveys considered comparable across this sampling period. However, the population dynamics of Atlantic salmon indicate that this may lead to further error in abundance estimates due to density-dependent losses (Nislow, Einum and Folt, 2004; Armstrong, 2005; Einum and Nislow, 2005). Furthermore, this pattern is also seen in many other salmonid species (Biro, Post and Parkinson, 2003; Johnston and Post, 2009; Grossman and Simon, 2020). Thus, by failing to account for the date on which the electrofishing survey was conducted, and so not accounting for this mortality, current practices may be leading to substantial errors in estimates of salmonid fry abundances. Consequently, there remains considerable uncertainty on the reliability of these time-delineated surveys completed over such extended sampling seasons.

1.5 Research aims and objectives

When considered as a whole, the overarching aim of this research was to use empirical field experiments and analyses of existing datasets to improve the conservation practices of Atlantic salmon and European eel, with the ultimate goal of applying these improvements to the conservation of salmonids and anguillids globally. This can be broken down further into four main objectives (O) that were designed to:

O1. Ground-truth the fundamental precision of time-delineated single pass electrofishing for estimating the population abundances of Atlantic salmon (and other salmonid species);

O2. Test the current application of time-delineated electrofishing, with respect to current survey timing and the density-dependent mortality concept;

O3. Further empirically test the efficacy of inter-catchment translocations for European eel within a field experiment;

O4. Develop and empirically test intra-catchment translocation as a novel population enhancement tool for Atlantic salmon, and;

O5. Refine the application of intra-catchment translocations in order to develop these as a practical and useful conservation method.

Data collected in conjunction with a series of large-scale field experiments was used to fulfil O1, with the results of time-delineated surveys ground-truthed against a more robust method with relatively well-known accuracy (area-delineated single pass electrofishing). For O2, a large-scale existing dataset was used to develop a depletion curve for Atlantic salmon abundance estimates from time-delineated single pass electrofishing surveys. This then provided a correction factor for the results of these surveys, based upon the date on which any specific survey was conducted. O3 was addressed through analysis of an existing dataset involving the capture and movement of juvenile European eels from the River Severn, England, to release sites located in headwater streams in North Wales, as part of a replicated ecosystem-scale inter-catchment translocation experiment. For O4 and O5, the efficacy of intra-catchment translocations for the conservation of Atlantic salmon was tested by mean of a series of large-scale field experiments conducted in Ireland. Data gathered in the first two field experiments was used to inform refinements to the experimental design for the final experiment.

1.6 Thesis structure

The subsequent chapters of this thesis are listed below, with each of Chapters 2-6 corresponding to one of the objectives outlined in section 1.5:

Chapter 2: Evaluation of timed single pass electrofishing for estimating abundances of stream-dwelling salmonids

Chapter 3: Developing a depletion factor for abundance estimation of stream-dwelling salmonids using timed single pass electrofishing surveys

Chapter 4: Experimental translocations reveal biotic resistance by native brown trout impedes European eel colonisation

Chapter 5: Efficacy of intra-basin translocations of post-emergent larvae as a population enhancement tool in Atlantic salmon

Chapter 6: Intra-catchment translocations of post-emergent larvae as a viable population enhancement management tool in Atlantic salmon

Chapter 7: Discussion; refining existing monitoring practices and applying novel enhancement strategies to populations of threatened diadromous species

Chapter 7 synthesises the findings of Chapters 2-6 and provides recommendations for how the findings of these chapters may be applied to the overarching aim of this research, as outlined in section 1.5.

Chapter 2: Evaluation of timed single pass electrofishing for estimating abundances of stream-dwelling salmonids

Abstract

Timed (or ‘time-delineated’) single pass electrofishing is a common method for estimating the abundance of salmonids in wade-able streams. This technique has become the standard population monitoring method for salmonids in Ireland and is also frequently used in Britain. Despite this, it remains relatively untested, with few studies comparing its accuracy relative to other, more established, electrofishing methods. Here, paired 5-minute time-delineated and area-delineated single pass electrofishing surveys were used to test hypotheses relating to its relative precision and sampling effort (as measured by area coverage) using Atlantic salmon as the focal species. Estimated area coverage during the 5-minute surveys varied by an order of magnitude, with linear models indicating that the precision of surveys was highly density-dependent, with the lowest precision when salmon densities were $\geq$ 69 fish 100 m^{-2}. There was a diminishing-returns relationship between salmon fry density (as estimated through area-delineated surveys) and the number of recorded fish in 5-minute timed surveys on the same riffles. Estimated area coverage during the 5-minute surveys was negatively correlated with salmon fry density, due to increased handling time and thus lower fishing time on high density riffles. When this area variation was accounted for in calculations of approximate 5-minute fry densities (by estimation of area coverage during 5-minute surveys), this pattern of diminishing catch returns was eliminated from the model, with the relationship between the predictor (area-delineated fry density) and response (estimated 5-minute fry density) variable being close to 1:1. Thus, accounting for the area sampled within timed surveys results in

population abundance estimates that can be considered as representative as those estimates derived from more intensive sampling efforts.

2.1 Introduction

Salmonids are among the most extensively studied and most heavily managed fish taxa worldwide (e.g. Cowx, 2003; Hansen *et al.*, 2012; Wells *et al.*, 2020; ICES, 2021). This is likely due to their substantial socio-economic value to both the commercial and recreational fisheries sectors (Wild Salmon Center, 2009; Myrvold *et al.*, 2019). Given their high socio-economic importance, salmonid populations are often subject to relatively extensive population monitoring activities, where monitoring generally consists of at least one of four observations: electrofishing surveys of juvenile freshwater life-stages (usually in summer), smolt counts (in spring), returning adult salmon counts (spring to autumn) and then winter redd counts (Michael and Chadwick, 1988; Gallagher and Gallagher, 2005; Matson *et al.*, 2018). Redd counting can require high sampling effort, with multiple observations often recorded over periods when river levels and water clarity can make observations difficult (Gallagher, Hahn and Johnson, 2007), while smolt and adult counts are generally reliant on the use of instream structures and technology to record data that often have issues with imperfect detection (Gregory *et al.*, 2019; Simmons *et al.*, 2021). These inherent issues in smolt and adult monitoring methods have likely contributed to the relative popularity of electrofishing surveys of the freshwater life-stages during the summer period that generally aim to generate population estimates of 0+ fish ('fry') and, where possible, relate these to future smolt production and adult return rates (Crozier and Kennedy, 1995). These surveys may also be used to provide population data on older salmonid juveniles, such as parr (1+ fish), although in the RoI fry data are used almost exclusively.

In recent decades, population monitoring of salmonids has increasingly shifted to using sampling strategies that use semi-quantitative approaches to improve the efficiency of the programme (Gargan *et al.*, 2008; Matson *et al.*, 2018). For this to be effective in generating comparable population abundance estimates, these methods require calibration with more quantitative methods, including quantification of their precision (Crozier and Kennedy, 1995; Honkanen, Dodd, *et al.*, 2018; Matson *et al.*, 2018). Precision is defined here as the extent of the difference between estimated fish abundance for a given technique versus true fish abundance, or the best estimate of abundance available. Quantitative electrofishing approaches generally involve multiple upstream passes within a defined river area (‘area-delineated multiple pass electrofishing’), with upstream and downstream stop nets generally providing a closed sampling area (Peterson, Thurow and Guzevich, 2004). While generating relatively precise population estimates (Arnason, Antonsson and Einarsson, 2005; Bertrand, Gido and Guy, 2006; Matson *et al.*, 2018), this method is resource intensive, inhibiting its deployment across multiple sites within large sampling programmes (Matson *et al.*, 2018). Correspondingly, semi-quantitative fishing using a single upstream pass, generally without stop nets, is often preferred (Arnason, Antonsson and Einarsson, 2005; Matson *et al.*, 2018). This can be performed either within a set area, generating fry density estimates (‘area-delineated single pass electrofishing’; Arnason et al., 2005; Matson et al., 2018), or in a set time period, generating information on the fry numbers captured per unit time (timed or ‘time-delineated’ single pass electrofishing; Crozier and Kennedy, 1994). The advantage of both approaches is that they greatly reduce sampling effort required versus multiple pass fishing (Matson *et al.*, 2018), thus enabling more extensive monitoring programmes, with time-delineated approaches considered the most rapid method for generating fry abundance data (Gargan *et al.*, 2008; Matson *et al.*, 2018) .

Although time-delineated electrofishing provides the advantage of rapid assessment of fry abundances, it presents several potential limitations in relation its overall precision with other methods (both semi-quantitative and quantitative). Firstly, estimating fry numbers per unit time introduces an extra source of variability in the abundance data. While there are inevitably sources of sampling error in all electrofishing methods, based upon operator, species catchability or abundance, and abiotic conditions such as turbidity and water velocity (Peterson, Thurow and Guzevich, 2004; Arnason, Antonsson and Einarsson, 2005; Hedger *et al.*, 2018), area-delineated methods ensure that, irrespective of whether they use single or multiple passes, estimated fish numbers are expressed as a density relating to a standardised unit of area (e.g. n m^{-2}; Hedger *et al.*, 2018; Matson *et al.*, 2018). Conversely, time-delineated electrofishing lacks an area coverage measurement, leading to difficulties in generating comparable data with area-based methods. Consequently, this may also result in problems incorporating their data with habitat assessment methods, such as HABSCORE, which uses recorded habitat data to predict population densities under pristine conditions, with these then compared against observed densities from electrofishing surveys (Milner, Wyatt and Broad, 1998), as well as hydraulic-based habitat modelling techniques such as PHABSIM (Bourgeois *et al.*, 1996). While the time taken to complete these surveys is consistent, and thus satisfies any requirement for standardised sampling effort, this does not necessarily equate to consistent sampling effort according to the area fished due to, for example, differences in stream wade-ability. Given that the standardisation of sampling effort is a fundamental requirement for effective population monitoring (Sutherland, 2008; Petrere and Giacomini, 2010), then the omission of accounting for the area fished and/or its standardisation within timed approaches is of potentially high concern. Moreover, in the absence of area coverage measurements from time-delineated surveys, it is often unclear whether their data are representative of larger stream reaches, despite representative sampling being a basic tenet of population-level studies (Petersen, Minkkinen and Esbensen, 2005).

Timed-delineated electrofishing approaches also fail to account for the actual time spent fishing versus time sorting the catch. For example, Honkanen *et al.* (2018) noted that density-dependent sampling errors can occur in these data that result from the proportion of time in a survey spent removing fish from nets increasing as the fry density increases. Ultimately, this can produce a relationship between fry abundance and operator fish handling time that is equivalent to a type-II functional response (Holling, 1965; Real, 1977). There is thus a diminishing-returns relationship between fry density and fish capture rates, with its asymptote representing the maximum fish capture rate that is no longer a function of the actual fish density. The point at which this asymptote is reached, relative to naturally occurring salmonid densities, is thus of great importance to the wider utility of the time-delineated method.

Time-delineated electrofishing methods thus have a series of inherent issues that require consideration if they are to be adopted as a standard and viable population monitoring tool. Given their potential to generate important population data in an efficient manner (e.g. analysing temporal changes in relative fry numbers in specific sites, where other sources of sampling error are minimised) then it is important to understand how these issues affect their data precision. However, there remain substantial knowledge gaps on these, despite there being a wide knowledge base on semi-quantitative and quantitative methods based on area (Temple and Pearsons, 2003; Peterson, Thurow and Guzevich, 2004; Arnason, Antonsson and Einarsson, 2005). Therefore, the aim here was to overcome these knowledge gaps through comparing data between paired time-delineated and area-delineated single pass electrofishing surveys of Atlantic salmon fry from the River Erriff catchment, Ireland. These data were used to test the following hypotheses

(H): (H_1) salmon fry numbers from time-delineated single pass electrofishing are significantly and positively correlated with fry densities from area-delineated single pass electrofishing; (H_2) as the area fished in individual time-delineated surveys is highly variable, incorporating an estimated area coverage metric into time-delineated survey results provides density estimates that have equivalence to area-delineated densities; and (H_3) increasing the area fished within time-delineated surveys leads to higher precision in survey results.

2.2 Methods

2.2.1 Study river

Time-delineated electrofishing validation was carried out in conjunction with a series of field experiments conducted in 2019 and 2020 within the River Erriff catchment, Ireland (Fig. 2.1A). This river is known for its substantial populations of both Atlantic salmon and anadromous brown trout, with a mean annual adult salmon run of 2533 fish since 1986 (IFI, unpublished), and is listed by Inland Fisheries Ireland (IFI) as the salmonid index catchment for the Republic of Ireland (RoI). Under this designation, the Erriff catchment has been subject to extensive population monitoring of Atlantic salmon and anadromous brown trout, both through time-delineated electrofishing surveys, and through monitoring of smolt numbers and returning adult numbers, as recorded through fish trapping activities.

2.2.2 Experimental design

A total of 76 individual electrofishing sites were surveyed within two distinct survey periods (June/July & August/September; hereafter ‘spring’ and ‘autumn’ surveys) in each of the two experimental years (2019 & 2020; Fig. 2.1B). This design provided four distinct sampling groups, with most sites surveyed in all of these, giving a total of 252 paired electrofishing surveys. Individual electrofishing sites consisted of 20-m instream length sections of primarily riffle habitat, selected based on suitability for salmon fry. This length was chosen as it closely matched the length of most individual riffle habitat units within the catchment (personal observation). Electrofishing sites were chosen to be as similar as possible in terms of riffle habitat, avoiding inclusion of features such as undercut banks, islands and split channels wherever possible. Electrofishing site widths, and hence areas, varied greatly (maximum area = 606 m^2, minimum area = 49 m^2), with this considered to provide a representative sample in terms of the size of most fry riffle habitats in river catchments in Ireland and further afield. Prior to the first survey period, upstream and downstream boundaries of all sites were marked on both banks using brightly coloured marker posts, which were then photographed *in-situ* and geo-referenced to enable their subsequent location without needing permanent site markers. This method ensured that the exact locations of all sites remained consistent throughout the study, enabling robust inter-survey period comparison.

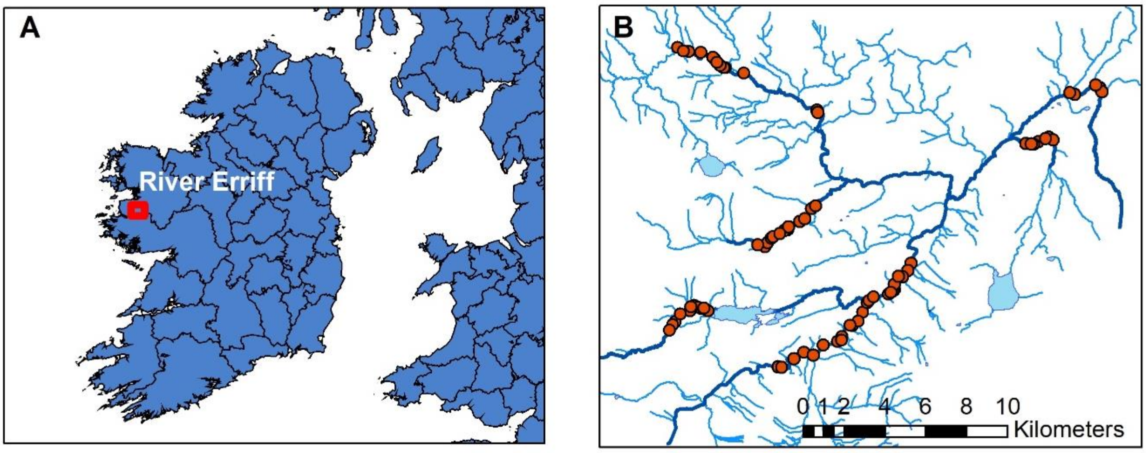

Figure 2.1: Maps showing; A) Location of the River Erriff catchment, and; B) Location of individual electrofishing sites within the Erriff catchment

As part of the broader experimental design, all sites were also surveyed in 2019 to provide habitat data. The primary aim of these habitat surveys was to obtain an accurate estimate of the area of each site, and thus allow calculation of fry densities from area-delineated electrofishing surveys. Several additional habitat variables were also recorded, with the aim of relating these to observed salmon fry densities at each electrofishing site. A number of these variables were also considered to have specific relevance to the area covered during time-delineated electrofishing surveys. Thus, the habitat surveys consisted of measurements of site area, river depth, proportion of site area covered by substrate within 4 categories (sand, gravel, cobble, boulder/bedrock), and the proportion of site area with macrophyte cover. In 2020, sites were visually assessed against photos from 2019 to determine whether any substantial changes to channel morphology, substrate or macrophyte cover had occurred. As this was never the case repetition of the habitat surveys was not considered necessary.

Site wetted area was estimated by repeat measurements taken immediately after spring and autumn electrofishing surveys at each site, with stream wetted width measured at 5-m intervals along each 20-m site. A mean area measurement, based upon both area estimates, was then used for statistics to account for differences in river flow condition between sampling periods. Depth was measured at 5 intervals along each of these cross-channel transects (left bankside edge, ¼ width, channel centre, ¾ width, right bankside edge). All other habitat variables were recorded following autumn surveys in 2019. Substrate composition was measured using a modified Wolman pebble count procedure and Wolman square. To create an approximate sampling grid, cross-channel transects beginning at either site boundary were walked at each site, with one substrate particle blindly selected per step, and macrophyte presence or absence recorded. Particles were measured by passing them through the smallest possible opening in the Wolman square. Once the far bank was reached, a single step was taken in an upstream or downstream direction and another transect completed until the 20-m site was covered. This method ensured at least 100 particles were measured for sites < 10 m mean width, ≥ 200 particles were measured for sites between 10 and 20 m mean width, and ≥ 300 particles for sites > 20 m mean width. Where these figures were exceeded, the number of particle and macrophyte records was reduced to the above figures (width < 10 m, n = 100 etc.) by randomly removing records, thus ensuring approximately equal sampling effort. The percentage of macrophyte cover and proportions of substrate particles within each of the substrate classes of sand (diameter; D ≤ 2 mm), gravel (2 < D ≤ 64mm), cobble (64 < D ≤ 256 mm) and boulder/bedrock (D > 256 mm) were then calculated.

2.2.3 Survey method

All electrofishing sites were surveyed using the same method, equipment and operator (LC) in all survey periods, to provide standardisation. The electrofishing equipment consisted of portable Hans Grassl backpack units (model IG600; Fig. 2.2) set between approximately 115 and 200V continuous direct current (DC). This differs slightly from the standard method in Ireland, where pulsed DC is used. This modification was made to reduce the mortality risk, as continuous DC has been shown to reduce injury risk in salmonids over pulsed DC (Dalbey, McMahon and Fredenberg, 1996; Ainslie, Post and Paul, 1998). This was considered of high importance given electrofishing took place in the weeks immediately following fry emergence, while most sites were also fished at least twice in each year, factors which might be considered to increase the overall fry mortality risk. The electrofishing anode used was triangular in shape, with a fine mesh net strung across the metal tubing of the anode used to capture fish, in line with the standard electrofishing equipment and method used in the RoI (Fig. 2.2). Thus, this method used a single operator, where one person operated the electrofishing gear and captured any fish, with an assistant then holding captured fish within a container (Fig. 2.2C). This differs from other electrofishing methods where nets separate to the anode are used, and thus capture of fish is handled by a second operator, or ‘netter’. Prior to fishing, water levels at each site were estimated and categorised as either ‘low’ or ‘normal’ (higher flow categories were unnecessary as fishing was not completed in such conditions). Fishing was always from the downstream boundary of each site to the upstream boundary and comprised a single pass, with this pass split into two distinct components.

Figure 2.2: Images showing; A) an example of the Hans Grasll IG600 electrofishing equipment used, excluding the backpack used to carry the battery, comprising the anode, cathode, battery and control unit; B) Close up image of the control unit, and; C) operation of the electrofishing equipment during this study

During fishing, captured fish were held in water, with fish that were observed but not captured also counted by species, with the exception of salmonid fry in autumn. During spring electrofishing surveys, salmon and trout fry could be easily distinguished due to differences in both size and colouration. Thus, any salmonid fry which were missed were assigned to either species based on visual ID. During autumn surveys, determination between salmonid species was more difficult. Hence, any salmonid fry observed but not captured were assigned as either salmon or trout based on the captured proportions of each species. Post-fishing, captured Atlantic salmon and brown trout fry and parr were identified to species, measured (total length; nearest mm), and then released. Larger trout and any other species captured were counted and released without measurement to enable rapid processing and release of all fish.

The first component of the single pass surveys consisted of the time-delineated electrofishing surveys. These were completed in an upstream direction, starting at the downstream boundary of each site, with fishing ceased once 5 minutes had elapsed from the start of electrofishing. At this point all fish captured were set aside on the stream bank by the assistant to the electrofishing operator. Fish captured or missed during this component were kept and/or recorded separately from those in the second survey component. Additionally, the upstream distance covered from the downstream boundary during this first time-delineated component was also recorded using a tape measure, with this laid out along one bank at each site prior to electrofishing. During this process, the electrofishing operator remained in the same position instream to ensure the entire area of each site was covered only once, with this process usually taking approximately 10-20 seconds. Thus, this was not considered to represent a significant interruption to the single electrofishing pass.

Following completion of this first component, electrofishing was then resumed until the upstream boundary of each electrofishing site was reached, with this forming the second component of the electrofishing surveys. Thus, the first component of each survey was considered to represent an accurate approximation of the 5-minute time-delineated electrofishing method, while the combination of the first and second components was considered to represent an area-delineated single-pass electrofishing survey.

2.2.4 Calculation of response variables

Total 20-m site area (m^2) was calculated as mean site width (m) x site length (20 m). Area-delineated salmon fry densities were then calculated based on the total number of salmon fry captured from both survey components, inclusive of both captured and missed fish, and total site area, and reported as fry n 100 m^{-2}. Salmon fry numbers from the time-delineated survey component were also reported inclusive of both fry captured and missed. The area coverage during the 5-minute time-delineated component (m^2) was estimated using the distance covered from the downstream site boundary until the completion of the 5-minute survey period (i.e. time-delineated area coverage = mean site width x upstream distance covered). For some analyses, this estimated area coverage was also reported as a percentage of the total site area. Estimated time-delineated fry density was then calculated based on the time-delineated fry numbers and estimated area coverage (m^2), and reported as fry n 100 m^{-2}. Densities of salmon parr and brown trout life stages from time-delineated survey components were calculated using the same method as for salmon fry. Prior to statistical modelling, Rosner’s tests were then used to identify and remove 7 statistical outliers based upon extremely high values for the time-delineated estimated area coverage and time-delineated estimated fry density.

2.2.5 Statistical approach

Linear models were used to model all relationships between predictor and response variables of interest, in line with H_1 to H_3. In all cases, bidirectional selection was used to select the predictor variables to be included in the final models. Specifically, both forward and backward stepwise selection was run on a range of habitat variables, with the Akaike information criterion (AIC) used to evaluate model fit at each stage. In cases where AIC scores were extremely similar between models containing different numbers of predictor variables, Bayesian information criterion (BIC) scores were also used to inform model selection, thus decreasing the risks of model over-parameterisation. Only predictor variables hypothesised to be of biological relevance were included in the selection process, with these listed for all models in Table 2.1. Only those variables selected through both forward and backward selection were included in the final models.

Correlation matrices and variance inflation factors (VIFs) were used to identify any sources of collinearity between predictor variables prior to model selection. Model validation was also applied at each stage during model selection and after selection of the final models to verify the underlying assumptions. Specifically, residuals were plotted versus fitted values to assess homogeneity of variance, and residuals versus each covariate to investigate model misfit. Additionally, VIFs were calculated at each stage of model selection to check for multicollinearity. Predictions for each model were then used to visualise the effects of each covariate within the model on a similar and easily interpretable scale, using a range of values from the minimum to the maximum recorded values for the covariate of interest, while all other covariates were fixed at their mean values.

2.2.6 Linear models

In order to test the accuracy of the time-delineated survey method, in line with H_1, salmon fry numbers for the time-delineated survey component were compared against area-delineated fry densities (fry n 100 m^{-2}). This was done using simple linear models, with time-delineated fry numbers used as a response variable, and with the predictor variable(s) consisting of either a single linear variable for area-delineated fry density, or both linear and quadratic components, thus testing whether this relationship best fit a type-I or type-II functional response curve. These two models were then compared using Akaike information criterion (AIC) scores, covariate p-values, and adjusted R^2 values to determine the best fitting model.

In line with H_2, and to further investigate the factors which affected the area covered in the time-delineated survey components, linear models were used to estimate the effect of a range of habitat variables, as well as estimated time-delineated salmon fry, salmon parr and trout fry densities, on area coverage. Estimated time-delineated area coverage was used as a response variable, with habitat variables and time-delineated salmon fry density used as predictor variables, with the variables available for selection listed in Table 2.1. Densities of other brown trout life stages and any other species present were not included in model selection due to extremely low overall abundance and absence from most surveyed sites.

In line with H_2, to test the accuracy of estimated fry density (fry n 100 m^{-2}) from the time-delineated survey components, simple linear models were then created using estimated time-delineated fry density as the response variable. Again, the predictor variable(s) consisted of either a single linear variable for area-delineated fry density, or both linear and quadratic components. These models were then compared using Akaike information criterion (AIC) scores, covariate p-values, and adjusted R^2 values to determine the best fitting model. Covariate p-values and adjusted R^2 values were then compared between the best fitting models for both time-delineated fry numbers and estimated time-delineated fry densities to determine the relative accuracy of both models (Table 2.1).

Further analyses were performed to determine the degree of combined under/overestimation of the estimated time-delineated fry densities, relative to the most accurate estimate of true fry densities available (area-delineated fry densities), as per H_3. The following formula was used to calculate the absolute values of the residuals (e) obtained from comparison of the area-delineated fry densities (fry n 100 m^{-2}; den_{total}) versus the estimated time-delineated densities (den_5), using data from all sites where fry were caught in the time-delineated component:

$$e = \left| \left(\frac{den_5}{den_{total}} \right) - 1 \right|$$

Thus, this model compared the relative precision, or total level of under/overestimation, of estimated time-delineated densities compared to area-delineated fry densities, rather than any specific trend towards over- or underestimation. These values were then used as the response variable, with area coverage per 5-minute sample expressed as a percentage of total site area and used as a predictor variable. Additional habitat variables were then included in the model selection process, with these included in Table 2.1. Area-delineated fry density was also included in model selection to test for density-dependent sampling error. The same process of bidirectional selection and model validation was then applied as in all models, with model predictions used to visualise the effects of individual covariates of interest.

2.3 Results

2.3.1 Time-delineated fry numbers

Atlantic salmon fry numbers recorded during the 5-minute time-delineated survey component were significantly and positively correlated with total fry densities from the overall area-delineated single-pass surveys. The final, best-fitting model describing their relationship contained both linear and quadratic components, demonstrating a type-II functional response (Table 2.1, Equation 1; Fig. 2.3A). Total fry density explained 64 % of the variation in time-delineated fry numbers, with both the linear and quadratic components of the final model being highly significant ($p < 0.01$, Table 2.1, Equation 1).

2.3.2 Area coverage

The estimated area coverage (in m^2) from the 5-minute time-delineated survey component was highly variable between individual electrofishing surveys (range = 16 to 167 m^2; mean ± SD = 62 ± 26 m^2; Fig. 2.3B). Linear models revealed time-delineated area coverage was significantly and negatively correlated with the densities of 0+ salmon fry, as well as trout fry and salmon parr, within the time-delineated survey component (Table 2.1, Equation 2; Fig. 2.3C, 2.3D). Additionally, the time-delineated area coverage was significantly and positively correlated with the total site area, mean site depth, and macrophyte proportion (Table 2.1, Equation 2). There were also significant differences in area coverage between years, once other variables were accounted for, with approximately 7 m^2 greater area coverage in 2020 versus 2019 (Table 2.1, Equation 2).

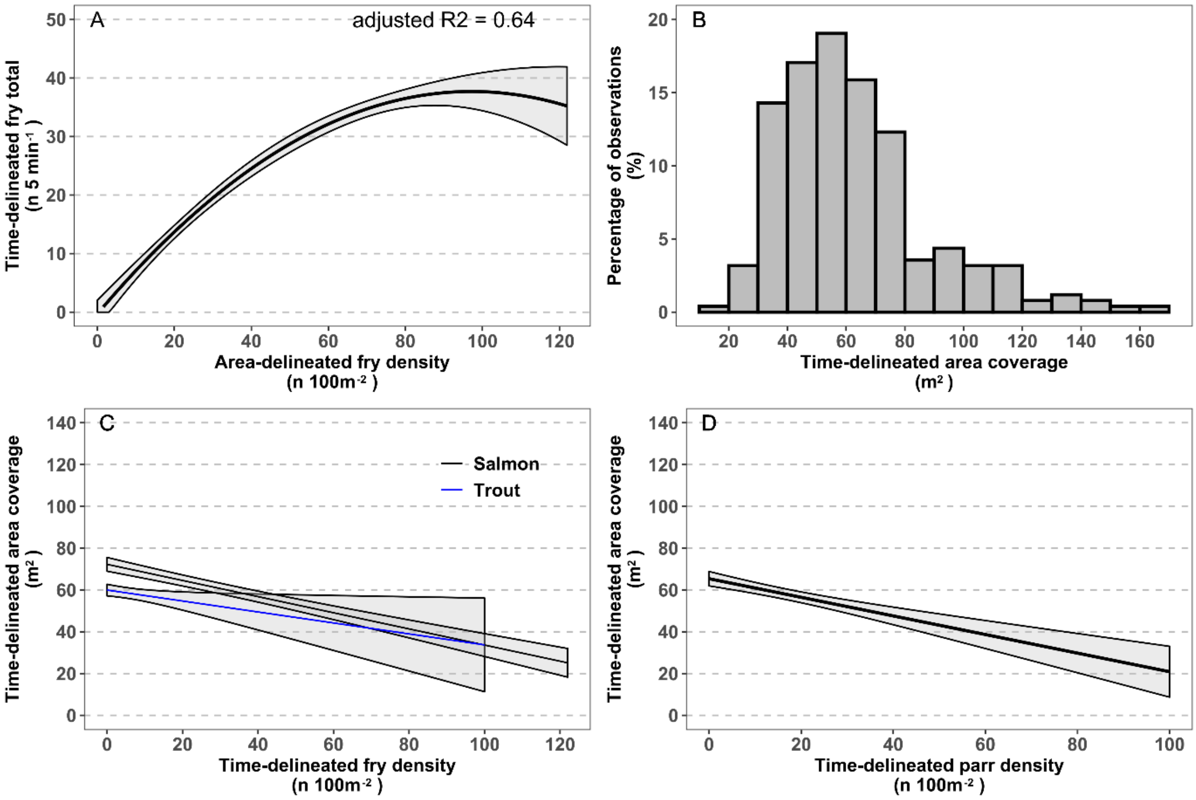

Figure 2.3: Predictions from linear models shown in equations 1 and 2 of table 2.1; A) Predicted relationship between area-delineated fry density and time-delineated fry number, from equation 1; B) Estimated time-delineated area coverage; C) Relationship between time-delineated salmon and trout fry densities and area coverage, from equation 2, and; D) Relationship between time-delineated salmon parr density and time-delineated area coverage, from equation 2. Shaded areas in all plots represent 95 % prediction intervals.

2.3.3 Density estimates

Models estimating fry densities from the time-delineated component increased the variation explained by overall area-delineated fry densities by approximately 12 % (R^2 = 0.76) when compared to modelling time-delineated fry numbers, with this relationship being non-linear (Table 2.1, Equation 3; Fig. 2.4A). Both the linear and quadratic components of this model were highly significant ($p < 0.01$, Table 2.1, Equation 3), although the magnitude of the quadratic component was lower, with this relationship closely matching a linear 1:1 relationship between the predictor (total area-delineated fry density) and response (estimated time-delineated fry density) variables (Fig. 2.4A).

The degree of under/overestimation of fry densities, based upon the estimated time-delineated fry densities, was negatively correlated with the percentage area coverage during this survey component. In practice, this meant that the greater the coverage of an individual riffle, the closer the estimate of fry densities from the time-delineated survey component was to the best estimate of fry density for the entire riffle (i.e. from area-delineated surveys; Table 2.1, Equation 4; Fig. 2.4B). Predictions from this model indicated that, for every 10 % of total site area covered in the time-delineated survey component, the mean survey imprecision (i.e. over/underestimation of fry densities), as indicated through absolute residuals, decreased by approximately 3.4 %. Average imprecision at 10 % and 90 % area coverage was approximately 38 % and 11 % respectively. Additionally, the survey precision was found to be 9 % lower on average in 2020 than 2019, once area coverage was accounted for (Table 2.1, Equation 4).

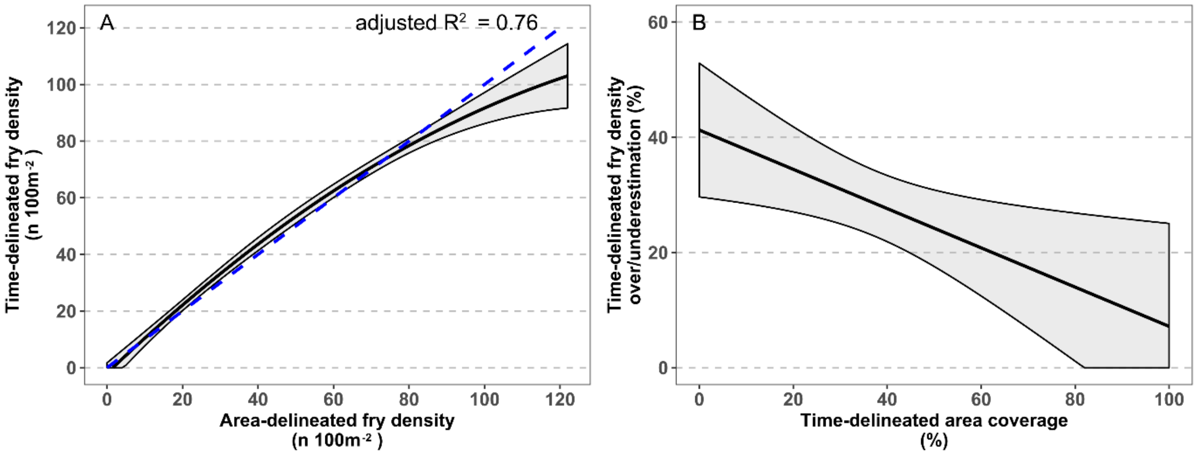

Figure 2.4: Predictions from linear models shown in equations 3 and 4 of table 2.1; A) Predicted relationship between area-delineated fry density and time-delineated fry density, from equation 3, and; B) Relationship between time-delineated percentage area coverage, and relative survey precision, as shown by modelling residuals of time-delineated fry density vs. area-delineated fry density, from equation 4, expressed as a percentage of area-delineated fry density. Shaded areas in all plots represent 95 % prediction intervals.

Table 2.1: linear model equations (#) and variables available for selection, statistically significant results are shown in bold

#	Formula	N obs.	Variables available for selection	Selection	Covariate(s)	Estimate	Standard error	Z value	P value
1	*Time-delineated fry number ~ Total fry density + Total fry density*^{2}	245	Total fry density, Total fry density^2	N/A	Intercept	-0.36	1.21	-0.30	0.77
					Total fry density	0.78	0.06	12.19	**$< 2 \times 10^{-16}$**
					Total fry density^2	-0.004	0.0007	-5.92	**1.11×10^{-8}**
2	*Time-delineated area coverage (m*^{2}*) ~ Total site area + Time-delineated parr density + Time-delineated fry density + Macrophyte proportion + Sampling year + Mean depth + Time-delineated trout fry density*	245	Time-delineated fry density, Time-delineated parr density, Time-delineated trout fry density, Sampling period, Sampling year, Total site area, Mean depth, Macrophyte proportion, Gravel proportion, Cobble proportion, Boulder proportion, Flow condition	Appendix 1, Table A1	Intercept	52.31	4.63	11.29	**$< 2 \times 10^{-16}$**
					Total site area	0.08	0.01	7.22	**6.89×10^{-12}**
					Time-delineated parr density	-0.45	0.07	-6.13	**3.57×10^{-9}**
					Time-delineated fry density	-0.39	0.04	-10.94	**$< 2 \times 10^{-16}$**
					Macrophyte proportion	34.99	8.67	4.04	**7.34×10^{-5}**
					Sampling year (2020)	6.77	1.99	3.40	**0.001**
					Mean depth	50.63	21.25	2.38	**0.02**
					Time-delineated trout fry density	-0.26226	0.11926	-2.20	**0.03**
3	*Time-delineated fry density ~ Total fry density + Total fry density*^{2}	245	Total fry density, Total fry density^2	N/A	Intercept	-2.30	2.05	-1.12	0.26
					Total fry density	1.29	0.11	11.85	**$< 2 \times 10^{-16}$**
					Total fry density^2	-0.003	0.001	-3.01	**0.003**
4	*|(Time-delineated fry density/Total fry density -1)| ~ Time-delineated area coverage (%) + Sampling year*	237	Time-delineated area coverage (%), Sampling year, Sampling period, Time-delineated fry density, Flow condition, Total site area	Appendix 1, Table A2	Intercept	0.41	0.06	6.97	**3.28×10^{-11}**
					Time-delineated area coverage (%)	-0.003	0.001	-2.47	**0.01**
					Sampling year (2020)	0.09	0.04	2.13	**0.03**

2.4 Discussion

The results of this experiment provide strong support for all of the hypotheses. Specifically, there was strong support for H_1, that salmon fry numbers obtained through time-delineated single pass electrofishing would be positively correlated with fry densities obtained through area-delineated single pass electrofishing surveys. In line with H_2, the area covered in individual time-delineated surveys was also found to be highly variable and so incorporation of an estimated area coverage metric into time-delineated survey results - thereby allowing approximate fry density calculation - increased the precision of these in relation to area-delineated densities. Finally, modelling of absolute residuals of time-delineated versus area-delineated densities indicated that greater area coverage in the time-delineated surveys lead to greater precision in survey results, when compared to area-delineated fry densities, with this in line with H_3.

The highly significant relationship between fry densities obtained through area-delineated electrofishing surveys and time-delineated fry numbers was as expected, with the adjusted R^2 value indicating that fry density, as obtained through area-delineated surveys, explained the majority of the variation in time-delineated fry numbers. However, the type-II, or diminishing-returns, nature of this relationship presents a practical issue for abundance estimation of salmonids, given the broad range of fry densities across which predicted time-delineated fry numbers remained consistent. In real-world terms, this means that a total of 35 to 38 fry recorded from a 5-minute electrofishing sample could theoretically correspond to an area-delineated fry density ranging between 69 and 122 fish 100 m^{-2}. Thus, the results from this study indicate that interpretation of higher abundance estimates, as obtained from time-delineated surveys, should therefore be subject to a relatively high degree of uncertainty, a finding in line with Honkanen et al. (2018).

The primary cause for this relationship appears to be shown by equation 2, with time-delineated area coverage (m^2) shown to be strongly negatively correlated with fry density from the time-delineated survey component. The most likely reason for this lies in the electrofishing method, as also shown by Honkanen *et al.* (2018). Upon noting the presence of salmonid fry on the anode during electrofishing, the electrofishing operator then had to transfer any captured fish from the anode into the container held by the electrofishing assistant. This process was estimated to take up to 2 seconds per transfer, during which time no further site area could be fished. Thus, at greater fry densities the number of transfers was also greater, with this likely resulting in the lower area coverage in the time-delineated survey component at sites with higher fry densities. Additionally, at sites with higher fry densities, it was also common for multiple fry to be captured during a single sweep of the electrofishing anode. When this occurred, it was also common for one or more of these fish to become trapped between the net surface and the metal tubing at the edges of the anode, requiring additional time to extricate these fish. This would therefore help to explain the diminishing-returns curve seen for the relationship between area-delineated fry densities and time-delineated fry numbers. Honkanen *et al.* (2018) proposed a similar explanation behind this relationship between fish density and time-delineated fish numbers, with the results here further building upon this work by empirically demonstrating an area coverage effect. This hence represents a significant issue, and one that is likely to be present across all time-delineated surveys, irrespective of the habitat, survey time period and species being sampled. This issue is also difficult to account for without obtaining some estimate of area coverage or total handling time during time-delineated surveys.

Given the relationship between estimated fry density and area coverage during the time-delineated survey component, as described above, it is perhaps unsurprising that calculation of an estimated fry density metric increased the variation explained by the area-delineated fry density. It is also important to note that, while still a non-linear relationship, as shown by the significance of the quadratic variable, this relationship was visually much closer to linear, with the magnitude of this quadratic effect lower. This relationship between the more robust area-delineated fry density estimate and the cruder time-delineated fry density estimate also very closely followed a 1:1 ratio. A 1:1 ratio represents the ideal scenario for survey interpretation, given it indicates that fry densities obtained by area coverage estimation during time-delineated surveys are equal to those which would be obtained by the more labour-intensive method of area-delineated single pass electrofishing. This is in contrast to the time-delineated fry numbers, which would be considerably more difficult to interpret, particularly in areas of higher fry density (e.g. ≥ 69 fish 100 m^{-2}). It should be noted, however, that estimation of total site area via width measurements during this study generally took approximately 5-15 minutes per site, dependent on river width and wading conditions. Albeit with the additional depth measurements recorded adding to the total time taken. Nevertheless, obtaining an area coverage metric would increase the time required to complete time-delineated surveys and is therefore somewhat contrary to their original purpose to provide a rapid abundance estimate.

A salmon fry density of ≈ 69 fish 100 m^{-2} therefore appears to represent the asymptote, above which the maximum number of fish that could be captured during the 5-minute survey period was no longer a function of the actual fish density, being constrained by handling time. This has some key implications, which are specific to interpretation of such survey data in the RoI, where the study was conducted, but also assist in broader interpretation. Currently, 5-minute electrofishing survey results are used primarily as a qualitative monitoring tool for river catchments in the RoI which are assessed to be close to or below their conservation limits, with a catchment average of 17 fry per 5-minute sample representing a cut-off point, below which rivers are subsequently subject to more intensive regulation and management, such as closure of recreational fisheries (Holmes *et al.*, 2021). From this perspective, the ability to determine the population trends within individual catchments is not significantly hindered by this method, provided intra-catchment variability in salmon fry abundance is relatively low (i.e. not characterised by extremely high and low values of fry density). Nevertheless, the ability to detect population trends across broader fish density ranges is likely hampered by such sampling. From a broader perspective, the utility of this method is therefore likely to be determined by the range of salmonid densities across which precise sampling is required.

The relationship between time-delineated area coverage and the densities of both salmon parr and trout fry also has key implications for both the abundance estimation of other species and of Atlantic salmon. For the abundance estimation of Atlantic salmon fry, these effects are likely to act as confounding variables, given that salmon parr will be present in any streams which contain fry, while Atlantic salmon and brown trout often occur sympatrically. Thus, where present, the densities of these will also affect the area coverage during time-delineated surveys, introducing a further source of sampling error. The effect of these two species and age class groups also strongly suggests that the same pattern of density-dependent sampling error is likely to be seen for other species. In the case of salmon parr, the effect on area coverage was higher than for salmon fry. This can be explained by their greater size and likely greater difficulty in handling these fish compared to salmon fry, and thus greater handling time per fish. This finding has important implications for the monitoring of other species as it demonstrates that density-dependent error will likely increase with the handling time for each species or specific life stage, in line with functional response predictions (Holling, 1965; Real, 1977).

The effect of brown trout fry on time-delineated area coverage was estimated to be around 32 % lower than that for Atlantic salmon fry. The mechanism behind this difference in effects is unclear, given the broadly similar size and morphology of these two species at this life stage. The broad confidence intervals for trout fry indicate that this difference was influenced by the large disparity in observed densities for the two species, with salmon fry far more abundant, being found within more sites and generally at higher densities than trout fry. This difference may also have been related to differences in catchability of these two species related to their microhabitat use, with brown trout fry generally considered to occupy slower flowing areas than salmon fry (Heggenes, Bagliniere and Cunjak, 1999; Armstrong *et al.*, 2003). This difference in habitat usage may therefore have made brown trout fry easier to capture, effectively reducing their total handling time.

The effect of several habitat variables on time-delineated area coverage has key implications for the broader application of this method, given these often vary greatly within lotic environments. Indeed, habitat complexity is generally considered to be a key factor in determining salmonid abundances (Fausch and Northcote, 1992; De Jalón and Gortazar, 2007; Hasegawa and Maekawa, 2008). The reason behind the positive correlation between mean site depth and area coverage was initially unclear, given deeper areas would often be associated with more difficult wading conditions, and might thus be expected to result in lower area coverage. The cause for this relationship may relate to lower sampling effort of deeper sections, and hence more rapid coverage of these areas. The primary purpose of these surveys was to capture salmonid fry, particularly those of Atlantic salmon. This life-stage is most associated with shallow riffle-type habitats (Heggenes, 1990; Heggenes, Bagliniere and Cunjak, 1999; Armstrong *et al.*, 2003), with deeper areas generally forming more suitable habitat for older salmon parr, as well as larger brown trout individuals (Armstrong *et al.*, 2003). Thus, deeper areas, while not deliberately ignored, were likely given lower sampling effort due to the absence of salmonid fry, resulting in more rapid coverage of these areas, and ultimately greater time-delineated area coverage.

The strong positive correlation between macrophyte proportion and area coverage is the most difficult to explain. This relationship was stronger than that between gravel proportion and area coverage, indicating that macrophyte proportion had a greater relative impact on area coverage during the time-delineated survey component. The cause for this remains uncertain. It is possible that areas of extremely thick macrophyte coverage, as generally found within clusters of *Potamogeton spp.*, were fished with less effort due to the inability to see salmonid fry and difficulty in extricating fry from these weeded areas when they could be observed. Additionally, sites where *Potamogeton spp.* was found in abundance were generally noted to be relatively slow flowing and low gradient, with this potentially making wading easier. However, several other macrophyte species were also present within the catchment, with most species forming much less dense coverage, and hence being unlikely to impact on electrofishing, while several species were also noted from faster flowing and higher gradient sites. Without recording the relative proportions of each macrophyte species, it is difficult to determine the relative contribution of each of these to site area coverage. Furthermore, while characterisation of stream flows via hydraulic modelling could provide further insight into the conditions affecting area coverage during these surveys, it is a relatively labour-intensive process (Ghanem *et al.*, 1996; De Jalón and Gortazar, 2007), and was considered logistically unfeasible in this study.

The higher precision of the time-delineated estimated fry densities with greater percentage area coverage likely relates to two mechanisms. The first being that, as the percentage area increased, so the relative accuracy of the estimated area coverage (m^2) increased, giving more accurate density estimates. Estimated area coverage was estimated relatively crudely, i.e. by calculating area coverage from the instream length coverage of the total site length, multiplied by the mean site width, and therefore did not take into account differences in wetted widths along each site. Therefore, sites with lower percentage area coverage would have been subject to greater inaccuracy, in terms of estimated area coverage, caused by variation in stream width along the site. As percentage area coverage increased, so the estimated area coverage became more representative of that actually fished. The second, and likely more important, mechanism was that fry abundances were noted to be spatially patchy, even within individual sites. This is in line with previous research, with salmonid species shown to distribute themselves according to instream habitat features, such as woody debris and boulders (van Zyll De Jong, Cowx and Scruton, 1997; Solazzi *et al.*, 2000; van Zyll De Jong and Cowx, 2016), as well as specific depth ranges, substrates and flow types (Heggenes, 1990; Heggenes, Bagliniere and Cunjak, 1999; Armstrong *et al.*, 2003). Additionally, suitable salmonid habitats are often characterised by high habitat complexity (Hasegawa and Maekawa, 2008). Therefore, coverage of smaller areas during time-delineated surveys likely resulted in non-representative sampling of the greater riffle area. At higher percentage area coverage, the estimated time-delineated fry densities then became more representative of those present across the entire site area. Additionally, at higher percentage area coverages the fry caught during the time-delineated fry survey component would have formed a greater proportion of the total fry count for each site, and thus it would be expected that the time-delineated and area-delineated densities would be necessarily correlated.

A further point of note was that the total site area was not found to be significant in the model from equation 4. This can be interpreted as suggesting that area coverage during time-delineated surveys, expressed in m^2, is of lesser importance than the relative percentage of the riffle area covered. If area coverage in m^2 was the main factor in determining the accuracy and precision of the estimated time-delineated density, then the total site area would be expected to be negatively correlated with the absolute residuals, as a set percentage of area coverage corresponds to greater area coverage in m^2 for larger sites. Thus, this result indicates that greater area coverage (m^2) was required for larger riffles to obtain a representative sample of fry densities within these. This finding is directly in line with the fundamental principles behind sample size determination, where larger sample sizes are considered necessary to maintain precision at set confidence intervals when sampling larger populations (Krejcie and Morgan, 1970; Dattalo, 2008). The results here indicate that, to maintain mean over/underestimation of salmon fry densities below approximately 20 % would require mean percentage area coverage of over 60 % in time-delineated surveys. In practical terms, this means that for any given riffle, at least 60 % of the total riffle area must be fished, and an estimated area coverage obtained, to ensure that the estimated fry density from that survey does not differ by more than 20 % from the density which would be obtained by true area-delineated single pass electrofishing of the entire riffle area.

2.5 Conclusions

Fundamentally, the results of this study show that area coverage is highly inconsistent between time-delineated single pass electrofishing surveys, even under near-ideal conditions (same operator, same catchment, similar flow conditions), and is strongly correlated with highly variable habitat features. Thus, the ability to compare time-delineated survey results across broader spatial and temporal scales may be limited. Additionally, given time-delineated surveys are often used to monitor temporal changes in fry abundances at the same locations, the within-site variation in area coverage observed here is an issue. These problems are further compounded by the difficulty in interpreting time-delineated surveys from high fry density sites. Furthermore, the results here indicate that use of a consistent 5-minute survey period will result in less representative sampling of larger riffle areas.

The results here also show that substantial improvements can be made to the time-delineated electrofishing protocol. Inclusion of an approximate area coverage measurement could greatly increase the accuracy and utility of time-delineated survey results at higher fish densities. For example, the overall area of individual riffles fished could be measured in a single year, with the percentage coverage during any subsequent time-delineated surveys then estimated visually and used to obtain an area coverage (m^2) estimate. Additionally, using variable sample times according to approximate riffle area (e.g. 5- and 10-minute surveys) could minimise the issue of non-representative sampling. In combination, these refinements could greatly increase the accuracy and utility of time-delineated survey results, while preserving the benefits of rapid and efficient sampling from this method.

Chapter 3: Developing a depletion factor for abundance estimation of stream-dwelling salmonids using timed single pass electrofishing surveys

Abstract

The relative accuracy of most electrofishing methods for abundance estimation of salmonids has been considered. In contrast, less consideration has been given to how electrofishing results may be affected by the population dynamics of salmonids. Substantial empirical evidence shows populations of many stream-dwelling salmonids undergo a phase of high mortality in their first summer following emergence from the spawning gravels. This period overlaps with the sampling period for most electrofishing surveys for salmonid species and so results from these surveys are likely subject to variation based on their timing. To date, little consideration has been given to this effect when interpreting these surveys in the context of population assessment. Here, generalised linear mixed effects models were used to derive a population depletion curve for Atlantic salmon, using a large 5-minute time-delineated single pass electrofishing survey dataset collected as part of statutory monitoring activities in the Republic of Ireland. Model predictions showed a depletion of approximately 34 % from a July 1st maximum by September 30th, corresponding to a depletion rate of 0.38 % d^{-1}. This depletion was broadly in line with similar depletion factors calculated from repeated timed-delineated electrofishing surveys conducted as part of a series of larger field experiments within the River Erriff catchment, Ireland. These findings hence have clear implications for the interpretation of such survey results, and thus management of salmonid species.

3.1 Introduction

Electrofishing surveys represent one of the most common ways by which stream-dwelling fish species, such as salmonids, are sampled. These are performed using a variety of techniques (e.g. area-delineated single and multiple pass surveys, time-delineated surveys etc.), with the relative accuracy, limitations and advantages well documented for most of these (Pusey *et al.*, 1998; Peterson, Thurow and Guzevich, 2004; Bertrand, Gido and Guy, 2006). Although some methods, such as time-delineated single pass surveys, are less well-proven, there are at least a limited number of studies into their relative accuracy (Crozier and Kennedy, 1995; Honkanen, Dodd, *et al.*, 2018; Matson *et al.*, 2018). The accuracy and limitations of the time-delineated method are also considered in Chapter 2, along with recommendations for how this method might be improved. Thus, the fundamental accuracy of each of these methods for monitoring of salmonids has been considered, to a greater or lesser extent, for each survey method. However, one factor which has not been fully addressed, and which is applicable to many salmonid species, relates to their practical application.

The majority of electrofishing surveys for salmonid species are performed over an approximate summer sampling period (e.g. July-September), with these targeted primarily at 0+ age class salmonids, or ‘fry’. Within Ireland, the general reasoning behind this survey period is that it ensures all salmonid fry have emerged from the spawning gravels prior to sampling (Gargan *et al.*, 2008). Additionally, the cut-off for electrofishing activities at the end of September is aimed at eliminating any disturbance to spawning salmonids, while also avoiding periods of inclement weather and unsuitable flow conditions later in the autumn. Although the fundamental reasoning behind use of this sampling period may vary between government agencies etc., the timing of most electrofishing surveys for salmonid species is broadly consistent, with most surveys aimed at the capture of summer or autumn fry.

The primary issue with this sampling period is that it overlaps with a period of extremely high mortality for many salmonid species. Many salmonid populations are generally considered to enter a phase of density-dependent mortality from the period immediately following emergence until the end of their first summer (Armstrong, 2005; Einum, Sundt-Hansen and Nislow, 2006; Einum, Nislow, Mckelvey, *et al.*, 2008; Honkanen, Boylan, *et al.*, 2018), with this period often considered to represent a population bottleneck (Jonsson and Jonsson, 2004; Armstrong, 2005; Kennedy, Nislow and Folt, 2008). Hence, given that this period of high mortality heavily overlaps with the approximate sampling period for most electrofishing surveys, it is likely that the results obtained from these surveys are highly dependent on the date of sampling. This is of particular importance given that, to the writers' knowledge, no government agency uses any form of scaling or depletion factor based upon the date on which a specific survey is undertaken. This is critical, given that fry numbers from these surveys are often a major factor used to assess the population status of many salmonids, and thus application of conservation strategies. Hence, from a conservation and management standpoint, it is of vital importance to understand and control for the effect of survey date to ensure the accuracy of these salmonid fry abundance estimates.

Here, an extensive time-delineated single pass electrofishing dataset, collected over 14 years by IFI, was used to develop a population depletion factor for a model salmonid species (native Atlantic salmon, 'salmon' hereafter), using generalised linear mixed effects models (GLMMs). These surveys were primarily aimed at the monitoring of salmon fry, where estimated fry abundances directly informed decision making in conservation management programmes (e.g. fisheries closures and catch-and-release policies). Calculation of a depletion factor then enabled the standardisation of electrofishing timed surveys through the application of a correction factor which could account for high fry mortality over their first summer of life. This depletion factor could benefit conservation outcomes for this species by allowing for more accurate population assessment and better-informed decisions around management strategies. The relatively broad spatial and temporal scale of the dataset, and abundance of observations, enabled testing of the following hypothesis: when all other relevant factors are accounted for, sampling date is a significant and negatively correlated predictor of the number of salmon fry captured in 5-minute time-delineated single pass electrofishing surveys.

3.2 Methods

3.2.1 Data Collection

All electrofishing data were collected by IFI over a 14-year period between 2007 and 2020 as part of statutory monitoring. During this period over 11,000 individual electrofishing surveys were conducted in over 150 river catchments, with the majority of these representing repeated surveys of the same electrofishing sites across multiple years. All survey sites were only subject to a single electrofishing survey in any given year, with surveys conducted between July 1st and September 30th except in exceptional circumstances (e.g. where heavy flooding delayed electrofishing surveys). The majority of sampling effort was concentrated towards the middle and end of this sampling period, with relatively fewer observation from July (Fig. 3.1).

Electrofishing surveys consisted of a single timed 5-minute upstream electrofishing pass without stop nets, a standardised method for the observation of salmonid fry by IFI (Gargan *et al.*, 2008; Holmes *et al.*, 2021). Although specific voltage ranges were not specified, these surveys used pulsed direct current, with a pulse rate of 60 p/s, and were conducted using a similar method and equipment to that outlined in Chapter 2 (i.e. backpack units, with triangular anodes including a mesh net), with the only major difference being the use of pulsed direct current being used instead of continuous direct current, in line with standard IFI practice. All salmonid fry captured during these surveys were identified to species, measured (fork length; nearest mm) and released. Salmonid fry numbers seen but not captured (i.e. missed) were also recorded and apportioned to either salmon or trout based on the captured proportions of each species. These missed fry numbers were not converted to integers and thus the overall fry counts for these surveys were often non-integer values. Older age classes of salmonids were not specifically targeted during these surveys, however, when captured these were identified to species level, assigned to an approximate age class and released without measurement. Any older salmonids missed were recorded to species level and assigned to an approximate age class based on visual identification. Additionally, any other fish species captured or missed during electrofishing surveys were also recorded to species level and counted, although the accuracy of these counts is likely lower due to the specific targeting of salmonid fry.

For each survey the percentage (%) area of substrate in five classes: bedrock, boulder (> 40 cm approximate diameter), cobble (10-40 cm), gravel (1-10 cm) and sand/silt (< 1 cm) was visually estimated. Additionally, average depth was also visually estimated for each survey. For each site which underwent repeated sampling, the mean values for each of the aforementioned variables were then calculated from all years of sampling. The stream order at each electrofishing site was also derived from GIS river network data.

For each individual electrofishing survey an approximate riffle grade was recorded by the electrofishing operator, based primarily upon the aforementioned variables. However, these gradings were not based upon specific values and must therefore be considered somewhat arbitrary. Riffles were graded between 1 and 5, with 1 representing excellent salmon fry habitat and 5 representing very poor fry habitat. Additionally, water level at the time of each survey was also graded between 1 and 5, with 1 representing very low water conditions and 5 representing high water. Some observations were also given scores between each of these values (i.e. intervals of 0.5). Hence, both riffle grade and water level can be considered single-point estimates of habitat quality and suitability of conditions to electrofishing respectively. In contrast, the substrate percentages and average depth relate to measurements taken over multiple years for most sites. It must be acknowledged that each of these habitat variables, and particularly riffle grade, had the potential to be biased by observed fry numbers if recorded post-electrofishing. For example, through higher or lower riffle grades being assigned post-survey where high or low fry numbers were recorded.

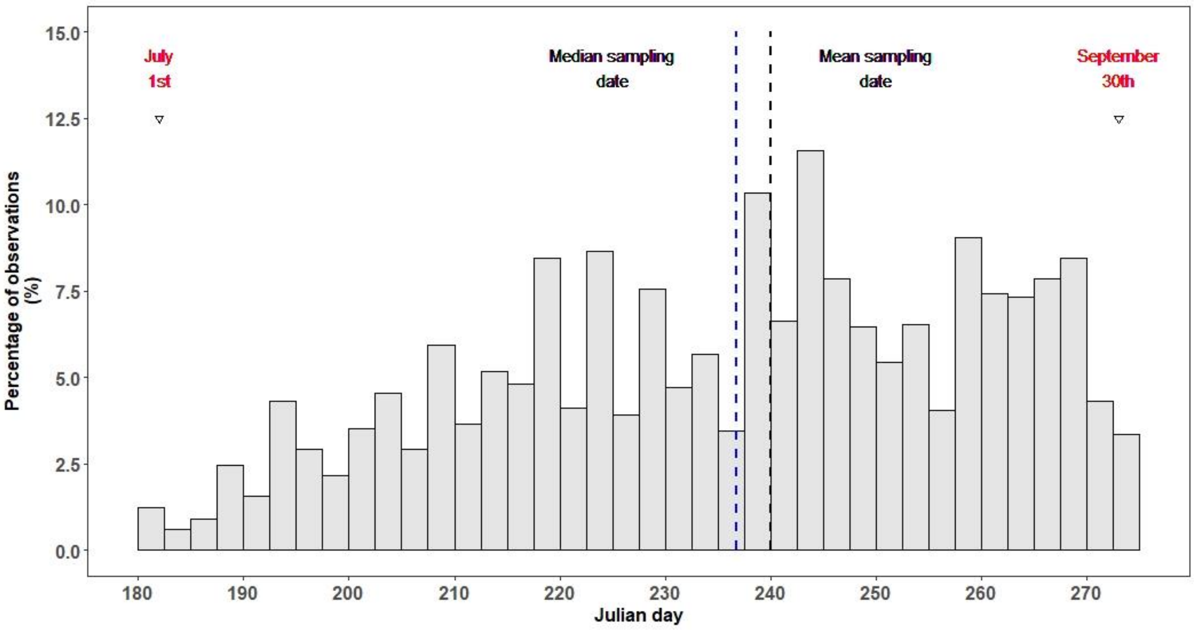

Figure 3.1: Time-delineated single pass electrofishing survey sampling effort across the 3-month summer survey period

3.2.2 Data subsampling

A subset of the original wider dataset was used to ensure all data used were suitable for the chosen statistical analyses. This was done both for ecological reasons (e.g. anthropogenic disturbances, sites inaccessible to spawning fish etc.), and for statistical reasons (e.g. missing data, number of observations per grouping level etc.). Data subsampling initially took place at the individual electrofishing survey-level and site-level. This was followed by further subsampling of the resultant dataset, to ensure the accuracy of GLMMs. Specifically, sufficient observations were required at each level of all random effects, while also ensuring enough levels were present for each random effect, to enable accurate estimation of both the within level and overall variance of each random effect term. This was of particular importance to ensure all random effects terms could be accurately modelled, given the use of multiple crossed random effects within the GLMMs.

At the survey-level, individual surveys were excluded from further analyses where anthropogenic disturbance through instream work, cattle crossings, fords, pollution, or siltation was suspected or observed. Furthermore, to ensure data quality, surveys where electrofishing operator, riffle grade or water levels were not recorded were excluded. Surveys where high water or low visibility were noted were also removed to ensure data quality and remove sources of confounding variation. Finally, surveys were removed where there was any uncertainty over the exact location of the survey or suspicion that the wrong location had been fished for any given electrofishing site (i.e. inconsistent location with other years of sampling from the same site).

At the site-level, individual sites were removed where substrate percentages or average depth were not recorded. Additionally, sites were removed where any note of downstream barriers to migration, such as improperly installed culverts, was made during any year of survey. Any sites where salmon fry were never recorded from any year of survey were also excluded. This reduced the level of unnecessary zero-inflation in terms of fry numbers, hence aiding in modelling of fry numbers.

To enable robust analysis using GLMMs, data were only included from both rivers and electrofishing operators with a total of at least 10 observations. Furthermore, a total of 35 observations with extremely high salmon fry values were removed from the dataset based on Rosner’s tests for outliers and individual inspection, with these values considered to be unrealistic and thus likely represented erroneous entries. This left a total of 4098 observations from 93 river catchments and 54 electrofishing operators across the entire 14-year sampling period. This dataset included some observations from both before (n =

20) and after (n = 67) the sampling period outlined above. These were retained to enable approximate predictions to be made from surveys conducted outside of the normal sampling period in extreme circumstances (e.g. where flooding delayed surveys) and to increase the accuracy of the depletion curve near the limits of the sampling period.

3.2.3 Statistical analyses

GLMMs were used to investigate the presence and level of population depletion over the sampling season (i.e. July-September) by modelling fry numbers from 5-minute time-delineated single pass electrofishing surveys, inclusive of missed fish. This model type was preferred over linear models and generalised linear models (GLMs) as it enabled use of non-gaussian response variable distributions and random effects.

Salmon fry number was modelled using a negative binomial distribution, with a hurdle model component used to account for zero inflation in the response variable distribution. A hurdle model structure was preferred over both zero-inflated poisson and negative binomial distributions based upon better fit, as estimated by comparing model residuals and AIC scores. The hurdle model structure accounts for zero inflation by using two model components. A binary model component is used to model the probability of any observation belonging to either the zero-value group or the positive-value (i.e. non-zero) group, with this model component often referred to as the ‘zero-inflation’ model (Feng, 2021). Non-zero data are then modelled using a truncated form of the specified frequency distribution (i.e. truncated negative binomial distribution), as per standard GLMM models, with this often referred to as the ‘conditional’ model.

To enable the use of a negative binomial distribution, the response variable (salmon fry per 5-minute sample) was rescaled by a factor of 10 to avoid loss of detail and converted to an integer value. Although negative binomial models commonly utilise a logged offset variable when used to model rate data, such as that modelled here, in this case the time component of the response variable was equal across all observations (5-minute sample). Thus, the response variable was considered to represent a count and therefore did not require an offset variable term.

The Julian day on which each electrofishing sample was taken was included in all models as a predictor variable, thus providing the temporal component of the model from which the depletion curve was estimated. Multiple crossed random effects terms were used to account for the year of sampling, which was modelled as a factor rather than as a numeric predictor variable, electrofishing operator, and the river catchment for each observation. Consideration was given to inclusion of an interaction term between Julian day and river catchment to enable inter-river differences in the fry depletion curve to be accounted for, with this approach being tested during data exploration. However, the relatively small number of observations for many rivers and consistency in terms of the sampling period between years (i.e. narrow span of Julian days for each river) created model convergence issues and led to a single depletion rate model structure being preferred. Additionally, having a single depletion curve was considered to be most useful from a management perspective.

Bidirectional selection was then used to select the additional variables to be included in the final model, with these variables used to reduce the level of confounding variation. Specifically, both forward and backward stepwise selection was run on a range of habitat variables, with the Akaike information criterion (AIC) used to evaluate model fit at each stage. Only variables hypothesised to be of biological relevance were included in the selection process and only those variables selected through both forward and backward selection were included in the final model. Hence, the substrate gravel percentage, cobble percentage, riffle percentage, average depth, riffle grade and flow condition were all included in the model selection to account for physical habitat variation between sites/surveys which may have affected both spawning effort and suitability for salmon fry. Riffle grade was scaled by a factor of 2 to aid in modelling, as the original scale containing non-integer values created model convergence issues. Additionally, the numbers of brown trout fry and parr, as well as salmon parr, were also included in the selection process to account for the impact of other species and age classes (e.g. through competitive interactions and/or niche partitioning).

Correlation matrices and variance inflation factors (VIFs) were used to identify any sources of collinearity between predictor variables prior to model selection. Model validation was applied at each stage during model selection and after selection of the final model to verify the underlying assumptions. Specifically, residuals were plotted versus fitted values to assess homogeneity of variance, and residuals versus each covariate to investigate model misfit. VIFs were also calculated at each stage of model selection to check for multicollinearity. GLMM predictions for the numbers of salmon fry across the entire sampling period were then calculated based upon the final model, with a fry depletion factor for the sampling period calculated based upon these.

3.2.4 Model ground-truthing

To ground-truth the final model, model predictions were compared to observations taken from time-delineated surveys conducted as part of a series of large-scale field experiments within the River Erriff catchment, Ireland. Under this experiment repeated electrofishing surveys of the same electrofishing sites were conducted during two approximate sampling periods (June-July & August-September) across two years, as outlined in Chapter 2, with these two sampling periods broadly overlapping with the survey season used by IFI. Within the above experiment, fry numbers were manipulated at some sites over the course of the summer period. Therefore, to ensure fair comparison, only sites where no manipulations took place were used for comparison.

To provide accurate comparison between empirical observations and predicted values, daily fry depletion rates (% d^{-1}) were calculated as the daily percentage depletion in fry numbers from the set date of July 1st. As most electrofishing surveys during the first of the two sampling periods were not conducted on this date, daily depletion rates were standardised to this date by using the raw depletion rates (i.e. change in fry n d^{-1}) to estimate the number of fry which would have been present on July 1st. Percentage depletion rates were then calculated based on this figure and the fry numbers during the second sampling period

3.3 Results

There was a highly significant and strongly negative relationship between Julian day of sampling and the number of salmon fry per 5-minute sample (GLMM, $p < 0.01$; Table 3.1; Fig. 3.2). Although technically non-linear due to the response variable distribution used, the negative relationship was visually close to linear. When calculated as a depletion rate in terms of percentage reduction in fry number from the July 1st maximum, this equates to approximately 0.38 % d^{-1}, or a total depletion of approximately 34 % across the entire sampling period (Fig. 3.2). There were, however, broad 95 % confidence intervals around these predictions, indicating the high degree of variation within the response variable (Fig. 3.2). Additionally, based on the zero-inflation model, Julian day was positively correlated with the probability of salmon fry number being a zero value (i.e. there was a greater probability of obtaining zero values for salmon fry number later during the sampling period; Table 3.1).

Depletion rates from repeat sampling within the River Erriff catchment were highly variable. Fry numbers from 5-minute time-delineated surveys increased between the June-July and August-September sampling periods for a number of sites, indicating net immigration was greater than mortality at these sites. When these were excluded the estimated depletion rates were broadly similar to those predicted from the GLMM (mean ± SD = 0.60 ± 0.34 % d^{-1}, n = 42, maximum = 1.24 % d^{-1}, minimum = 0 % d^{-1}).

In the final model, in addition to Julian date, the following predictor variables were also included: stream order, gravel and cobble percentages, riffle grade, salmon parr number, trout parr number and trout fry number. Stream order, gravel and cobble percentages, and salmon parr number, were all positively correlated with salmon fry number, with the remainder of the predictor variables negatively correlated with salmon fry number (Table 3.1). Additionally, riffle grade, trout parr number and trout fry number were all positively correlated with the probability of salmon fry number being a zero value (Table 3.1). Water level was not found to be significantly correlated with salmon fry number during model selection, indicating that surveys conducted within an approximately normal range of flow conditions gave broadly similar fry numbers.

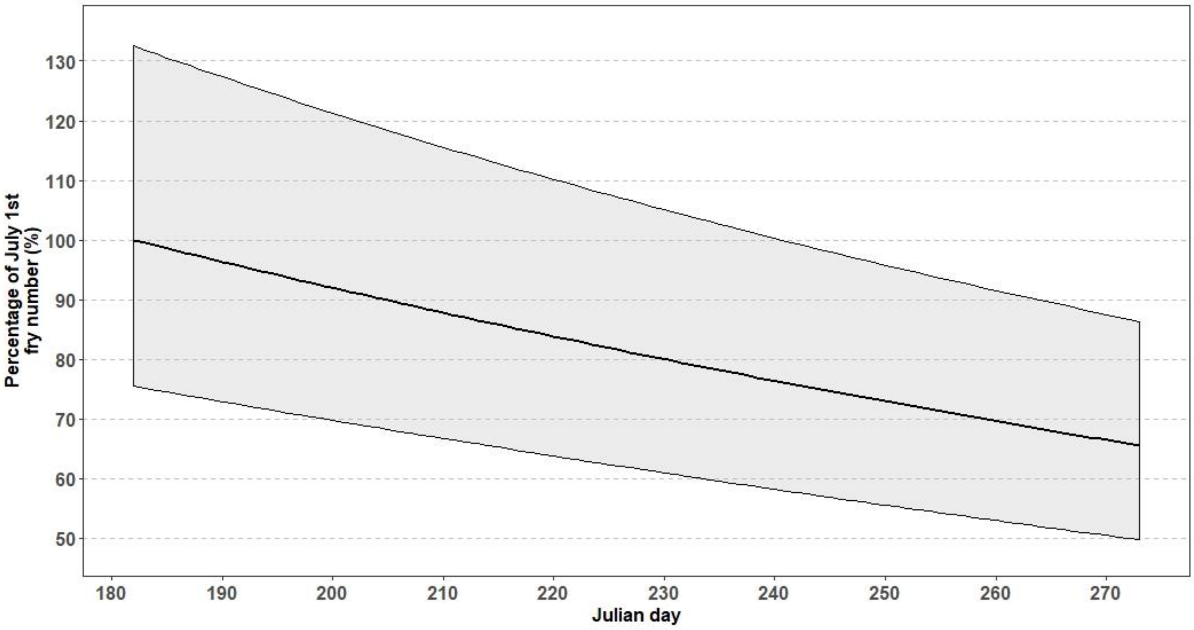

Figure 3.2: Model predictions from the generalised linear mixed-effects model shown in Table 3.1, showing the depletion curve for Atlantic salmon fry throughout the Inland Fisheries Ireland sampling period, with predicted fry abundance and 95 % prediction intervals shown as a proportion of the maximum fry abundance which would theoretically be obtained on the first day of sampling (July 1st)

Table 3.1: generalised linear mixed effects model equation and variables available for selection, statistically significant results are shown in bold

Formula	N obs.	Variables available for selection	Selection	Model component	Covariate(s)	Estimate	Standard error	Z value	P value
Salmon fry number ~ Stream Order + Riffle grade + Salmon parr number + Trout parr number + Trout fry number + Gravel percentage + Cobble percentage + (1|River catchment) + (1|Year) + (1|Operator) Response variable distribution = Negative binomial	4098	Salmon parr number, Trout parr number, Trout fry number, Gravel percentage, Cobble percentage, Mean depth, Stream Order, Riffle grade, Flow condition	Appendix 2, Table A1	Conditional model	Intercept	5.75	0.20	28.67	**$< 2 \times 10^{-16}$**
					Julian day	-0.005	0.0007	-7.11	**1.20×10^{-12}**
					Stream order	0.12	0.01	9.03	**$< 2 \times 10^{-16}$**
					Riffle grade	-0.13	0.01	-12.22	**$< 2 \times 10^{-16}$**
					Salmon parr number	0.01	0.003	5.40	**6.69×10^{-8}**
					Trout parr number	-0.04	0.005	-7.67	**1.68×10^{-14}**
					Trout fry number	-0.006	0.002	-3.92	**8.23×10^{-5}**
					Gravel percentage	0.01	0.001	5.78	**7.37×10^{-9}**
					Cobble percentage	0.004	0.001	3.93	**8.69×10^{-5}**
				Zero-inflation model	Intercept	-2.04	0.91	-2.24	**0.03**
					Julian day	0.006	0.003	2.04	**0.04**
					Stream order	-0.47	0.07	-7.08	**1.48×10^{-12}**
					Riffle grade	0.27	0.05	5.76	**8.50×10^{-9}**
					Salmon parr number	-0.19	0.02	-8.95	**$< 2 \times 10^{-16}$**
					Trout parr number	0.08	0.02	4.76	**1.90×10^{-6}**
					Trout fry number	0.03	0.01	5.25	**1.56×10^{-7}**
					Gravel percentage	-0.01	0.004	-2.37	**0.02**
					Cobble percentage	-0.01	0.005	-2.66	**0.008**

3.4 Discussion

In showing a highly significant and steep population depletion curve, the results of this study strongly support the initial hypothesis and highlight the issue of failing to account for seasonal depletion in Atlantic salmon fry numbers. This finding also has broader implications for other salmonid species, where similar patterns are also likely to apply. Given the level by which fry numbers appear to decline from these results, it is likely that, by failing to account for a date effect, many catchments are at risk of mis-management due to significant over- or underestimation of fry abundance, depending on the sampling period during which electrofishing surveys are carried out. Overestimation of fry abundances could have severe negative impacts on threatened and/or declining salmonid populations, particularly where strict fry abundance cut-offs are used to determine implementation of conservation measures such as fisheries restrictions (e.g. through conservation limits).

A practical example of the above is demonstrated by the qualitative assessment of salmonid population statuses within catchments close to or below conservation limits, by IFI, with this used as a demonstrative example of the issues of this method. Based on correlation of time-delineated electrofishing abundance estimates with returning adult salmon numbers, 17 fry per 5-minute sample was chosen as a cut-off value, below which rivers are subject to more intensive management (Holmes *et al.*, 2021). In practical terms the depletion rate shown here means a total of 17 salmon fry from a sample taken on July 1st would theoretically equate to 11 salmon fry by September 30th, while 17 salmon fry on September 30th would equate to 26 salmon fry on July 1st. Thus, this clearly demonstrates the issue of failing to account for fry mortality over this period.

While highly significant, these results do present some limitations. It is worth noting that, while the calculation of a single depletion factor for all river catchments aids in ensuring broad applicability, it is highly likely that depletion factors will vary between rivers and individual sites. This is demonstrated by the high degree of variation in the depletion factors calculated for the River Erriff catchment alone. However, it was considered impractical from a management perspective to use separate depletion factors for each individual river. Additionally, data exploration indicated that the relatively narrow and consistent sampling period for many rivers would limit the ability to make accurate predictions for all catchments. Nonetheless, with sufficient resources and historical data it might be possible in future to calculate catchment-specific depletion factors, providing more accurate data for individual rivers, such as those within Natura 2000 Special Areas of Conservation (SACs) and/or those with salmonid populations of particularly high socioeconomic value e.g. rivers which support large recreational fisheries.

A potential further limitation in the results here is related to the nature of salmonid population dynamics. As previously noted, many authors have hypothesised that mortality of Atlantic salmon is primarily density-dependent during their first summer, with numerous studies providing empirical data to support this hypothesis (Armstrong, 2005; Einum, Sundt-Hansen and Nislow, 2006; Einum, Nislow, Mckelvey, *et al.*, 2008; Honkanen, Boylan, *et al.*, 2018). Thus, it would be expected that electrofishing sites with higher fry abundances at the beginning of the sampling period would experience higher mortality, and thus a higher depletion rate, than those with lower initial fry abundances.

Despite this, model validation showed no significant relationship between Julian day and the model residuals, suggesting that density-dependent mortality was either not evident from the original dataset or was successfully accounted for by the final model. There are two primary explanations for this. The first lies in the time-delineated electrofishing method used to gather these data. Using this method leads to density-dependent error in fry abundance estimates, as shown in Chapter 2, and by (Honkanen, Dodd, *et al.*, 2018). Based on Chapter 2, fry numbers of over approximately 35 fish per 5-minute sample likely corresponded to a wide range of fry densities (69-122 fish 100 m^{-2}). Thus, the initial period of high density-dependent mortality may not have been observed in terms of fry numbers during these samples. It is also possible that this difference in depletion rates was at least partially accounted for by the GLMM, in which the Julian day effect (i.e. depletion curve) is proportionally, rather than numerically, identical across all predicted values of fry abundance. In practical terms this means that, for sites with higher abundance, the same percentage depletion would equate to a greater reduction in actual fry numbers than sites with lower fry abundance.

Nevertheless, salmonid population dynamics do suggest that predictions for the beginning of the electrofishing period are likely to be subject to greater inaccuracy due to higher overall variation in fry abundances. This is likely to be of greater importance to more accurate area-delineated electrofishing methods, for which density-dependent errors are less of an issue (Honkanen, Dodd, *et al.*, 2018). However, this still has key implications for the standardisation of time-delineated electrofishing survey results. To allow accurate comparison of survey results, the depletion factor calculated here could be used as a correction factor to standardise survey results to a specific sampling date. As noted above, fry densities are likely to be subject to the highest variability at the start of the electrofishing period. Thus, use of a standardised sampling date at the beginning of the survey period would give the highest uncertainty around standardised predicted fry abundances.

It could be argued that, from a population dynamics perspective, September 30th represents the most optimal standardised sampling date, given this is the period when fry abundances are likely to have the lowest overall variability due to density-dependent mortality. Thus, fry abundance predictions for this date should theoretically show the lowest inaccuracy in terms of fry numbers. Additionally, September 30th fry numbers are likely to be most closely related to migrating smolt numbers, and hence to returning adult numbers, so provide the most useful indicator of a catchment's population status.

However, consideration must also be given to sampling effort. The relative accuracy of predictions based upon the depletion rate calculated here is likely to be heavily affected by the number of days between the standardised sampling date and the date on which a given electrofishing survey is carried out. Given the mean and median survey dates correspond to August 26th and 28th respectively, it is likely that a standardised sampling date close to these will give the highest mean accuracy of standardised fry abundance predictions. Thus, choice of such a standardised date must be weighed based upon both the biological principles which apply to salmonid populations, and the statistical considerations of prediction accuracy.

Given that observations from the extremes of the sampling period are always likely to result in less accurate fry abundance predictions, irrespective of the standardised sampling date used, shortening the sampling period to ensure broader comparability could also be considered as a first resort, where feasible. However, it is recognised that in many cases this is likely to be impossible, given practical considerations such as staff numbers, restricted fieldwork seasons and the possibility of long periods of unsuitable water levels, thereby demonstrating the practical need for depletion factors such as this one.

3.5 Conclusions

It is clear from the findings reported here that current salmonid population monitoring techniques are likely to be subject to substantial inaccuracy, given the failure to account for population depletion when the results of electrofishing surveys are reported. This seems a significant oversight, which could lead to mismanagement of salmonid populations, as these surveys are often used to inform management strategies and conservation measures. Given the evidence provided here, it is recommended that, where possible, similar depletion factors are developed as a matter of urgency for a range of salmonid species to enable more accurate estimation of abundance and aid in monitoring population trends.

In order to ensure that the depletion factor developed here is robust, this model should also be ground-truthed against empirical data based on multiple observations of fry abundance from similar catchments, including those not included in the original model, both within Ireland and further afield, to determine its broader applicability. However, irrespective of the exact rate of depletion, some level of population depletion is likely to occur in all salmonid populations over the course of a summer sampling period, and this should be accounted for to enable effective management of declining salmonid populations.

Chapter 4: Experimental translocations reveal biotic resistance by native brown trout impedes European eel colonisation

Abstract

Anthropogenic impacts have exponentially increased the extinction risk of countless species, necessitating a step-change away from traditional conservation measures. Methods such as species reintroductions and assisted colonisations through translocations have gained support as viable means to safeguard vulnerable populations and species. However, there is a need to expand the environmental scale and increase the level of replication of studies into these methods to increase their wider relevance. To address this knowledge gap, critically endangered European eels were used to carry out a replicated ecosystem-scale translocation experiment. Eels are of particular relevance given European Union mandates to make 60 % of commercially caught eels available for reintroduction, with some of these released outside the catchments where they were captured (inter-catchment translocation). Eels were released into 13 headwater streams where natural stream conditions created two treatments: (1) streams populated by native brown trout, and; (2) trout-free streams above impassable waterfalls. Trout presence reduced eel recapture rates by approximately 70 %, and predicted eel survival from approximately 4 % to 2 %, after 3-months. A strong negative relationship was observed between the number of recaptured eels and the density of 2+ year age class trout, with eels usually absent at 2+ trout densities ≥ 5 fish 100 m^{-2}. Recaptured eels were slightly larger in trout-populated streams (5 ± 9 mm difference), suggesting smaller eels may be more vulnerable to predation. These results demonstrate the potential success of large-

scale translocation programmes (e.g. through European Union eel management plans) for this and other anguillid species, but highlight the need for further research across a greater range of predator densities and within more speciose ecosystems, given the strong effect exerted by a single species here.

4.1 Introduction

Anthropogenic impacts on earth's flora and fauna are greater than ever before, with even historically abundant and widespread species now at risk of extinction (Lande, Landweberg and Dobson, 1999; Urban, 2015; Maheshwari, 2021). This risk is increased by the synergistic nature of anthropogenic impacts (Richmond, 1993; Laurance and Cochrane, 2001; Rosa and Seibel, 2008), for example when climate-induced species range shifts are hampered by habitat fragmentation (Opdam and Wascher, 2004). Hence, it is vital to facilitate species range shifts through fragmented habitat with greatly reduced propagule density. Consequently, there is now increasing agreement that assisted colonisations and reintroductions of many species (e.g. through translocations) will be required to facilitate their future survival (Griffith *et al.*, 1989; George *et al.*, 2009; Seddon, 2010; Lawler and Olden, 2011).

To ensure the success of such translocations, it is critical to understand the biotic and abiotic factors which affect the survival of translocated individuals (e.g. Laws and Kesler, 2012). The scale of translocation studies is thus of paramount importance, given the need to apply translocation programmes across diverse ecosystems and habitats (Seddon, 2010; Laws and Kesler, 2012). While the increased prominence of such programmes has created an increase in such studies (e.g. Chiarello *et al.*, 2004; Etheridge *et al.*, 2010; Nussear *et al.*, 2012; Spurgeon *et al.*, 2015), their scope has often been limited. The use of replicated designs is rare and, where applied, replication is often within the same ecosystem (e.g. a single stream reach; Spurgeon *et al.*, 2015).

Given these challenges, headwater stream ecosystems are ideally suited in several ways to the evaluation of such translocation projects. Firstly, stream dispersal pathways are restricted to dendritic networks, with dispersal primarily occurring in only two directions (upstream or downstream), allowing simple assessment of dispersal (Dias *et al.*, 2013; Fuller, Doyle and Strayer, 2015). Secondly, headwater streams are small and are often fragmented, either naturally or by anthropogenic obstructions (Dias *et al.*, 2013; Fuller, Doyle and Strayer, 2015; Grill *et al.*, 2015). This allows isolation of entire populations, more accurate assessment of survival and aids replication. Thirdly, the simple fish assemblages of headwater streams create more readily discernible species interaction networks (Richardson and Danehy, 2007; Tylianakis *et al.*, 2010). Finally, many streams are already being affected by anthropogenic impacts, with climate-mediated changes to flow regimes and water temperatures, reduced abundance of many fish species and ever-increasing levels of habitat fragmentation (Arnell and Gosling, 2013; Grill et al., 2015; van Vliet et al., 2013; WWF, 2006).

Headwater streams are also habitats for the model species of this study, the European eel. Anguillid species are facultatively catadromous, spending a proportion of their life in freshwater but having to return to the marine environment to reproduce (Aoyama, 2009). This life history strategy can render Anguillid species particularly vulnerable to the effects of over-exploitation (Jessop, 2000; Bru, Prouzet and Lejeune, 2009) and habitat fragmentation, such as through barriers to migration (Verreault, Dumont and Mailhot, 2004; Acou *et al.*, 2008; Verhelst, Buysse, *et al.*, 2018). European eels are listed as ‘critically endangered’ by the IUCN, having experienced a decline of approximately 99 % in recruitment between the early 1960s and early 2000s (Dekker, 2003; Jacoby and Gollock, 2014a).

In response to this severe and prolonged decline, European Union (EU) legislation has established a target of 40 % escapement of silver (migratory adult) eel biomass relative to the best estimate of escapement without anthropogenic influences (European Commission, 2007). Crucially, this legislation requires 60 % of the commercial catch of juvenile eels (elvers) to be released, of which a proportion are advised to be stocked into other catchments. While this represents one of the largest translocation programmes worldwide, little research has been carried out on the impact of these translocations. An understanding of the determinant factors for the success of translocations is a vital component of such projects, and one which requires urgent investigation. If reintroduction is to play a major role in this species' recovery, it is necessary to make the best use of the limited numbers of juveniles available without incurring detrimental effects.

In this study, European eels and brown trout were used to conduct a replicated ecosystem-scale colonisation experiment. Both species occur in sympatry across much of their ranges, yet little is known about their interspecific interactions. Given brown trout possess a number of traits that might inhibit eel colonization success (e.g. territorial aggrssion and piscivory; Titus, 1990; Jonsson *et al.*, 1999) this information is of great relevance to conservation and management practices globally, with salmonids co-occurring with anguillids across extensive native and non-native ranges. Correspondingly, eels were translocated into trout-populated and trout-free reaches of headwater streams devoid of other fish species, with these revisited three months post-translocation, with the survival and dispersal of eels recorded in relation to the presence, densities, and estimated ages of trout. The following hypotheses (H) were tested: (H_1) brown trout presence would negatively affect eel colonisation success (as estimated from recapture rates); (H_2) in trout-populated stream reaches there would be a negative relationship between eel recapture rate and trout density, and; (H_3) lengths of surviving eels in trout-populated streams would be larger through size-selective predation by trout.

4.2 Methods

4.2.1 Study area & experimental design

This study was carried out in 13 headwater streams within 4 watersheds in Wales, United Kingdom (Fig. 4.1A, 4.1B). For each stream only a single stream reach was used, with all stream reaches located above impassable man-made dams and/or natural waterfalls, rendering them inaccessible to eels prior to the study. Six stream reaches were also inaccessible to resident brown trout (confirmed by electrofishing surveys). This created two experimental treatments; trout-populated (n = 7), and trout-free stream reaches (n = 6). For the purposes of this study, “stream reach” is defined as the section of each stream, approximately 1 km in length, within which eels were released and surveys took place. Each stream reach was considered a single replicate.

4.2.2 Eel collection, housing & translocation protocol

Juvenile glass eels collected from the River Severn, England were transported to the Natural Resource Wales Fish Culture Unit on April 28th, 2015. Eels were housed in a 300-litre tank filled with well water maintained at 24 ˚C (± 0.89 SD) and reared for one month on a diet of cod roe and fish pellets. Water temperatures were then gradually decreased to 12 ˚C to match the conditions of the study streams, allowing acclimatisation. Following this, eels were randomly selected from the rearing tank and transported in aerated containers to the study sites. Juvenile eels, now considered elvers, were then released at all 13 stream reaches between the 1st and 5th June 2016, in a random order.

Approximately 900 eels were released into a 50-m section in the centre of every stream reach (hereafter: “the release site”, Fig 4.1C), with eel numbers estimated by extrapolating the recorded mass of 100 eels. This represents an approximate density of 10 eels m^{-2} within each release site, greater than that recommended for stocking into areas of predicted high natural mortality (6 eels m^{-2}; Environment Agency, 2010), and was chosen to maximize dispersal and successful colonization, and therefore increase the likelihood of recapture.

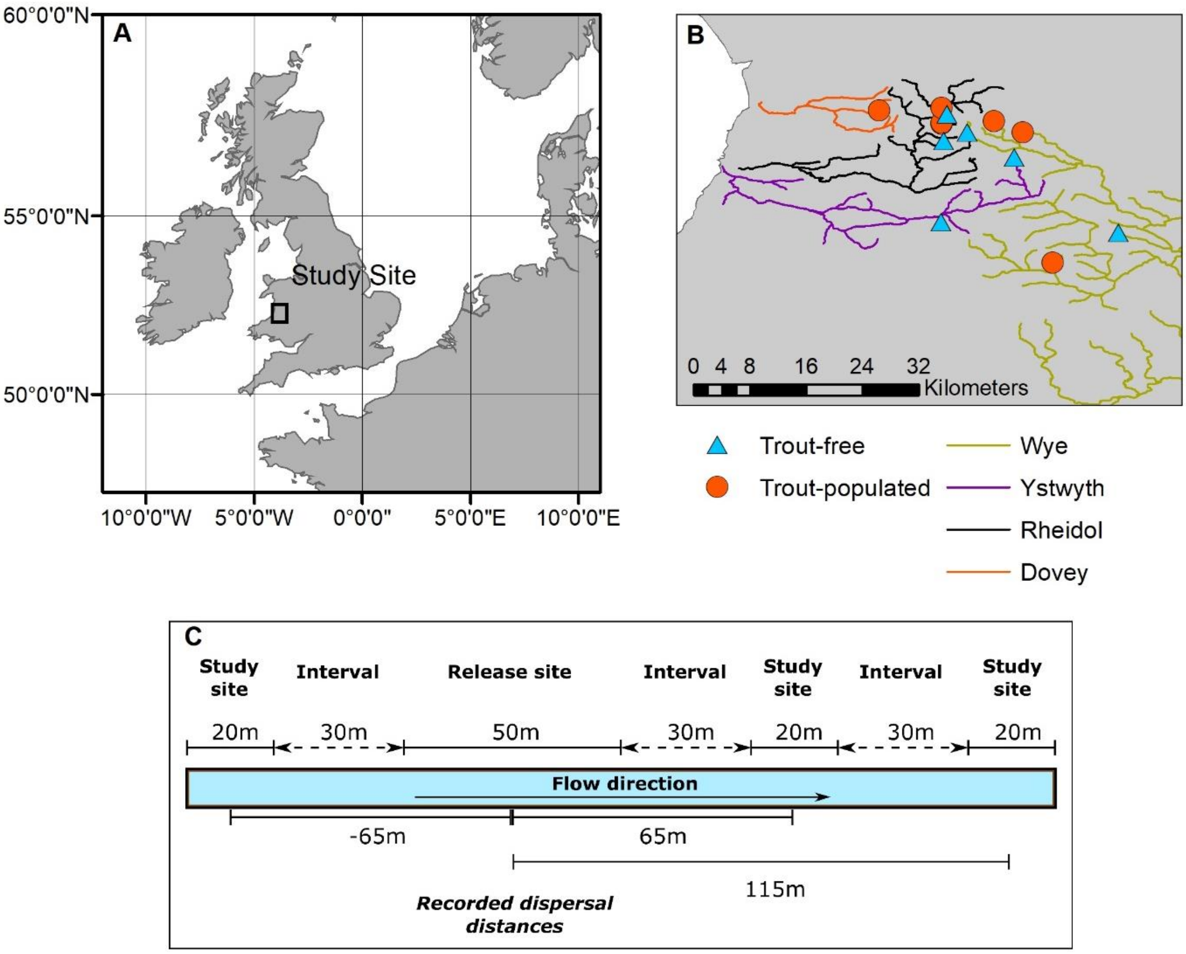

Figure 4.1: A) Location of study site within the UK; B) Locations of stream reaches in Wales according to treatment group and river catchment, and; C) Diagrammatic representation of release and study sites within each stream reach, with site lengths, intervals and recorded dispersal distances labelled.

4.2.3 Electrofishing surveys

Between September 1st and 13th, 2016, all stream reaches were surveyed in a random order to recapture the translocated eels to assess their survival and growth. This used area-delineated upstream single-pass electrofishing (300-500 V, continuous direct current) without stop nets, an effective method for surveying both eels and trout (Baldwin and Aprahamian, 2012). For each stream reach, an electrofishing survey was initially conducted within the 50-m release site, followed by subsequent surveys sampling 20-m sections of stream at 30-m intervals upstream and downstream of the release site (Fig. 4.1C). Surveys were carried out in both directions until zero eels were captured in three consecutive 20-m sites or an impassable barrier was encountered (Pedersen 2009). Any eels or trout seen but not captured during these surveys were recorded. At five randomly chosen sites, multiple-pass electrofishing surveys were conducted, with three upstream passes conducted without stop nets. In all cases, 100 % of trout and eels were caught or counted as ‘missed’ during the first upstream pass (Appendix 3, Table A1). All captured eels and trout were measured (total length; nearest mm) and released, with trout age classes assigned using length-frequency histograms (Fig. 4.2).

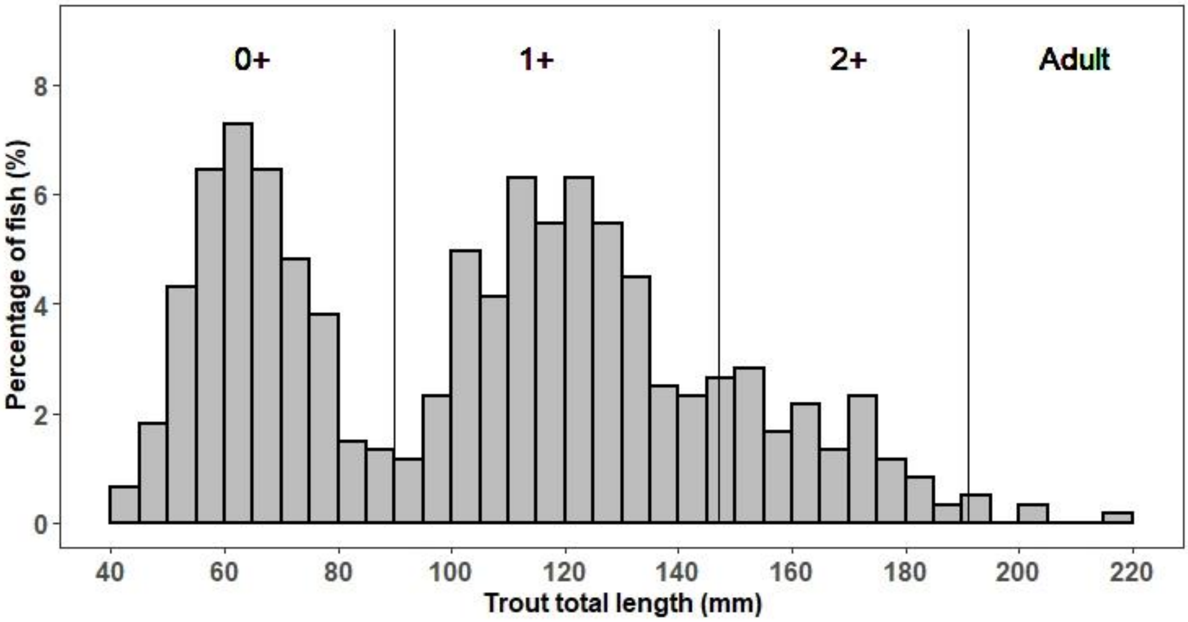

Figure 4.2: Length frequency histogram showing all brown trout captured during electrofishing surveys, as used to assign captured trout to approximate age classes

4.2.4 Stream habitat characterization

To ensure comparability between streams, a suite of physiochemical variables were recorded across three main spatial scales: (1) stream-level; (2) stream reach-level, and; (3) site-level (Fig. 4.3A, 4.3B; Appendix 3, Tables A2, A3):

For each stream, the following physical variables were recorded: total stream length above impassable barrier (km), highest stream altitude (m), channel gradient (%) and watershed area (km^2), with the latter two variables encompassing the catchment from the stream source to the first confluence downstream of the experimental stream reach. As only a single stream reach was stocked within each stream, all stream-level variables were also specific to individual stream reaches.

At a single location within each stream reach, the stream pH, temperature (°C) and conductivity (μmhos cm^{-1}) were recorded, with all major trace elements and heavy metals determined using inductively coupled-plasma mass spectrometry (ICPMS; Appendix 3, Table A3).

The following variables were also collected at every site: average channel width (m; measured across transects set perpendicular to the stream thalweg at four-meter intervals); average channel depth (cm; five depth recordings per width transect). The following site-level variables were estimated visually (%): proportion of wetted channel made up of pools, riffle, and smooth habitat; proportions of substrate within the following classes; boulder (diameter: $D > 40$ cm), cobble ($10 < D \leq 40$ cm), gravel ($1 < D \leq 10$ cm) and sand/silt ($D \leq 1$ cm); and a fish cover index (proportion of wetted channel with large/small woody debris, undercut banks, aquatic vegetation, boulder cover and overhanging vegetation).

4.2.5 Statistical analyses

Two separate Principal Component Analyses (PCAs) were carried out for stream reach-level chemical variables and for stream- and site-level physical variables. This was to ensure observed differences in eel numbers and lengths were not due to underlying habitat differences. Any elements recorded at concentrations under 0.05 ng ml^{-1} at all stream reaches were excluded from PCAs, as these were unlikely to affect fish health based on the recommended levels from the EU Water Framework Directive (European Commission, 2000). PCA calculations were then done via singular value decomposition of the centred and scaled data matrix.

Rosner's tests revealed 2 stream reaches (TL3 and TL7; Fig. 4.3B) to be mathematical outliers, based upon principal component 2 (PC2) scores from the chemical PCA. TL3 had elevated levels of magnesium (Mg), potassium (K) and nitrates (NO3) compared to all other stream reaches, indicative of fertiliser runoff/leaching from farmland (Withers and Lord, 2002). TL7 was found to have elevated levels of sulphates (SO4). Both had elevated levels of lead (Pb), with concentrations of 38.6 and 9.3 ng ml^{-1} respectively. Although lead bioaccumulation has well documented negative effects on aquatic life (Lee *et al.*, 2019), data from these stream reaches were not excluded from further analyses given the short overall duration of the study, and hence reduced potential for bioaccumulation, with a previous study indicating that short term exposure to higher concentrations of lead (300 ng ml^{-1} over 28 days) has minimal negative effects on juvenile eel biomarkers (Nunes *et al.*, 2014). Any bias as a result of this pollution would have been conservative (i.e. reducing observed differences between treatments) as both stream reaches were within the trout-free treatment group. All recorded chemical elements listed under the EU Water Framework Directive were within safe levels (Appendix 3, Table A3; European Commission, 2000).

Generalised additive mixed-effect models (GAMMs) were used to evaluate colonisation success, as indicated by surviving eel densities, with generalised linear mixed-effect models (GLMMs) used to investigate differences in eel lengths. For both model types, a combination of hypothesis testing and bidirectional model selection using the Akaike information criterion (AIC) was used to select the best fitting model. Specifically, variables of interest were included in all models. Both forward and backward stepwise selection was then run on a range of habitat variables to explain additional variation in the response variable, with the Akaike information criterion (AIC) used to evaluate model fit at each stage. In cases where AIC scores were extremely similar between models containing different numbers of predictor variables, Bayesian information criterion (BIC) scores were also used to inform model selection, thus decreasing the risks of model over-parameterisation. Only variables hypothesised to be of biological relevance were included during model selection, with these listed in Table 4.1, and only those covariates selected through both forward and backward selection were included in the final model.

Correlation matrices and variance inflation factors (VIFs) were used to identify any sources of collinearity between predictor variables prior to model selection. Model validation was applied to verify the underlying assumptions. Specifically, residuals were plotted versus fitted values to assess homogeneity of variance, and residuals versus each covariate to investigate model fit. Additionally, VIFs were calculated at each stage of model selection to check for multicollinearity. Predictions for each model were then used to visualise the effects of each covariate within the model on a similar and easily interpretable scale, using a range of values from the minimum to the maximum recorded values for the covariate of interest, while all other covariates were fixed at their mean values.

GAMMs were used to test whether the presence of trout affected eel survival, in line with H_1. These were preferred over GLMMs as they allowed prediction of more complex relationships between upstream and downstream dispersal distances and eel numbers than was possible through GLMMs. The three confirmatory zero electrofishing sites both upstream and downstream within each stream reach were removed from the data set, both for biological reasons since eels did not disperse this far, and to minimise zero-inflation. Eel number per site was then tested using a negative binomial distribution and with natural-logged site area as an offset variable. This was favoured over modelling density directly, due to extremely high zero-inflation (63 % zero values), positive skew (skewness = 4.2) and kurtosis (kurtosis = 19.4) in the response variable distribution. Dispersal distance (instream distance from the centre of each electrofishing site to the centre of the release site) was included in all models as the only smoothed term, with upstream dispersal recorded as a negative value. Trout presence/absence was included as a factor in all models, with stream reach included as a random effect. Bidirectional selection, as outlined above, was then used to select the best fitting model. GAMM predictions for the total survival of eels within both trout-free and trout-populated stream reaches (i.e. including areas not sampled) were then compared, assuming equal and constant stream widths, and with all other covariates included in the final model fixed at their mean values.

To test for a negative relationship between eel recapture rates and overall trout density (H_2), GAMMs were used to investigate the effect of trout densities on surviving eel densities within trout-populated stream reaches (n = 9). Eel number per site was tested using the same model structure as before, with two different modelling approaches then used, and with bidirectional selection again used to find the best fitting model from each approach. For the first approach, the response variable was modelled as a function of total trout density per site, whereas in the second the response variable was modelled versus trout densities within specific age classes. The final models from both approaches were then compared using AIC scores and covariate p-values. Predictions from the final model were then used to estimate eel survival and dispersal across varying densities of trout.

The relationship between eel length and trout abundance was investigated through generalised linear mixed-effect models (GLMMs), using the same model selection process as for GAMMs. Only data from sites where eels were recaptured, and hence measured (n = 21), were used. Mean eel length at each site was used as a response variable, using a normal distribution, and modelled as a function of the abundance of trout within specific age classes, with stream reach used as a random effect. Bidirectional selection was then applied to find the optimum model. Under ideal conditions, the dataset used for this analysis would be further subset to remove sites where only small numbers of eels (e.g. < 10) were recaptured to reduce the effects of individual variation in eel lengths. However, given the already small number of observations, including many sites where only a few eels were recaptured, this approach was considered unfeasible.

4.3 Results

4.3.1 Habitat data

No physical or chemical habitat variables differed significantly between the trout-free and trout-populated stream reaches. Both treatments were also physically and chemically similar based upon PCAs (Fig. 4.3A, 4.3B), with no significant differences between principal component scores for either the physical or chemical habitat variables between treatments (p > 0.05; Appendix 3, Tables A2, A3).

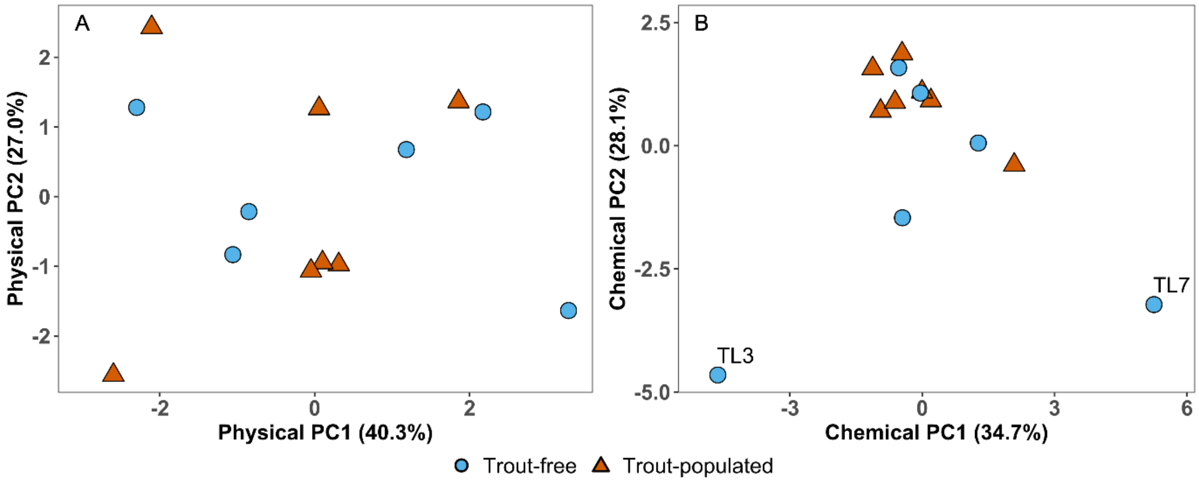

Figure 4.3: Principal component analysis summary, showing principal component scores based upon; A) physical variables, and; B) chemical variables. Outliers identified using Rosner’s tests are annotated

4.3.2 Eel survival and colonisation success

Of the approximately 11,700 eels released, 261 were recaptured in electrofishing surveys (recapture rate = 2.2 %), with the majority recaptured from trout-free stream reaches (n = 192; recapture rate = 3.6 %) rather than the trout-populated stream reaches (n = 69;

recapture rate = 1.1 %). This difference across treatments was highly significant when stream reach recapture numbers were compared by treatment (Welch's two sample t-test; $t = -5.0$, $df = 8.5$, $p < 0.001$).

Analysis of site data from both treatments through GAMMs showed a rapid decrease in eel numbers with increasing dispersal distance, both upstream and downstream from the release site (Table 4.1, Equation 1; Fig. 4.4A). Predictions from the final model indicated that for 900 eels released into a stream reach measuring 780 m instream length (265 m upstream, 515 m downstream of release site), with a constant stream width equal to the average from all sites (1.7 m), eel survival would be approximately twice as high in trout-free stream reaches as trout-populated stream reaches (trout-free eel number ± SE = 32.6 ± 9.6, trout-populated eel number ± SE = 15.0 ± 4.5). This equates to 3.6 ± 1.1 % and 1.7 ± 0.5 % survival for trout-free and trout-populated stream reaches respectively (Fig. 4.4A). This model also showed a significant and positive relationship between pool percentage and eel density (Fig. 4.4B)

Analysis of site data from trout-populated stream reaches using GAMMs indicated that 2+ trout density is significantly and negatively correlated with eel density (Table 4.1, Equation 2; Fig. 4.4C, 4.4D). 0+ trout density was weakly and positively correlated with eel density, while riffle percentage was weakly and negatively correlated with eel density, although both variables were excluded from the final model (Appendix 3, Table A5). Overall trout density was not significantly correlated with eel density, being excluded during model selection in all cases.

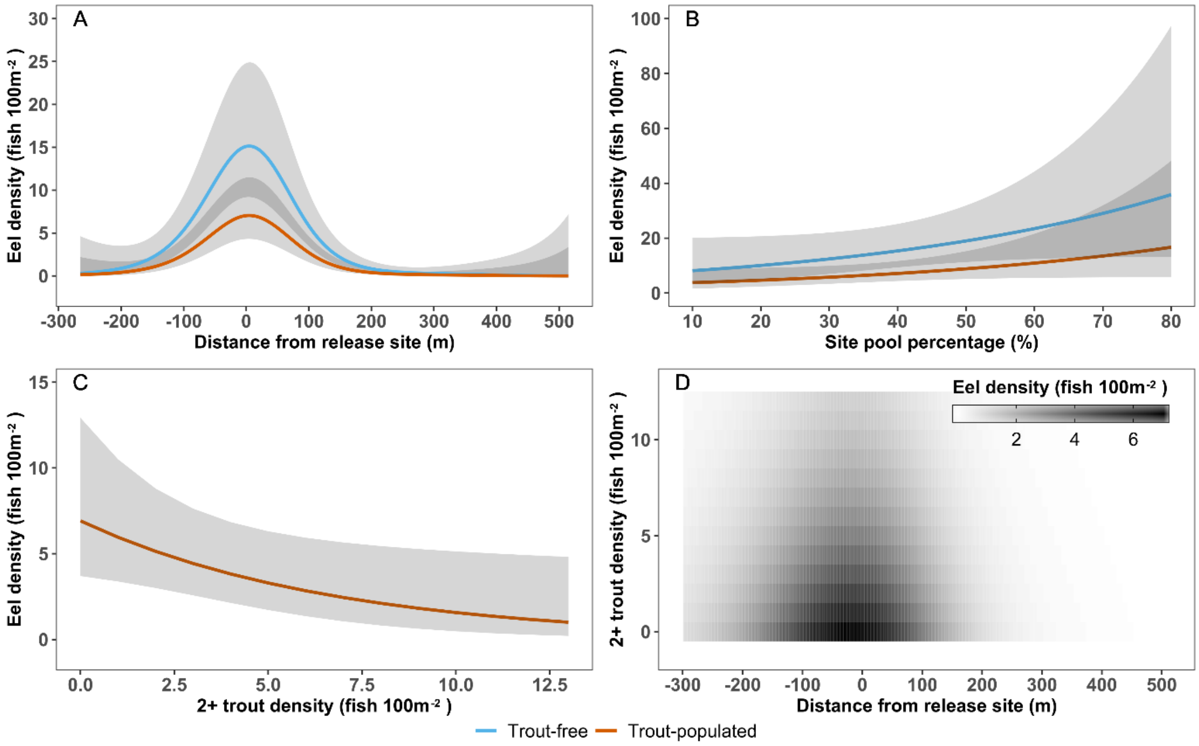

Figure 4.4: Predicted eel densities in relation to; A) dispersal distances for trout-free and trout-populated stream reaches, based on equation 1 (negative dispersal distances indicate upstream dispersal); B) pool percentages for trout-free and trout-populated stream reaches at the release site, from equation 1; C) varying densities of 2+ trout at the release site, from equation 2, and; D) dispersal distances and densities of 2+ trout for a trout-populated stream reach, from equation 2. Predictions were calculated with all other model covariates set to their mean values. Shaded areas represent 95 % prediction intervals.

4.3.3 Eel lengths

Eels recaptured from trout-populated stream reaches were slightly larger than those from trout-free stream reaches (mean trout-free total length ± SD = 84.2 ± 9.1 mm, n = 115; mean trout-populated total length ± SD = 88.9 ± 13.5 mm, n = 51; Fig. 4.5A, 4.5B), with this difference near-significant (Mann-Whitney U test; U = 3468, p = 0.06). Analysis of site data from trout-populated stream reaches through GLMMs showed that 0+ trout density was significantly and negatively correlated with eel length (Table 4.1, Equation 3; Fig. 4.5C), while 1+ trout density was positively correlated with eel length. 2+ and adult trout densities were both positively correlated with eel length but were excluded from the final model, likely due to relatively lower abundances (Appendix 3, Table A6). Accordingly, when trout in the 1+, 2+ and adult age classes were grouped into a combined density variable, this was significantly and positively correlated with eel length (Table 4.1, Equation 3; Fig. 4.5D), and produced a model with a lower AIC score than when age classes were modelled separately. In this model 0+ trout density, mean depth and substrate gravel proportion were all found to be negatively correlated with eel length (Table 4.1, Equation 3). Neither overall trout density nor eel density were found to be significantly correlated with eel length, with both being excluded during model selection in all cases.

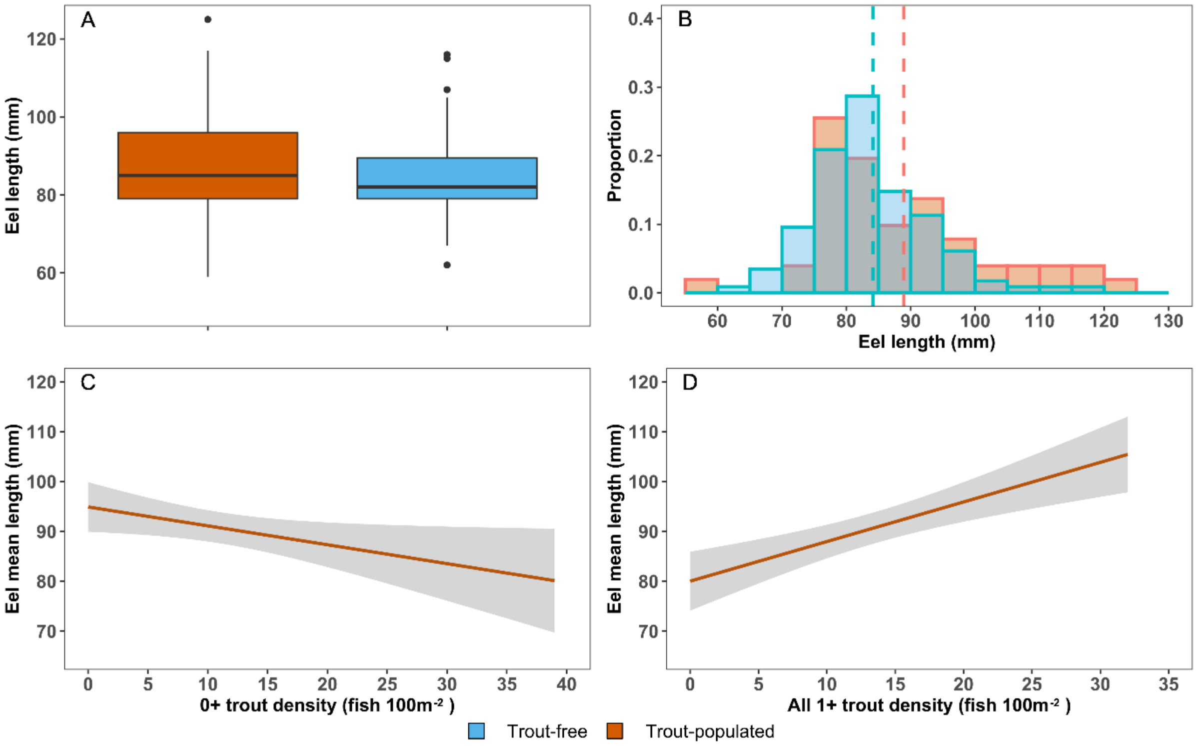

Figure 4.5: A) Recaptured eel lengths within trout-free and trout-populated stream reaches; B) Eel length frequency histogram for trout-free and trout-populated stream reaches, dashed lines represent group means; C) Predicted eel length at recapture with varying densities of 0+ brown trout, and; D) Predicted eel length at recapture with varying densities of 2+ brown trout. Predictions are based upon equation 3, with all other covariates within the model set to their mean values and for the same stream reach. Shaded areas represent 95 % prediction intervals

Table 4.1: GAMM and GLMM equations (#) and covariates. Statistically significant results are shown in bold

#	Model type	Formula	Dataset	N obs.	Variables available for selection	Selection	Covariate(s)	Estimate/ *edf.*	Standard error/ *ref df.*	Z value/ *chi squared*	P value
1	GAMM	*Eel number ~ s(Dispersal distance) + Treatment + Pool percentage + (1|Stream reach), Offset = log$_n$(Site area)* Response variable distribution = Negative binomial	All sites	131	Pool percentage, Riffle percentage, Mean depth, Gravel percentage, Cobble percentage, Boulder percentage	Appendix 3, Table A4	Intercept	-5.58	0.56	-9.89	**< 2 x *10^{-16}***
							Treatment	0.78	0.29	2.71	**0.007**
							Pool percentage	0.02	0.01	1.85	**0.06**
							s(Dispersal distance)	*3.57*	*3.57*	*57.17*	***5.34 x 10^{-10}***
2	GAMM	*Eel number ~ s(Dispersal distance) + 2^+ trout density + (1|Stream reach), Offset = log$_n$(Site area)* Response variable distribution = Negative binomial	All sites within trout populated stream reaches	72	0^+ trout density, 1^+ trout density, 2^+ trout density, adult trout density, Pool percentage, Riffle percentage, Mean depth, Gravel percentage, Cobble percentage, Boulder percentage	Appendix 3, Table A5	Intercept	-4.19	0.41	-10.18	**<2 x 10^{-16}**
							2^+ trout density	-0.20	0.08	-2.39	**0.02**
							s(Dispersal distance)	*2.42*	*2.42*	*11.48*	***0.004***
3	GLMM	*Eel length ~ All 1^+ trout density + Mean depth + Gravel proportion + 0^+ trout density + (1|Stream reach)* Response variable distribution = Gaussian	All sites within trout populated stream reaches with 1 or more eels captured	21	0^+ trout density, all 1^+ trout density, Eel density, Pool percentage, Riffle percentage, Mean depth, Gravel percentage, Cobble percentage, Boulder percentage	Appendix 3, Table A6	Intercept	120.00	8.63	13.91	**< 2 x 10^{-16}**
							All 1^+ trout density	0.81	0.19	4.21	**2.61 x 10^{-5}**
							Mean depth	-1.12	0.32	-3.56	**0.0004**
							Gravel proportion	-0.50	0.17	-3.00	**0.003**
							0^+ trout density	-0.39	0.18	-2.16	**0.03**

4.4 Discussion

The main aim of this study was to investigate the effects of brown trout presence and abundance on the success of eel colonisation. There was strong support for the initial hypothesis (H_1) that the presence of brown trout would negatively affect colonisation success. There was no direct support for the hypothesis (H_2) that there would be a negative relationship between eel recapture rates and overall trout density. However, the results do highlight a strong link between age 2+ trout density and eel survival, while also providing evidence for selective pressure towards larger individuals in trout-populated stream reaches. Extremely low overall recapture rates and limited dispersal were recorded across both treatments, findings also reported from other eel colonisation studies (Pedersen, 2009b). These findings hence have clear implications for translocation and stocking programmes for this and other species.

Recorded eel densities across both treatments were lower than those of naturally recruited populations of upland streams (Laffaille *et al.*, 2003). Three likely explanations were considered for this finding. Firstly, the harsh, high velocity, low temperature lotic environment may have reduced survival rates, as noted from a previous study on elver stocking (Pedersen, 2009a). Secondly, the act of translocating small juveniles to novel habitats likely increased mortality rates. Finally, the survival of introduced animals following captive rearing is often low (Mathews *et al.*, 2005), with this often linked to reduced natural selection and imposed artificial selection for traits which may be deleterious under natural conditions (McDougall *et al.*, 2006; Araki, Cooper and Blouin, 2007; Araki *et al.*, 2008). The short captive rearing period may have minimised these effects, while also providing a buffer to mortality during a period when natural mortality is likely very high for this species (White and Knights, 1997), although it could be argued that high natural mortality may also result in intensive natural selection. These points are particularly relevant given the likely naivety of these juvenile eels to upland stream environments, given their capture in an estuary and subsequent holding in captivity.

As well as an overall effect of trout presence, the results of this experiment also appear to show a clear threshold, in terms of trout densities, for successful colonisation by juvenile eels. 85 % of the electrofishing sites with 2+ trout densities of 5 fish 100 m^{-2} or greater had no eels, with the remaining sites each having a single eel. This may therefore represent a density above which translocated eel juveniles struggle to survive in these environments, with this also demonstrated in GAMM results. Predation and competition represent the most likely mechanisms behind the negative effect of trout presence, and 2+ trout densities, on eel numbers. Brown trout are piscivorous at larger sizes (≥ 100 mm total length; Mittelbach and Persson, 1998), and are highly aggressive and territorial within fluvial environments (Titus, 1990; Jonsson *et al.*, 1999), frequently causing population declines in other fish species (Crowl *et al*. 1992; McIntosh *et al*. 1994; Townsend, 1996). The predation hypothesis is in line with previous research, which has indicated that the primary mechanism for biotic resistance to species colonisation in aquatic ecosystems is generally predation rather than competition (Alofs and Jackson, 2014). Moreover, brown trout and European eels generally have little overlap in their diet (Mann and Blackburn, 1991), meaning that competitive interactions between these species are likely to be minimal. However, while inferences may be drawn from the results of this study, in the absence of study-specific dietary data, the possibility that this effect relates to competition between these species cannot be entirely eliminated.

Although some 1+ trout exceeded the ‘threshold’ size for piscivory (Mittelbach and Persson, 1998), it is unlikely that these fish would have been able to feed upon eels in this study. Salmonids are gape-limited predators (Winters and Budy, 2015), although they can consume large prey relative to their own body size (> 60 % of total length in cutthroat trout, *Oncorhychus clarkii,* and 48 % of total length in tiger trout *Salmo trutta* x *Salvelinus fontinalis*; Winters and Budy, 2015). Given mean eel total length was ≈ 86 % of the total length of the smallest piscivorous trout, most eels were likely too large for 1+ trout to predate upon. Hence, the non-significant effect of 1+ trout is in line with predation being the driving factor behind the observed differences between treatment groups, as all trout age classes exhibit aggression and territorial behaviour (Titus, 1990). However, it must be noted that the significant effect of the combined 1+ through to adult trout age class variable on eel lengths does suggest either that some predation by 1+ trout upon eels did occur, potentially on the smallest eel individuals, or that these fish exhibited other behaviours (e.g. territoriality) which reduced survival of smaller eels.

In comparison, all trout within the 2+ age class exceeded the threshold size for piscivory, and were within the relative predator vs. prey size ranges reported by Winters and Budy (2015), with the significant effect of these on eel numbers potentially providing support for the predation hypothesis. Although the non-significant effect of adult trout is in contrast with this hypothesis, this may have been due to their low abundance. Within trout-populated stream reaches adult trout mean density ± SD was 1.25 ± 2.26 fish 100 m^{-2} and densities never exceeded 11.11 fish 100 m^{-2}.

The reason behind the weak positive correlation between 0+ trout density and eel density, despite the former being excluded from the final model, remains unclear. Collinearity, where both eel density and 0+ trout density were negatively correlated with 2+ trout density, was not a factor, as 0+ and 2+ trout densities were not significantly correlated. Previous studies suggest this effect is unlikely to be due to overlap in habitat utilisation, with eels favouring benthic habitat and slower flows, whereas salmonids, and particularly juveniles, inhabit faster flows (Bjornn and Reiser, 1991; Lamouroux *et al.*, 1999; Foldvik *et al.*, 2012). Furthermore, eel density was found to be negatively correlated with riffle percentage, with riffles forming a key habitat for 0+ trout (Heggenes, Bagliniere and Cunjak, 1999). However, the negative correlation between 0+ trout density and eel length may indicate some degree of niche overlap, with interspecific competition potentially reducing growth rates of juvenile eels (Larkin, 1956; Cuenco, Stickney and Grant, 1985; Welker, Pierce and Wahl, 1994).

This study highlights both the benefits of such translocation programmes as those employed by EU countries, and the challenges behind ensuring their success. The low survival rate of eels in this study means the use of such methods should be carefully considered in the context of the global decline in juvenile glass eel abundance, with the investment in terms of juveniles high relative to the potential return in terms of migratory adults. This is critical given survival was only studied over a short period (3 months), while the freshwater feeding phase of eels frequently lasts over 15 years (Vøllestad, 1992; Svedaung, Neuman and Wickström, 1996). Total mortality over this period may be much higher, even accounting for decreasing mortality with increasing size (Lorenzen, 1996).

Given the conflicting and inconclusive evidence for multiple hypotheses relating to interspecific interactions, it seems likely that the observed relationships are underpinned by a more complex web of such interactions. More research is clearly required across a wider range of habitats and fish densities to make firmer conclusions regarding the extent and mechanisms of these interactions. Additionally, while the ability to isolate the effect of a single species on colonisation success was valuable for this study, it is generally accepted that increasing species richness will reduce colonisation success (Elton, 1958). Hence, colonisation success may be hampered in higher order streams with greater species richness, and thus a greater array of competitors and predators, although this may be offset by more favourable environmental conditions (e.g. slower flows, higher macroinvertebrate abundance). Such research would also have direct implications for the conservation of other anguillids. Many Anguillid species (e.g. *A. rostrata, A. japonica, A. dieffenbachii*) are classified as endangered by the IUCN (Jacoby and Gollock, 2014b, 2017; Pike, Crook and Gollock, 2019) and all co-occur with native or invasive salmonids, or both, within their ranges. Given that piscivory and aggressive territorialism are shared traits among most salmonids, similar relationships are likely present (Milner *et al.*, 2003).

4.5 Conclusions

In summary, there is a clear and pressing need to understand the conditions under which translocation programmes can be successfully applied and how they may be adapted to account for environmental factors, including existing species assemblages. This research has clearly shown that failing to account for such factors, for example by stocking eels into harsh upland streams populated by brown trout, will result in poor eel survival and may in fact act against conservation aims for this species. Notwithstanding, where appropriately applied with consideration given to the above factors, such methods show evident promise and their application to other species which face similar population decline, including other Anguillids, should be tested as a matter of urgency.

Chapter 5: Efficacy of intra-basin translocations of post-emergent larvae as a population enhancement tool in Atlantic salmon

Abstract

Atlantic salmon populations have experienced significant declines across their range over the last 50 years, with established management practices, such as supplemental stocking of hatchery reared fish, having little beneficial effect and potentially exacerbating population declines. This study tested a novel method by which freshwater production of salmon may be increased by reducing the naturally high level of density-dependent mortality in the initial weeks and months following fry emergence from spawning gravels. Emergent fry densities were recorded through area-delineated single pass electrofishing surveys across two years within 6 areas of the River Erriff catchment, Ireland. Fry were then translocated from identified high fry density sites, characterised by large quantities of suitable substrate for spawning, adipose fin clipped, and released at identified low density sites, generally characterised by lower quantities of suitable spawning substrate. Electrofishing surveys were carried out in autumn of both years to determine autumn fry densities. At the degree of density manipulations carried out in this study translocations were found not to have a significant effect on autumn fry densities, either at sites where fry were removed or where fry were released. Thus, while the beneficial effects of translocations in recipient sites might only be measurable when higher numbers of fish are moved, the process did not affect autumn densities at donor sites, indicating the method should not have deleterious impacts on fry densities across larger spatial scales.

5.1 Introduction

Population declines are an increasing feature of many anadromous species, where anthropogenic pressures, such as climate change, exploitation and habitat fragmentation, are impacting their ability to complete their complex lifecycles (Parrish *et al.*, 1998; Limburg and Waldman, 2009; Mills *et al.*, 2013). Atlantic salmon, a species of high cultural, recreational and economic importance (Morton *et al.*, 2016; Ignatius and Haapasaari, 2018), are no exception, having experienced considerable declines in populations across their range in the last 50 years (Parrish *et al.*, 1998; Limburg and Waldman, 2009; Mills *et al.*, 2013; ICES, 2018). These declines have resulted in their populations being subject to high conservation and management efforts that aim to restore population sustainability (Skaala *et al.*, 2014).

Management efforts to ensure sustainability of Atlantic salmon populations have tended to focus on the freshwater phases of their lifecycle (Skaala *et al.*, 2014; Gibson, 2017; Koed *et al.*, 2020). Attempts to increase the spawning effort of adults have included improving upstream passage at migration barriers, sometimes by their removal, but more usually by installing fish passes (De Leaniz, 2008; Koed *et al.*, 2020), and by improving spawning habitats, such as by cleaning gravels of silt and/or gravel reinstatement (Semple, 1987; Hendry *et al.*, 2003; Cawley, 2017; Rachelly *et al.*, 2021). While juvenile recruitment can then be enhanced through habitat works to improve nursery areas (Hendry *et al.*, 2003; Koljonen *et al.*, 2013), attempts to increase the overall numbers of juveniles and emigrating smolts are often unsuccessful (Mitchell *et al.*, 1998; Solazzi *et al.*, 2000; De Jalón and Gortazar, 2007). An alternative approach is releasing large numbers of hatchery reared fish (Naish *et al.*, 2007; Bacon *et al.*, 2015). The driver of this is often to improve long-term success in recreational fisheries, as increasing the number of juveniles is posited as increasing numbers of emigrating smolts and, subsequently, the number of returning adults available for capture (Aas *et al.*, 2018). However, studies increasingly suggest that stocking is often unsuccessful due to, for example, low survival rates of hatchery reared fish (Jonsson, Jonsson and Hansen, 2003; Araki *et al.*, 2008; Thorstad *et al.*, 2011). This low survival is, at least in part, due to artificial selection for traits which are beneficial in the hatchery but have negative consequences in the wild (Araki *et al.*, 2008; Roberts, Taylor and Garcia de Leaniz, 2011; Stringwell *et al.*, 2014). Consequently, the number of returning adults produced from these hatcheries relative to the level of investment can be low (Jonsson, Jonsson and Hansen, 2003; Araki *et al.*, 2008), while hatchery fish can also detrimentally impact wild salmonid populations through genetic introgression where interbreeding occurs (Araki, Cooper and Blouin, 2007; Christie *et al.*, 2012).

As a consequence of the negative impacts of hatchery reared salmon, there has been an increasing shift towards the decommissioning of hatcheries, with alternative conservation strategies, such as habitat improvement schemes and imposition of stricter regulations on commercial and/or recreational fishing now being more commonly applied (Harrison, Hauer, *et al.*, 2019). However, both the removal of fish hatcheries and enforcement of alternative conservation measures, and particularly catch-and-release fishing regulations, may be contentious with some recreational anglers and riparian owners. There are multiple examples where controversy amongst stakeholders has surrounded the closure of salmon hatcheries (Harrison, Rybråten and Aas, 2018; Harrison, Hauer, *et al.*, 2019; Harrison, Kochalski, *et al.*, 2019). Additionally, although qualitative data are limited, previous studies on other species have indicated that imposition of mandatory catch-and-release fishing regulations may be unpopular with some anglers and can lead to decreased angling participation in fisheries (Arlinghaus *et al.*, 2007), as shown for Atlantic salmon and other salmonid species (Johnston *et al.*, 2011; Olaussen, 2016). These latter points are important, as these stakeholders often fund conservation activities directly or indirectly, for example through angling licence sales, angling clubs, and fishing permit sales, the values of which are often considerable (Pitcher and Hollingworth, 2008; Butler *et al.*, 2009; Liu, Bailey and Davidsen, 2019).

There is thus an increasing need for an alternative management approach that can increase juvenile salmon production and does not impact long-term population sustainability, while also accounting for recreational anglers' and other stakeholders' concerns. This could be based on manipulating the high intra-catchment variability in juvenile salmon production, where sites of strong spawning effort are often restricted spatially (Moir *et al.*, 2004; Armstrong, 2005; Finstad *et al.*, 2010; Foldvik, Finstad and Einum, 2010). Areas of high spawning effort tend to be characterised by good quality spawning gravels, with these generally being patchily distributed within catchments, resulting in spatial variations in egg densities and larval production (Webb *et al.*, 2001; Armstrong, 2005; Finstad *et al.*, 2010; Foldvik, Finstad and Einum, 2010). With the dispersal of these juvenile salmon life stages being limited in their first summer of life, areas of high larval production are then subject to strong density-dependent mechanisms, which have direct negative effects on survival rates in an early life regulatory phase (Einum and Nislow, 2005; Imre, Grant and Cunjak, 2005; Einum, Sundt-Hansen and Nislow, 2006; Einum, Nislow, Mckelvey, *et al.*, 2008). These mechanisms may also result in later indirect effects following this regulatory phase, for example through lower initial growth and subsequent smaller body size affecting predation risk (Hyvärinen and Vehanen, 2004; Fritts and Pearsons, 2006), and size and/or age at smoltification, which can then affect survival at sea (Jonsson, Jonsson and Hansen, 1998a; Milner *et al.*, 2003; Saloniemi *et al.*, 2004; Gregory *et al.*, 2019). Correspondingly, Atlantic salmon stock-recruitment curves are generally theorized as dome-shaped, as described by the Ricker model (Schnute and Kronlund, 2002; Honkanen, Boylan, *et al.*, 2018), or flat-topped (Buck and Hay, 1984; Jonsson, Jonsson and Hansen, 1998b), as reviewed in Milner *et al.* (2003).

Here, it was posited that net salmon production for a catchment can be increased by intra-catchment translocation of post-emergent salmon larvae (‘fry’ hereafter) from areas of high fry density to lower density sites. As sites of high fry production would otherwise be subject to high density-dependent mortality rates, the removal of surplus fish in the initial post-emergence period should reduce the strength of these mechanisms, offsetting the initial reduction in fry numbers through increased survival rates, while also theoretically increasing growth rates. Increasing densities in the low production areas should then result in increased numbers surviving their first summer of life, with no significant effect on growth or mortality, providing densities do not exceed those at which density-dependent mechanisms act, and such areas contain sufficient suitable habitat for salmon fry (i.e. stream carrying capacity is not exceeded). This should then result in increased smolt production rates and average smolt lengths (and/or reduced smolt ages) at a catchment level, increasing marine survival probabilities, and result in higher numbers of returning adults (Gregory, Armstrong and Britton, 2018; Gregory *et al.*, 2019). This method also eliminates or minimises many of the problems associated with hatchery rearing practices, such as artificial selection processes and subsequent genetic introgression with wild fish.

Thus, the aim of this study was to test the efficacy of a novel management tool for improving juvenile salmon production through translocating post-emergent fry from sites of high density (i.e. those sites with optimum spawning habitat) to low density sites (i.e. sites with poor spawning habitat but good nursery habitat). Use of control and treatment experimental sites of low- and high post-emergent larval densities on the River Erriff, Ireland, enabled the following hypotheses (H) to be tested: (H_1) spring (post-emergent) juvenile abundances vary spatially across the study area, with higher abundances in areas of higher gravel abundance; (H_2) autumn juvenile salmon abundances are higher at low density fry recipient sites than their equivalent low density control sites, and abundances at high density donor sites are not significantly lower than at high density control sites; (H_3) net autumn fry density across all treatment sites, considered together, is greater than the net density at control sites when considered together; (H_4) growth rates at recipient low density sites are not significantly lower than their control sites, and growth rates at high density donor sites are higher than at high density control sites.

5.2 Methods

5.2.1 Study river and sites

The River Erriff catchment is located on the west coast of Ireland on the border between counties Mayo and Galway, with the watershed covering an area of approximately 163 km^2 (MacCarthaigh, 1997; Fig. 5.1A, 5.1B). This spate river has been renowned for its substantial populations of both Atlantic salmon and anadromous brown trout, with a mean annual adult salmon run of 2533 fish since 1986 (IFI, unpublished), and is listed as the salmonid index catchment for the RoI. Within the Natura 2000 network, the River Erriff forms part of the Mweelrea/Sheeffry/Erriff Complex Special Area of Conservation

(SAC), for which Atlantic salmon are listed as one of the features of interest (NPWS, 2017).

The river catchment comprises the Erriff mainstem, formed by the confluence of the Owenmore and Owenwee Rivers, and 4 further major tributaries (Fig. 5.1C). The Owenmore River is the largest tributary of the Erriff and can be split into two distinct sections, the upper and lower Owenmore, delineated by its confluence with the Sheeffry river. The rivers Derrinkee and Derrycraff form the Owenwee at their confluence. The Glendavoc river flows directly into Tawnyard Lough, with the outflow from this lake, known locally as the black river, flowing directly into the Erriff mainstem (Fig. 5.1C). The primary land use throughout the catchment is sheep grazing, with varying levels of stream boundary protection, although some areas of the upper Erriff mainstem are characterised by ancient oak woodland (approximately 0.2 km^2). All areas of the catchment also contain small (total area $\approx$ 15 km^2) coniferous plantations, of which approximately 3.6 km^2 directly adjoin river sections included in this experiment.

For the purposes of this experiment, only the rivers Sheeffry, Owenmore (upper), Glendavoc, Derrinkee and Derrycraff, plus the Erriff mainstem, were included, forming 6 major catchment areas (Fig. 5.1C, 5.1D). Historical electrofishing data, collected from time-delineated September electrofishing surveys (5-minute single pass surveys) conducted since 2007 as part of statutory monitoring, indicates that higher fry densities are generally found within the upper and middle reaches of the Erriff mainstem, as well as the Owenmore and some lower stretches of the Sheeffry and Glendavoc, while lower fry densities are generally found within the upper reaches of each of the 4 aforementioned tributaries (IFI, unpublished). While these data only provide a proxy for spawning effort, given the poor dispersal ability of salmon fry outlined earlier, they suggest the spatial distribution of spawning effort and densities of juveniles are unevenly distributed through the catchment.

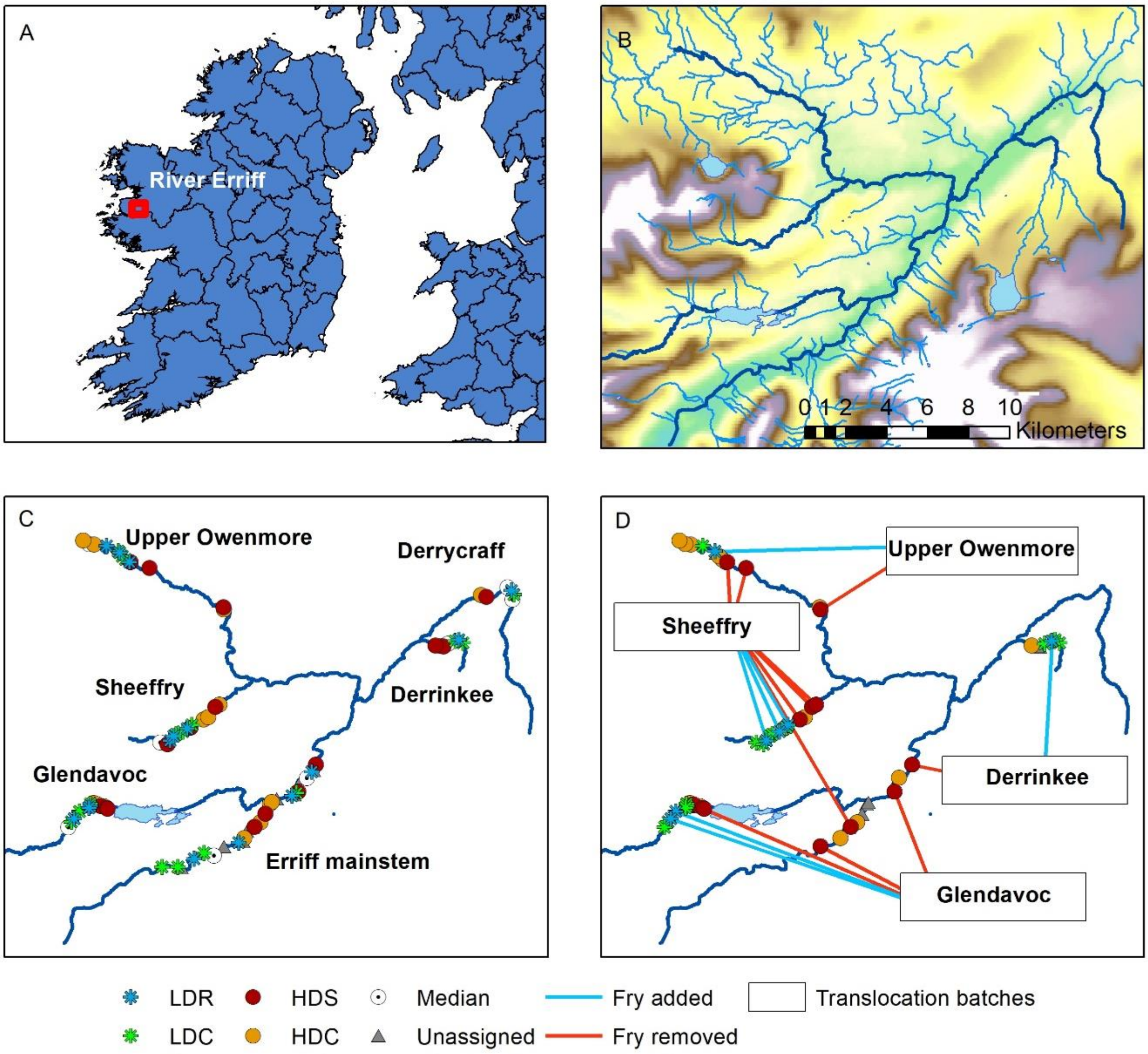

Figure 5.1: Maps showing; A) Location of Erriff catchment; B) greater Erriff catchment, including smaller tributaries not included in the experiment, with elevation shown; C) location and designation of experimental sites in 2019, with catchment areas labelled; and D) location and designation of experimental sites in 2020, with translocation batches labelled

5.2.2 Experimental design

Two sets of translocation experiments were completed in this study: summer 2019 ('Year 1 experiment') and summer 2020 ('Year 2 experiment'). While there were some differences between the two experiments in how they were designed, their basic components were similar, involving pre-translocation surveys (late spring/summer), translocation (June/July), and assessment of fry numbers at the beginning of autumn (August/September).

5.2.2.1 Pre-translocation surveys

The aim of these surveys (hereafter 'spring fry surveys') was to determine densities of post-emergent salmon fry prior to translocation to provide baseline comparative data to post-translocation surveys at the beginning of autumn. Prospective experimental sites that contained suitable fry riffle habitat were selected after completion of preliminary walkover surveys throughout all 6 catchment areas between the 5th and 10th of June 2019. Each site consisted of a 20-m instream length section of river channel, and sites were chosen to be as similar as possible, avoiding inclusion of features such as undercut banks, islands and split channels wherever possible. Of the prospective sites, 80 were then chosen for electrofishing surveys between June 25th and July 8th of Year 1 (2019), and 58 between June 16th and 25th of Year 2 (2020). Prior to sampling, upstream and downstream boundaries of all sites were marked on both banks using brightly coloured marker posts, which were then photographed *in-situ* after survey completion and geo-referenced to enable their subsequent location without needing permanent site markers.

The electrofishing equipment consisted of portable Hans Grassl backpack units (model IG600) set between approximately 115 and 200 V continuous direct current (DC), as per Chapter 2. Electrofishing surveys in both years were conducted by the same operator (LC) to provide standardisation. Prior to fishing, water levels at each site were estimated and categorised as either 'very low', 'low' or 'normal' (higher flow categories were unnecessary as fishing was not completed in such conditions). Fishing was always in an upstream direction, starting from the downstream site boundary, and comprised a single pass. During fishing, captured fish were held in water, with fish observed but not captured also counted by species. Post-fishing, captured Atlantic salmon and brown trout fry and parr were identified to species, measured for total lengths (TL, nearest mm) and then released. Larger trout and any other species captured were counted and released without measurement. During spring electrofishing surveys salmon and trout fry could be easily distinguished due to differences in both size and colouration. Thus, any salmonid fry which were missed were assigned to either species based on visual ID.

After the completion of electrofishing, the physical parameters of the sites were measured. This was completed by setting transects perpendicular to the direction of flow at 5-m intervals along each 20-m site, starting at the upstream boundary markers and finishing at the downstream boundary. Wetted width (m) was recorded for each transect and river depth (m) was recorded at 5 points along each transect (left bankside edge, ¼ width from the left bank, channel centre, ¼ width from the right bank, right bankside edge). These data enabled post-emergent salmon and trout fry densities to be determined (n 100 m^{-2}).

5.2.2.2 Translocation method: Year 1

In Year 1, the salmon fry densities for sites within each catchment area were analysed for their distributions, with median site-level fry densities assigned for each of these areas, based on up to 2 sites. Median values were considered to best represent the average spawning potential (and hence post-emergent salmon fry density) for each catchment area due to the non-parametric (zero-inflated and positively skewed) distribution of the fry densities. Sites with fry densities below the median were then assigned as low density (LD), whereas those above the median were assigned as high density (HD). LD and HD sites were then evenly split to provide two groups: controls (no manipulation) and treatment (manipulation; Appendix 4, Table A1). In LD treatments, salmon fry were translocated into the sites and so these were labelled ‘Low Density Recipient’ (LDR) sites; ‘LD Control’ (LDC) sites were then their comparator group in autumn surveys. In HD treatments, salmon fry were removed and translocated into LDR sites, and thus these were fry source sites, referred to hereafter as ‘High Density Source’ (HDS) sites, HD controls were labelled ‘High Density Control’ (HDC) sites and were the comparator group for HDS sites in autumn. The designation of sites to control or treatment groups was initially done numerically, involving the ranking of sites according to fry density and designation as alternating treatments and controls. This was then adjusted to account for the geographical position of sites to ensure site independence where possible, for example, by avoiding placing LDR sites immediately upstream from LDC sites (Fig. 5.1C).

Following the selection of the LDR, LDC, HDS and HDC sites in each area of the catchment, the translocations were executed. In year 1, translocations always occurred within the catchment areas, with no movements between areas (Appendix 4, Table A1).

The numbers of fish to be removed from HDS sites were calculated as the number of fry that could be removed from each site without reducing fry density below the density of the median site(s) for that catchment area. For example, for a HDS site with a fry density of 120 fish 100 m^{-2} in a catchment area with a median density of 50 fish 100 m^{-2}, then a maximum of 70 fish per 100 m^2 of HDS site area could therefore be removed for translocation (i.e. reducing density from 120 to 50 fish 100 m^{-2}). The translocations were completed using the same electrofishing equipment and survey design as outlined previously (upstream, single pass). In all cases, to avoid edge effects (i.e. immigration of fish into HDS sites from surrounding areas that were also of relatively high density), the area fished consisted of the 20-m site plus 10 m upstream and downstream of the upstream and downstream boundary markers respectively. Most sites within this study were situated in riffle-pool-run type habitat, with large pools between suitable riffle habitats. This habitat structure likely serves to partially isolate individual riffles, with deeper pools mostly unsuitable for colonisation by post-emergent salmonid fry, primarily due to competition and predation from older salmonids, and particularly brown trout (Kennedy and Strange, 1986; Bardonnet and Heland, 1994; Heggenes, Bagliniere and Cunjak, 1999; Armstrong and Nislow, 2006). Hence, this was considered the most effective way of minimising immigration into source sites. Collection of fry from HDS sites was conducted rapidly to minimise the risk of mortality, with fishing within each area of the site conducted in a downstream-upstream order (i.e. downstream marginal area, within-site area, upstream marginal area). Fishing was concluded when the maximum number of fry for donation was reached or when all 3 areas had been fished, whichever occurred first.

To enable identification of translocated versus non-translocated (i.e. native) salmon fry in subsequent surveys, a non-lethal marking technique was required. With the fish too small to have tags applied to them, adipose fin excision (‘clipping’) was used, which is considered to be suitable for mass marking of salmonid fishes where individual identification is not required (Andrews *et al.*, 2015). This was completed through placing the fish into an anaesthetic bath (MS-222; approximate concentration = 15 mg l^{-1}) until stage 2 anaesthesia (loss of reactivity to external stimulu and partial loss of equlibirum; Iversen et al., 2003), before their placement on a wetted v-cut sponge for support, with adipose fin excision carried out using micro-point scissors. Fish were then placed into freshwater in a separate designated container for recovery. Following recovery, the fish were then transferred to a 60-litre, aerated transport tank for transportation. This procedure of capture, marking and transport was then repeated for all fry source sites within each given catchment area before their release, resulting in a single pooled batch of fish from all sites combined. Bags containing ice were submerged in the transport tank to prevent water temperatures exceeding 16 °C.

The number of fry to be released into each LDR site was calculated as the number required to raise each site to the density of the median site(s), as a proportion of the total number of fry required to raise all LDR sites within that catchment area to the median. For example, for a catchment area with 3 LDR sites of equal areas with densities of 10, 20 and 30 fish 100 m^{-2} respectively and a median density of 50 fish 100 m^{-2}, the target numbers of fry to be released for each LDR site would be 40, 30 and 20 fish per 100 m^2 of site area respectively (representing approximately 44 %, 33 % and 22 % of the captured fry total). The number of fry actually collected was then divided between LDR sites according to these proportions (Appendix 4, Table A1). As with HDS sites, and in order to reduce edge effects, fry were also stocked into two 10-m sections immediately upstream and downstream of each LDR site at the same stocking rate (i.e. half the number of fry as the central 20-m section per 10-m section). Therefore, at each recipient site, donated fry were released according to the numbers designated for each of the three areas of each release site (downstream 10-m section, within-site 20-m monitored section, upstream 10-m section) resulting in a 40-m stocked section of channel per site. This was done by walking upstream releasing fry in small numbers as evenly as possible throughout the channel. All translocations took place between July 9th and 12th in 2019.

5.2.2.3 Translocation method: Year 2

For the Year 2 experiment, some modifications were made to the Year 1 method. Spring fry surveys were earlier (between June 16th and 25th) to enable earlier translocations. LDC sites within the Erriff mainstem catchment area were not included and the Derrycraff catchment area was excluded from the 2020 experiment, with the number of LDR sites reduced from 15 to 7 (Fig. 5.1D; Appendix 4, Table A1). Additionally, to expedite the process of carrying out these surveys and enable earlier translocation, width measurements were not recorded and no new sites were added to the experiment for 2020, with width measurements recorded in 2019 used for calculations and analysis. Site designations in 2020 (as LDC, LDR, HDC and HDS sites) were based on 2019 fry numbers/densities from autumn electrofishing surveys and fry numbers/densities from 2020 spring surveys. For each site, the spring fry surplus or deficit was calculated as the 2020 spring fry number minus the 2019 autumn fry number. Sites where this value was positive (i.e. spring 2020 density > autumn 2019 density) were assigned as high density, while those where this value was approximately zero or negative (i.e. spring density $\lessapprox$ autumn density) were assigned as low density. No correction was applied to this method for sites which had been designated as HDS or LDR sites in 2019, based upon preliminary results from the 2019 experiment, which indicated that there were no significant differences between autumn densities for these two treatments.

Site assignment to control or treatment groups was as per the Year 1 experiment. However, for 2020 translocations occurred between some catchment areas (i.e. translocation batches for all catchment areas except the Owenmore were supplemented with fish from another catchment area, while the Derrinkee batch consisted of only fish from the Erriff catchment area; Fig. 5.1D; Appendix 4, Table A1). Additionally, no translocations occurred within the Erriff catchment area in 2020. These amendments were to allow for a greater overall level of density manipulation over a larger area at LDR sites compared to the Year 1 experiment. These inter-catchment area translocations were structured to minimise the instream distance between source and recipient sites (e.g. by translocating fish from the upper Owenmore to the Sheeffry, based upon their proximity; Fig. 5.1D; Appendix 4, Table A1) to reduce the likelihood of genetic differentiation between translocated and non-translocated fish, as intra-catchment genetic differentiation has been noted in other Irish catchments (Dillane *et al.*, 2008). The number of fry removed from each HDS site was calculated as the number of fry that could be removed from each site without lowering the fry density below 110 % of the 2019 autumn fry density. The 10 % buffer was included to account for inter-year changes in carrying capacity of each site (and hence potential autumn fry density). In addition, the upstream and downstream areas of each HDS site to be fished were extended from 10 m instream length to 20 m instream length.

The number of fry to be released at each LDR site was calculated as the number of fry required to raise each LDR site to the maximum autumn fry density recorded from the 2019 experiment for the entire catchment (74 fish 100 m^{-2}), as a proportion of the total number of fry required to raise all LDR sites within the same catchment area to this density. For example, using a catchment area with 3 LDR sites of equal areas with spring densities of 10, 20 and 30 fish 100 m^{-2} respectively, the target number of fry to be released for each LDR site would be 64, 54 and 44 fish per 100 m^2 of site area respectively (representing approximately 40 %, 33 % and 27 % of the captured fry total). As in year 1, upstream and downstream areas were also stocked at the same rate, however as with HDS sites, these were extended to 20 m instream length. The method of fry capture, adipose fin excision and release was the same as in year 1, although adverse weather meant that the Sheeffry and Glendavoc translocations had to be carried out in 2 and 3 batches respectively.

5.2.2.4 Autumn surveys

To enable assessment of the effect of the translocations on autumn fry densities, electrofishing surveys were completed between September 2nd and 19th for Year 1 (minimum translocation-autumn survey interval = 59 days, maximum = 81 days). For Year 2, they were conducted earlier (August 27th to September 4th; minimum interval = 63 days, maximum = 75 days) to reduce the likelihood of dispersal outside of the stocked 60 m area for LDR sites. The same electrofishing equipment was used as per the spring surveys, with the same sites resampled.

To estimate the dispersal of translocated fish from LDR sites, ‘hotspot’ surveys were also conducted at 5-m instream length sections of each riffle upstream and downstream of each LDR site. These took place until either a barrier to dispersal was encountered (e.g. a waterfall), another experimental site was encountered, or three consecutive hotspot sites had no translocated fish. These surveys used the same single-pass upstream electrofishing method as that of experimental sites. The extent of displacement from the associated LDR site for each of these sites was then estimated by geo-referencing and geographic information system (GIS) software. The area of each hotspot site was also estimated by taking wetted width measurements at both the top and bottom of the 5-m section. In year 2, the length of each hotspot site was increased from 5 to 10-m to increase the chances of capturing translocated fry, and hence 3 width measurements were taken. Additionally, the 20-m upstream and downstream stocked sections of each LDR site were fished in year 2 to indicate the level of small-scale fish movement within the areas where supplemental fry were added. Fishing within the central 20-m section was completed first to ensure this was not affected by fishing adjacent areas, followed by the downstream section and then the upstream section, before all fish were measured and released. In the surveys of both years, all captured fish were identified to species and all 0+ salmon fry were examined for adipose fin clips to identify recaptured translocated fish. During autumn surveys, determination between salmonid species was more difficult than in spring. Hence, any salmonid fry observed but not captured were assigned as either salmon or trout based on the captured proportions of each species. The same method was also used for assignation of salmon fry as either translocated or non-translocated fish, although in practice assignation as translocated fry was rare.

5.2.2.5 Habitat surveys

These habitat surveys were designed to enable any physical habitat differences to be accounted for in subsequent data analyses on fry densities. These surveys were completed in Year 1 only. In Year 2, sites were visually assessed against photos from 2019 to determine whether any substantial changes to channel morphology, substrate or macrophyte cover had occurred. As this was never the case, repetition of the habitat surveys was not necessary. The habitat surveys were conducted at each site and consisted of measurements of site area, depth, proportion of substrate within 4 categories (sand, gravel, cobble, boulder/bedrock), and macrophyte cover (%).

Site wetted area was estimated following autumn electrofishing surveys, using the same method as in spring surveys, with width measured at 5-m intervals along each 20-m site. A mean area measurement based upon both area estimates was then used for statistics to account for differences in river level between sampling periods. Depth was measured at 5 intervals along each of these cross-channel transects (left bankside edge, ¼ width, channel centre, ¾ width, right bankside edge). Substrate composition was measured using a modified Wolman pebble count procedure and Wolman square. To create an approximate sampling grid, cross-channel transects beginning at either site boundary were walked at each site, with one substrate particle blindly selected per step, and macrophyte presence or absence recorded. Particles were measured by passing them through the smallest possible opening in the Wolman square. Once the far bank was reached, a single step was taken in an upstream or downstream direction and another transect completed until the 20-m site was covered. This method ensured at least 100 particles were measured for sites < 10 m mean width, ≥ 200 particles were measured for sites between 10 and 20 m mean width, and ≥ 300 particles for sites > 20 m mean width.

Where these figures were exceeded, the number of particle and macrophyte records was reduced to the above figures (width < 10 m, n = 100 etc.) by randomly removing records, thus ensuring approximately even sampling effort. The percentage of macrophyte cover and proportions of substrate particles within each of the substrate classes of sand (diameter; $D \leq 2$ mm), gravel ($2 < D \leq 64$mm), cobble ($64 < D \leq 256$ mm) and boulder/bedrock ($D > 256$ mm) were then calculated.

5.2.3 Data and statistical analyses

5.2.3.1 Habitat data

To account for any habitat driven differences in fry densities, the habitat data were analysed through univariate tests (Mann Whitney U tests, Welch’s two sample t-tests) before a principal component analysis (PCA) was conducted. The PCA incorporated the proportion of substrate particles in each of the four classes, macrophyte cover, mean site depth and site area. The PCA input incorporated all sites for which these variables were recorded (habitat variables were not recorded for 2 sites), including those sites not assigned to one of the 4 treatment groups, and included each site only once to avoid pseudo-replication, as habitat data were only recorded in year 1 (n = 80 sites). PCA calculations were then undertaken via singular value decomposition of the centred and scaled data matrix. Individual habitat variables and PC1 and PC2 scores were then compared between LDR and LDC sites, HDS and HDC sites, and HD versus LD sites. For actual comparison between treatments, PCA scores and individual habitat variable values for sites used in both years were included twice.

5.2.3.2 Generalised linear mixed-effect models (GLMMs)

Fry lengths and densities in both the spring and autumn sampling periods were modelled using GLMMs. These were preferred over linear models and generalised linear models (GLMs) due to their ability to model multiple frequency distributions for the response variable, as well as random effects. In all cases data exploration was applied prior to modelling, with the relationships between response variables and covariates visualised using scatterplots or boxplots. In all models, data from all 6 catchment areas and both years were considered together, with year modelled as a random effect in all models and catchment area included as a random effect for models with response variables recorded in spring, to account for possible catchment area differences in spawning effort. A combination of hypothesis testing and bidirectional model selection was used. Specifically, predictor variables of interest were included in all models, with both forward and backward stepwise selection then run on a range of habitat variables. These predictor habitat variables were used to reduce the level of confounding variation in the response variable. Covariate significance values and the Akaike information criterion (AIC) were then used to evaluate model fit at each stage. In cases where AIC scores were extremely similar between models containing different numbers of predictor variables, Bayesian information criterion (BIC) scores were also used to inform model selection, thus decreasing the risks of model over-parameterisation. Only habitat variables hypothesised to be of biological relevance were available for selection, with these listed for all models in Table 5.1, and only those covariates selected through both forward and backward selection were included in the final models.

Correlation matrices and variance inflation factors (VIFs) were used to identify any sources of collinearity between predictor variables prior to model selection. Model validation was also applied at each stage during model selection and after selection of the final model to verify the underlying assumptions. Specifically, residuals were plotted versus fitted values to assess homogeneity of variance, and residuals versus each covariate to investigate model misfit. Additionally, VIFs were calculated at each stage of selection to test for multicollinearity.

For all models, brown trout age class density variables were simplified to 0+ (fry) and all 1+ (i.e. all trout parr, sub-adults and adults) age classes, given the low numbers of brown trout, and particularly older age classes, recorded at almost all experimental sites. The nature of the interactions between salmon fry and all age classes of trout over 1+ (and thus the relationships between these and salmon fry response variables) were also hypothesised to be similar (i.e. negatively correlated due to competition and predation). Pre-translocation densities for each of these fish density variables were used as these were considered most likely to impact on fry survival immediately post-emergence, with fish larvae most vulnerable to mortality, and particularly predation, at smaller body sizes (Peterson and Wroblewski, 1984; McGurk, 1986; Houde, 1997).

5.2.3.3 Spring fry densities

Site-level differences in the spring (pre-translocation) fry densities of both years' experiments were tested using GLMMs. Given the high degree of zero inflation of the response variable (spring fry density), overdispersion was assessed for each model. Site-level spring fry densities were then modelled using GLMMs incorporating random catchment area and year effects and a gaussian distribution for the response variable, based upon QQ plots of the model residuals. Spring fry density predictions for each model were then used to visualise the effects of each covariate within the model on a similar and easily interpretable scale, using a range of values from the minimum to the maximum recorded values for the covariate of interest, while all other covariates were fixed at their mean values.

5.2.3.4 Pre-translocation fry lengths

To investigate density-dependent and independent effects on emergence size and initial fry growth, site-level mean TL (mm), as calculated from spring electrofishing surveys, was used. Only sites where 20 or more salmon fry were caught during the spring sampling period were used for this analysis to ensure the accuracy of mean TLs. Again, univariate analyses were first performed to identify patterns of interest and potential covariates for use in later modelling. Mean TLs were then modelled using GLMMs incorporating random catchment area and year effects and a gaussian distribution for the response variable (spring fry mean TL), based upon QQ plots of the model residuals. Predictions for the response variable were again used to visualise the effect of covariates included in the final model.

5.2.3.5 Autumn fry densities

Autumn fry densities were modelled using GLMMs which incorporated both a linear and quadratic term for spring fry density, in order to best represent the hypothesised non-linear relationship between these two variables, as seen in stock recruitment curves for this species (Milner *et al.*, 2003). Again, data from all 6 catchment areas and both years were considered together, with year modelled as a random effect. Catchment area was not included as a random effect to avoid overparameterization and as differences in spawning effort were accounted for through the spring fry density covariate, while differences in fry survival between catchment areas were hypothesised to be accounted for through recorded habitat variables. A gaussian distribution was used for the response variable (autumn fry density) based upon QQ plots of residuals. Two approaches were used to test for differences in fry densities between treatments. The first approach excluded any treatment variable, with the residuals for each treatment then compared using univariate analyses to determine whether statistical differences in fry densities were apparent once other confounding habitat variables had been accounted for. In the second approach, both the linear and quadratic terms for spring fry density available for selection were modelled by treatment/control, with all other covariates modelled without this effect. This approach was used to test for treatment-related differences in the shape of the autumn fry recruitment curve. Again, autumn density predictions were used to visualise the effect of each covariate of interest, with all other covariates except the covariate of interest fixed at their mean values.

5.2.3.6 Fry growth in the post-translocation period

Site-level autumn fry mean TL (mm), was used as a proxy for growth rate, with both sampling interval (days) and spring fry mean TL (mm) included in model selection to allow differences in these variables between sites to be accounted for. This method assumes no immigration/emigration and no size-dependent differences in mortality between sampling periods and hence the results must be interpreted cautiously. Again, univariate analyses were first performed to identify patterns of interest and potential covariates for use in later modelling. To ensure the results were not skewed by translocations of larger or smaller individuals into LDR sites, only the TLs of non-translocated fry were used for calculation of autumn fry mean TLs. Additionally, to ensure the accuracy of site-level mean TLs, only sites where at least 20 non-translocated fry were caught in both the spring and autumn sampling periods were used for this analysis. Autumn fry mean TL was modelled using GLMMs incorporating a random year effect and a gaussian distribution for the response variable, with fry mean TL predictions used to visualise the results.

5.3 Results

5.3.1 Habitat data

There were no significant differences in the measured habitat variables for LDR versus LDC sites and HDS versus HDC sites (Mann Whitney U tests, all $p > 0.05$; Appendix 4, Table A2). The PCA revealed no clear patterns in the clustering of these site categories (Fig. 5.2), with no significant differences detected in PC1 and PC2 scores in comparisons between the site designations (Mann Whitney U tests/Welch's two sample t-tests: $p > 0.05$; Appendix 4, Table A2). There were significant differences in PC1 and PC2 values between high- and low density sites and, at a univariate level, significant differences were apparent between all measured variables for these two density categories (Mann Whitney U tests, $p < 0.05$; Appendix 4, Table A2).

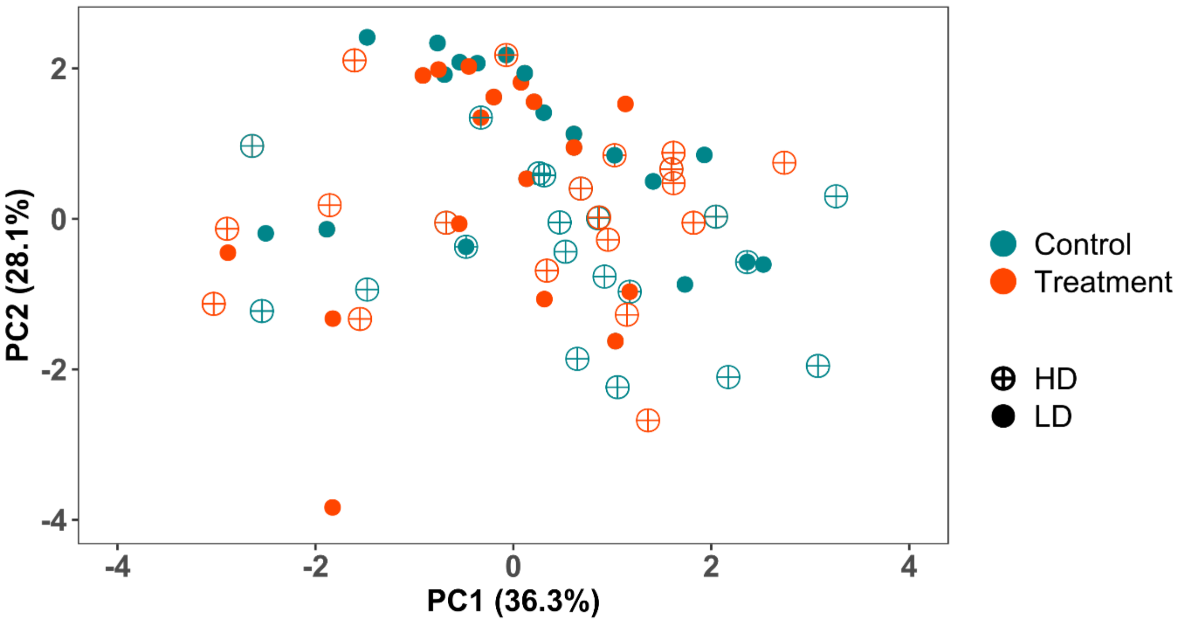

Figure 5.2: Habitat variables principal component analysis summary of all experimental sites

5.3.2 Spring fry densities and lengths

The differences in the spring fry densities of the LDR versus LDC and HDS versus HDC sites were not significant for either year, or when these data were combined (Mann Whitney U tests/Welch's two sample t-tests: $p > 0.05$; Appendix 4, Table A3). There were significantly higher fry densities at the HD vs. the LD sites in both years and in the combined data (Mann Whitney U tests/ Welch's two sample t-tests: $p < 0.05$; Appendix 4, Table A3). There were also significant differences between catchment areas and years (Appendix 4, Table A4). Across all sites, GLMMs revealed significant and positive correlation between the proportions of gravel, cobbles and macrophyte cover, and spring fry density ($p < 0.05$; Table 5.1, Equation 1; Fig. 5.3). Additionally, there was a negative relationship between Julian day of sampling and fry density.

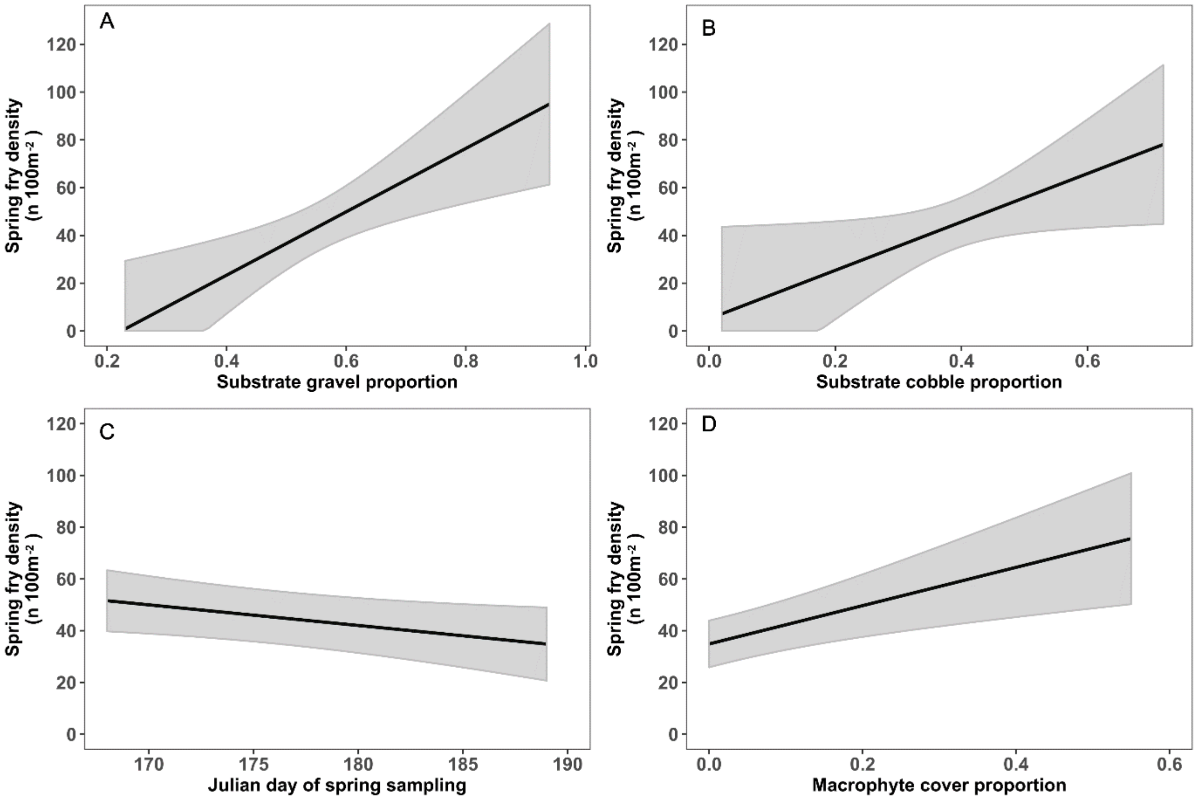

Figure 5.3: Predicted spring 0+ fry density plotted against habitat variables included in the GLMM shown in equation 1; A) gravel proportion by streambed area; B) cobble proportion by streambed area; C) Julian day of survey, and; D) macrophyte cover by streambed area; Solid lines represent predictions from the GLMM where all other covariates included in the model were fixed at the mean. Shaded areas represent 95 % prediction intervals. All predictions were calculated for a single catchment area (Glendavoc) and year (Year 1 – 2019)

For the lengths of the spring fry, univariate analyses revealed no significant differences in mean TLs between LDR and LDC sites, between HDS and HDC sites, or between LD and HD sites in either year or in both years combined (Mann Whitney U tests/ Welch's two sample t-tests: $p > 0.05$; Appendix 4, Table A5). Significant differences were, however, present between years for all these treatments (Welch's two sample t-tests: $p < 0.05$; Appendix 4, Table A5). Significant differences in spring fry mean TLs were also observed between some catchment areas, both in individual years and in both years combined, as well as within all catchment areas between years (Mann Whitney U tests/Welch's two sample t-tests: $p < 0.05$; Appendix 4, Table A6). GLMMs indicated that spring mean TL was significantly and negatively correlated with fry densities and gravel proportion ($p < 0.05$), and was positively correlated with macrophyte cover ($p < 0.05$; Table 5.1, Equation 2; Fig. 5.4).

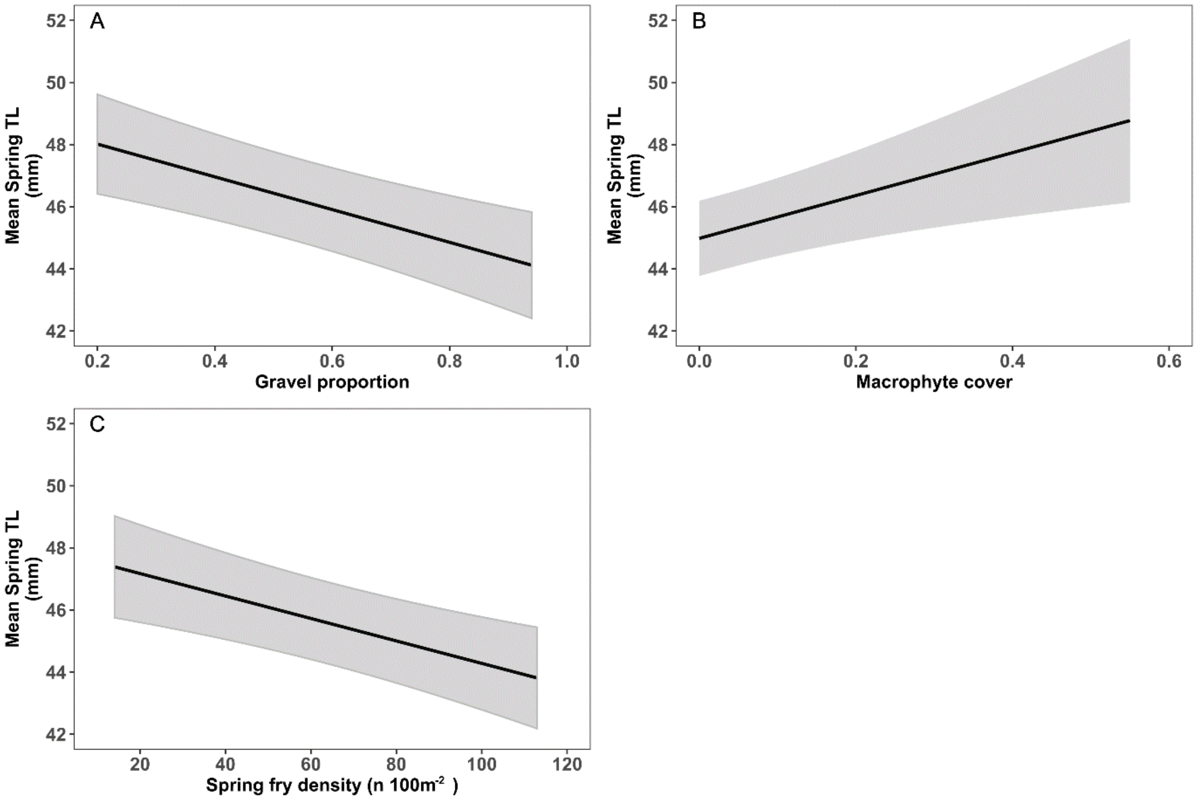

Figure 5.4: Predicted spring mean total length plotted against variables included in the GLMM shown in equation 2 of Table 5.1; A) Gravel proportion; B) Macrophyte cover, and; C) Spring fry density. Solid lines represent predictions from the GLMM where all other covariates included in the model were fixed at the mean. Shaded areas represent 95 % prediction intervals. All predictions in part C-E are calculated for a single catchment area (Glendavoc) and year (Year 1 – 2019).

5.3.3 Numbers of translocated fry

A total of 2238 0+ salmon fry were captured, adipose fin clipped and translocated within the catchment across both years (2019 = 1138; 2020 = 1100). The mortality rate during the translocation process in both years was low (2019 = 1.5 %; 2020 = 1.2 %, combined = 1.3 %).

5.3.4 Post-translocation fry recapture rates and dispersal

The estimated recapture rate of translocated fry in autumn surveys, including missed fish which were assigned as translocated, was low in both years (2019 = 61 fry, 5.4 %; 2020 = 41 fry, 3.7 %; combined = 4.6 %). Totals of 12 and 17 fish which had been translocated in 2019 were also subsequently recaptured in spring and autumn surveys in 2020 respectively, representing recapture rates of 1.1 % and 1.5 % respectively. Of the 61 estimated recaptured fry in 2019, 35 were recaptured from the central 20-m stocked sections (LDR sites), 13 from hotspot surveys of riffles upstream and downstream of these sites, and a further 13 from non LDR experimental sites. Of the 41 translocated fry recaptured in 2020, 11 came from the central 20-m sections, 9 from the 20-m downstream stocked sections and 4 from the 20-m upstream sections of the stocked 60 m areas themselves. A further 12 fish came from hotspot surveys and 5 from a single upstream adjacent LDC site.

The maximum recorded upstream dispersal distances in 2019 and 2020 were 396 m and 130 m respectively, with mean (± SD) dispersal distances for those fish found upstream of the stocked sections being 171 ± 108 m (n =13) and 83 ± 22 m (n = 16) in each year respectively, as measured from the centre of the stocked section to the centre of the hotspot or experimental site. Mean downstream dispersal distance in 2019 was 212 ± 362 m ($n = 13$), with a maximum recorded downstream dispersal distance of 1021 m. Only a single translocated 0+ fish was caught downstream of any of the stocked sections in 2020 (60 m dispersal distance).

5.3.5 Autumn fry densities and growth rates

Regarding autumn fry densities, univariate tests indicated that differences in densities in LDR versus LDC sites, and HDS versus HDC sites, were not significant in either year or when their data were combined for both years (Mann Whitney U tests/ Welch's two sample t-tests: $p > 0.05$; Appendix 4, Table A3). Differences were apparent between catchment areas and within catchment areas between years (Appendix 4, Table A7). The significant differences detected in the fry densities between HD and LD sites in the spring survey (pre-translocation) period remained in the autumn surveys (Mann Whitney U tests/ Welch's two sample t-tests: $p < 0.05$; Appendix 4, Table A3).

Testing of all autumn fry density data across both years via GLMMs revealed that the significant and positive predictors of autumn fry densities were the spring fry densities, the proportions of gravel and cobble within the streambed area and the Julian day of spring sampling ($p < 0.05$; Table 5.1, Equation 3; Fig. 5.5), with the density of 1+ salmon near-significant ($p = 0.10$). There was also significant and negative correlation between spring 1+ trout density and autumn salmon fry density ($p < 0.05$; Table 5.1, Equation 3), with mean site depth near-significant ($p = 0.08$). Univariate analysis of the residuals from the final model showed no significant difference between LDR and LDC sites (Welch's two sample t test; t = 0.1, df = 21.0, p = 0.89; Appendix 4, Table A3), and a near significant difference between HDS and HDC sites (Mann Whitney U test; U = 326.0, p = 0.1; Appendix 4, Table A3), with HDS sites having lower (i.e. lower values and/or more negative) residuals on average. Modelling spring vs. autumn fry density by treatment/control using GLMMs indicated that there was little difference between treatment and control sites, with the differences in the shapes of the autumn fry recruitment curves being non-significant (Table 5.1, Equation 4; Fig. 5.5B).

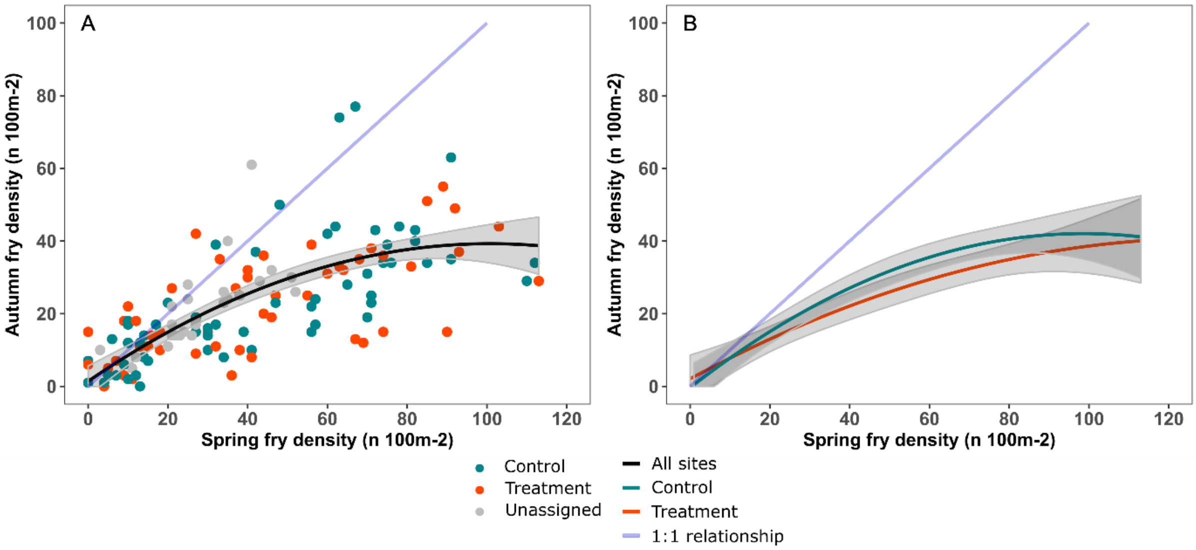

Figure 5.5: Recorded and predicted autumn 0+ fry density values plotted against variables included in the GLMMs in equations 3 and 4 of Table 5.1, with all other variables included in the models fixed at the mean; A) Observed values for autumn fry density based upon treatment, plotted with predictions from equation 3 including all treatment and control sites in a single model, and; B) predictions for equation 4 including a treatment (i.e. HDS and LDR) and control (HDC and LDC) covariate within the model. Shaded areas represent 95 % prediction intervals. Blue lines represent a 1:1 relationship between Spring and autumn fry densities. All predictions are calculated for a single year (Year 1 – 2019) and with all other covariates within the model set to their mean values.

Much like those observed in spring, non-translocated autumn fry mean TLs were found to differ significantly between some catchment areas (Appendix 4, Table A8). In particular, the upper Owenmore had the largest autumn fry on average in both years combined, with the Derrinkee having the smallest fry on average. The Derrycraff had the largest autumn fry in 2019 (70.9 ± 3.8 mm TL; Appendix 4, Table A8), with these found to be significantly larger than fry from all other catchment areas in 2019. Differences in autumn fry mean TLs were not observed between years for any catchment area, with the exception of the Derrinkee. Differences in autumn fry mean TLs were not seen between treatments but were observed within all treatments, except HDS, between years (Appendix 4, Table A5).

The GLMMs indicated autumn fry mean TL was significantly and positively correlated with spring mean TL, as expected, but was not correlated with any habitat variables. (Table 5.1, Equation 5; Fig. 5.5). No effect of spring or autumn densities, treatment assignation or density manipulation was found on autumn fry mean TL from this analysis (Table 5.1, Equation 5).

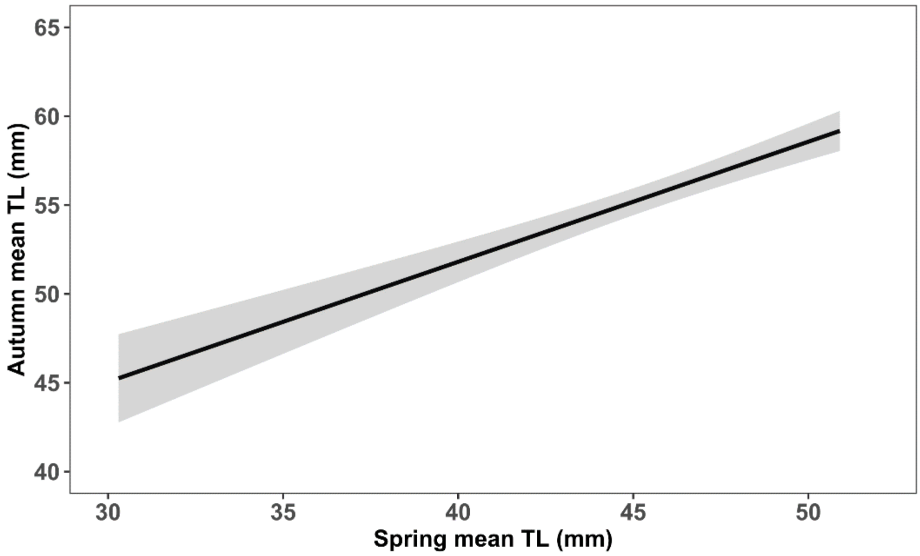

Figure 5.6: Predicted autumn mean total length (TL) plotted against spring fry mean TL, as shown in equation 5 of Table 5.1. The solid line in part represents predictions from the GLMM where all other covariates included in the model were fixed at the mean. Shaded areas represent 95 % prediction intervals. All predictions were calculated for year 1 (2019).

Table 5.1: GLMM equations (#), statistically significant results are shown in bold

#	Formula	Dataset	N obs.	Variables available for selection	Selection	Covariate(s)	Estimate	Standard error	Z value	P value
1	*Spring fry density ~ gravel prop. + macrophyte cover + Julian day + cobble prop. + (1|catchment area) + (1|Year)* Response variable distribution = Gaussian	Treatment, control and unassigned sites	134	Gravel proportion, Cobble proportion, Macrophyte proportion, Mean depth, Julian day, 0^+ trout density, 1^+ trout density, 1^+ salmon density	Appendix 4, Table A9	Intercept	59.34	86.24	0.69	0.49
						Gravel proportion	132.63	42.22	3.14	**0.002**
						Macrophyte cover	73.99	22.73	3.26	**0.001**
						Julian day	-0.80	0.39	-2.07	**0.04**
						Cobble proportion	101.29	48.62	2.08	**0.04**
2	*Spring mean TL ~ Spring fry density + gravel prop. + macrophyte cover + (1|catchment area) + (1|Year)* Response variable distribution = Gaussian	Treatment, control and unassigned sites with over 20 fry captured in spring	100	Gravel proportion, Cobble proportion, Macrophyte proportion, Mean depth, Julian day, 0^+ trout density, 1^+ trout density, 1^+ salmon density, Spring fry density	Appendix 4, Table A10	Intercept	46.92	4.03	11.63	**$< 2 \times 10^{-16}$**
						Spring fry density	-0.04	0.01	-3.61	**0.0003**
						Gravel proportion	-5.27	1.35	-3.90	**9.51×10^{-5}**
						Macrophyte cover	6.90	2.27	3.04	**0.002**
3	*Autumn fry density* ~ Spring fry density + (Spring fry density)^2 + cobble prop. + Julian day of Spring sampling + gravel prop. + mean site depth + 1^+ trout density + 1^+ salmon density + (1|Year)* Response variable distribution = Gaussian	Treatment, control and unassigned sites	134	Gravel proportion, Cobble proportion, Macrophyte proportion, Mean depth, Julian day of spring sampling, Julian day of autumn sampling, 0^+ trout density, 1^+ trout density, 1^+ salmon density, Spring fry density, Spring fry density^2	Appendix 4, Table A11	Intercept	-130.30	33.85	-3.85	**0.0001**
						Spring fry density	0.75	0.10	7.21	**5.53×10^{-13}**
						Spring fry density^2	-0.004	0.001	-3.67	**0.0002**
						Cobble proportion	53.86	19.87	2.71	**0.007**
						Julian day spring	0.53	0.15	3.44	**0.0006**
						Gravel proportion	37.90	18.62	2.04	**0.04**
						Mean site depth	-32.47	18.83	-1.72	0.08
						1^+ trout density	-1.12	0.54	-2.08	**0.04**
						1^+ salmon density	0.13	0.08	1.67	0.10
4	*Autumn fry density* ~ Spring fry density, by = treatment/control + (Spring fry density)^2, by = treatment/control + Julian day of spring sampling + cobble prop. + 1^+ trout density + site mean depth + (1|Year)* Response variable distribution = Gaussian	Treatment, control and unassigned sites	134	Gravel proportion, Cobble proportion, Macrophyte proportion, Mean depth, Julian day of spring sampling, Julian day of autumn sampling, 0^+ trout density, 1^+ trout density, 1^+ salmon density, Spring fry density, Spring fry density^2	Appendix 4, Table A12	Intercept	-133.20	30.89	-4.31	**1.62×10^{-5}**
						Spring fry density	8.60	0.15	5.64	**1.71×10^{-8}**
						Treatment/control; treatment	2.46	4.62	0.53	0.59
						Spring fry density^2	-0.004	0.002	-2.91	**0.004**
						Julian day spring	0.76	0.17	4.52	**6.23×10^{-6}**
						Cobble proportion	20.47	6.83	3.00	**0.003**
						1^+ trout density	-1.44	0.50	-2.90	**0.004**
						Site mean depth	-52.39	22.25	-2.36	**0.02**
						Spring fry density: treatment/control (treatment)	-0.27	0.22	-1.24	0.22
						Spring fry density^2: treatment/control (treatment)	0.002	0.002	0.98	0.33
5	*Autumn mean TL ~ Spring mean TL + sampling interval + (1|Year)* Response variable distribution = Gaussian	Treatment, control and unassigned sites with over 20 non-translocated fry captured in both spring and autumn	84	Gravel proportion, Cobble proportion, Macrophyte proportion, Mean depth, Sampling interval, 0^+ trout density, 1^+ trout density, 1^+ salmon density, Spring mean TL, Spring fry density, Post-translocation fry density, Autumn fry density	Appendix 4, Table A13	Intercept	40.91	5.71	7.16	**8.02×10^{-13}**
						Spring mean TL	0.68	0.08	8.53	**$< 2.00 \times 10^{-16}$**
						Sampling interval	-0.20	0.06	-3.46	**0.0005**

5.4 Discussion

The results of the translocation experiments were mixed; although they were ultimately unsuccessful in their primary aim of increasing fry densities at LDR sites, a result contrary to H_2, the impacts of the removal of fry in spring on September densities in the HDS sites were relatively low, in line with H_2. The overall effects of the translocations were therefore largely neutral, contrary to H_3, but with the finding that HDS autumn densities were relatively unimpacted by fry removals arguably being a highly important result in the context of applying translocations elsewhere. The results were consistent with H_1, as the spring (post-emergent) salmon fry densities were strongly and positively correlated with the proportion of gravel within the riverbed. Finally, there was strong support for H_4, as there was no evidence suggesting that growth rates at LDR sites were negatively affected by translocations.

Evaluating the effects of the translocations on the different site categories was relatively complex. For example, at the LDR and HDS sites, there were slightly different results provided between univariate tests (no overall effect) and the multivariate GLMMs (potential minor effect on HDS sites) in terms of autumn fry densities. Several habitat variables were strong predictors according to the GLMMs. In particular, gravel proportion had strong positive correlation with spring fry density, with this relationship likely to be directly associated with the spawning requirements of Atlantic salmon, which have been shown to preferentially utilise substrate of between 2-64 mm in diameter for spawning, based upon Wentworth substrate increments (Louhi, Mäki-Petäys and Erkinaro, 2008). The similar relationship between cobble proportion and spring fry density may indicate that salmon are also able to successfully utilise larger substrate particles for spawning within the catchment ($64 < D \geq 256$ mm), as found in other studies

(Peterson, 1978; Fluskey, 1989; Louhi, Mäki-Petäys and Erkinaro, 2008). The strong negative relationship between Julian day of sampling and spring fry density was considered to mainly be a direct result of high fry mortality during the initial weeks following emergence, although dispersal may also play a role in this observed pattern. High post-emergence mortality rates are a feature of salmon populations generally (Nislow, Einum and Folt, 2004; Armstrong, 2005; Einum, Nislow, Mckelvey, *et al.*, 2008; Honkanen, Boylan, *et al.*, 2018). Here, the strength of the relationship between Julian day and fry density indicates that initial mortality and/or dispersal may be high across a broad range of emergent fry densities, not just at the highest density sites. Hence, this may suggest some level of density-independence in initial mortality and/or dispersal. This finding fits with other studies that suggest mortality rates in teleost fishes generally decline with body size, with the highest mortality in the early larval stages (Peterson and Wroblewski, 1984; McGurk, 1986; Houde, 1997).

Importantly, the results also indicated a strong habitat effect on the autumn fry densities, which is at least partially independent of any habitat effect on emergent densities. Correspondingly, the effects of these habitat variables on fry survival (and hence autumn fry densities) may have been greater than those from translocation density manipulations, and so contributed to their overall non-significant effects. The positive relationships between the proportions of gravel and cobbles within the substrate of each site and autumn fry density may relate to spawning effort at each site, as both variables were found to have a positive effect on spring fry density. However, given this model also accounted for spring fry density, it is likely that these variables also confer some degree of habitat suitability for salmon fry, with other studies finding that juvenile salmon tend to occupy stream areas with finer substrate than brown trout, particularly where both species occur in sympatry (Heggenes, 1990; Heggenes, Bagliniere and Cunjak, 1999). Likewise, the negative relationship between depth and autumn fry density may relate to juvenile habitat suitability, as Atlantic salmon fry have been found to preferentially inhabit faster, shallower areas within river systems compared to brown trout and older conspecifics (Heggenes, 1990; Heggenes, Bagliniere and Cunjak, 1999; Armstrong *et al.*, 2003), although the positive relationship between 1+ salmon density and autumn fry density observed here indicates overlap in habitat usage between age classes.

Based on the above, the negative relationship between 1+ trout and autumn salmon fry densities may therefore indicate differential habitat usage, with 1+ trout inhabiting deeper sections with larger substrate, such as boulders, as noted by Heggenes, Bagliniere and Cunjak (1999). This may also be interpreted as evidence of competitive interactions between these species, which are also well documented (Armstrong *et al.*, 2003; Houde, Wilson and Neff, 2015). These two factors are likely interlinked, with a previous study from the River Bush, Northern Ireland suggesting that usage of shallower areas by juvenile salmon may be driven by competition with trout (Kennedy and Strange, 1986).

The highly significant positive relationship between Julian day of spring sampling and autumn fry density can be interpreted as further evidence of high initial post-emergence mortality, as hypothesised by other authors (Nislow, Einum and Folt, 2004; Armstrong, 2005; Einum, Nislow, Mckelvey, *et al.*, 2008; Honkanen, Boylan, *et al.*, 2018), and shown here in equation 1. This relationship indicates that identical fry densities recorded later in the immediate post-emergence period much more closely resemble those recorded in autumn, versus the same densities recorded only 1-2 weeks earlier in the immediate post-emergence period.

In the translocation experiment, due to the way the fish were sampled, spring and autumn mean fry total lengths (TL; mm) at each site had to be used for assessments of growth rates. It is acknowledged that these represent a proxy measure of growth rates and do not capture the individual variability that would be expected. Indeed, Atlantic salmon are noted for their extreme variability in individual growth rates and life history patterns (Økland *et al.*, 1993; Hutchings and Jones, 1998). Irrespective, these results provided minimal evidence for density-dependent growth during the first summer, with univariate analyses showing no significant differences in fry length between any treatments in autumn. Furthermore, the GLMMs indicated that autumn fry length was not correlated with any measures of fry density, while GLMM residuals showed no evidence of differential growth between treatments. Conversely, spring fry length was found to be negatively correlated with fry density, although this effect was relatively small, suggesting density-dependent effects may be greatest in the days immediately following fry emergence in spring. This fits with the hypothesis that the strength and scale of density-dependent processes is directly related to fry dispersal ability (Einum, Sundt-Hansen and Nislow, 2006), with dispersal ability thought to be lowest immediately post-emergence (Kennedy, 1988; Beall *et al.*, 1994; Einum, Sundt-Hansen and Nislow, 2006). However, this finding is in contrast with Einum et al. (2006), who hypothesised that density-dependence within salmon fry is predominantly seen in mortality rates, as opposed to growth rates. This effect may also relate to the timing of electrofishing surveys relative to emergence, with density expected to decline following emergence, as shown in equation 1, while fry lengths would be expected to increase. Thus, inter-site variability in emergence timing could also have produced this effect, even with Julian day of sampling accounted for.

The apparent relationships between several habitat variables and spring fry lengths suggest habitat variables could have played key roles in density-independent processes. Macrophyte cover was strongly and positively correlated with spring fry lengths, a largely expected result given macrophytes directly increase invertebrate production, thus providing food for salmonids and other fish species (Riley *et al.*, 2009; Lusardi, Jeffres and Moyle, 2018), and may also provide refuge from predators (Allouche, 2002), with predator exposure known to affect foraging behaviour in juvenile Atlantic salmon (Gotceitas and Godin, 1991). It is possible that the negative relationship between gravel proportion and spring fry length resulted from collinearity and was a direct result of the positive correlation between gravel proportion and spring fry density. However, this is unlikely given that spring fry density was accounted for within the model, and the VIF values for each covariate. This suggests an alternative density-independent relationship between substrate composition and fry growth. The size range of gravels recorded in this study also closely matches those reported by Bourassa and Morin (1995) to support the highest densities of stream macroinvertebrates, suggesting that food availability is also not a major driver of this observed relationship. Hence the primary cause for this pattern remains unclear.

5.5 Conclusions

In summary, the results of this study indicate that habitat variables, and particularly gravel proportion, are strong predictors for emergent fry densities, and would be useful for identification of potential fry source sites where historical electrofishing data are absent. Furthermore, the results of this study demonstrate that translocations from such sites and marking of salmon fry can be feasibly achieved with extremely low initial mortality and with some instances of survival after as much as 15 months at liberty. However, at the levels of density manipulation used in this study, a conservation/management benefit of translocations could not be demonstrated in terms of autumn fry densities. Although the results also suggested some potential for negative effects on autumn densities to be incurred on some source sites, these were considered to be minor and able to be eliminated by refinements to the translocation design. Furthermore, this is considered unlikely to be an issue within river systems with higher emergent fry densities, although this requires further work. Thus, whilst translocations of post-emergent salmon fry within catchments and sub-catchments potentially provide a conservation mechanism to increase smolt production, their utility to achieve this here was not able to be demonstrated fully.

Chapter 6: Intra-catchment translocations of post-emergent larvae as a viable population enhancement management tool in Atlantic salmon

Abstract

Although previous experiments have indicated that intra-catchment translocations of Atlantic salmon fry can be conducted with low initial mortality, and little to no effect on fry densities at high density fry source sites or on growth of non-translocated fry at low density fry recipient sites, these experiments have been unable to show an overall benefit in terms of fry densities at such low density recipient sites. These previous experiments were hindered by higher than predicted dispersal of released salmon fry at low density recipient sites, and by the relatively low level of density manipulations. Here, extensive refinements to the experimental design allowed more thorough review of the efficacy of intra-catchment translocations as a novel management tool for this salmonid species. Translocations of fry from identified high density sites, to low density release sites at the centre of larger (≈ 500-m instream length) stream reaches allowed more effective testing of the impact of fry translocations, as measured by autumn fry densities recorded from single pass area-delineated electrofishing surveys. The experimental results were complicated by much higher natural autumn fry recruitment than in previous years, treatment bias between pre-translocation fry densities at low density control and recipient stream reaches, and the carrying out of pre-translocation surveys during the fry emergence period. Thus, comparisons between treatments were severely limited. However, within low density recipient stream reaches, translocated fry were shown to have an overall positive effect on autumn fry densities, with little to no impact on native fry survival or growth.

6.1 Introduction

Intra-catchment translocation as a concept is based upon the overarching hypothesis that movement of post-emergent salmonid larvae (fry) from sites of high fry density to sites of relatively lower fry density can be used to decrease the overall level of density-dependent fry mortality over the first summer following fry emergence, thereby increasing overall fry abundance at the end of this summer period (Chapter 1, 5). As salmonid populations tend to be subject to high density-dependent mortality in their post-emergence phase, this can result in higher mortality within areas with an abundance of suitable spawning gravel due to higher egg - and thus larval - densities (Webb *et al.*, 2001; Armstrong, 2005; Finstad *et al.*, 2010; Foldvik, Finstad and Einum, 2010). This effect is likely compounded by the relatively low dispersal abilities of salmonid fry compared to older age classes (Einum, Sundt-Hansen and Nislow, 2006; Finstad *et al.*, 2010; Foldvik, Finstad and Einum, 2010).

This post-emergence period is thus considered a population bottleneck, after which higher dispersal abilities and changes in habitat use result in the effects of density-dependence acting more on growth than survival (Jonsson and Jonsson, 2004; Armstrong, 2005; Einum, Sundt-Hansen and Nislow, 2006). Correspondingly, in this post-emergence period, there is the potential to work in tandem with these processes by manipulation of fry densities between high- and low density areas, i.e. to remove ‘surplus’ fry from high density areas where they are unlikely to survive and translocate them to areas of lower density where survival rates will be less impacted by density-dependent processes. Previous translocation field trials, completed in 2019 and 2020, indicated intra-catchment translocations of post-emergent Atlantic salmon fry were both logistically feasible and did not significantly impact autumn fry densities in donor sites (Chapter 5). However, these trials were unable to demonstrate increased autumn fry abundances in the translocated recipient sites, with this relating to an experimental design that had insufficiently accounted for the dispersal of fry outside of the experimental sites. Indeed, these relatively high fry dispersal rates present a potential confounding issue for the evaluation of fry translocations, as it is difficult to differentiate between mortality and emigration within non-contained, large-scale field experiments, and with autumn electrofishing survey data in the translocation trials revealing translocated salmon fry in non-translocated riffle habitats that were adjacent to the release sites. Consequently, this largely unexpected pattern of dispersal needs to be considered within the translocation design. Additionally, the use of many such sites meant that, even prior to fry dispersal, the initial number of salmon fry released at each site was relatively low. This may have further compounded the effects of high fry dispersal.

The aim of this study was thus to test how intra-catchment translocations of post-emergent salmon fry could increase autumn fry densities, using an experimental design that built on the trials of 2019 and 2020 by basing its assessments at the stream reach level and within streams where post-emergent fry abundances are naturally low, and thus below the level at which density-dependent mortality is expected to be a significant factor in post-emergent survival and, ultimately, autumn fry densities. Additionally, given the potential side-effects of substantially increasing natural fry abundances (e.g. inducing density-dependent effects), it was again important to test whether translocations could be carried out without incurring negative effects on either the survival or growth of non-translocated salmon fry within streams where fry numbers were supplemented with translocated fish. Therefore, through the use of control and treatment experimental sites and stream reaches of low- and high post-emergent fry densities within the River Erriff catchment, Ireland, it was hypothesised (H) that: (H_1) high fry density donor reaches would have autumn fry densities that did not significantly differ from high fry density control reaches; (H_2) low density stream reaches that received translocated fry would have significantly higher autumn fry densities versus low density control stream reaches where no fry were added; (H_3) in recipient reaches, total autumn fry densities would be positively correlated with autumn translocated fry densities; and (H_4) in recipient reaches, the translocated fry would not then negatively impact the growth or survival of non-translocated fry, as abundances would remain below the level at which density-dependence acts on either process. Thus, in combination, support for both H_3 and H_4 would demonstrate an overall positive impact on reaches which received additional fry through translocations.

6.2 Methods

6.2.1 Study river and sites

The River Erriff is a spate river located on the west coast of Ireland which has been renowned for its substantial populations of both Atlantic salmon and anadromous brown trout (Chapter 5). The river catchment comprises the Erriff mainstem, formed by the confluence of the Owenmore and Owenwee Rivers, and 4 further major tributaries (Chapter 5), of which two were included in this experiment (Fig. 6.1). The size of the Owenmore and lack of migration barriers mean it was considered an extension of the Erriff mainstem in this experiment. Thus, for the purposes of this experiment, the Erriff mainstem (including the Owenmore), as well as the Sheeffry and Glendavoc rivers were included, forming 3 major catchment areas (Fig. 6.1).

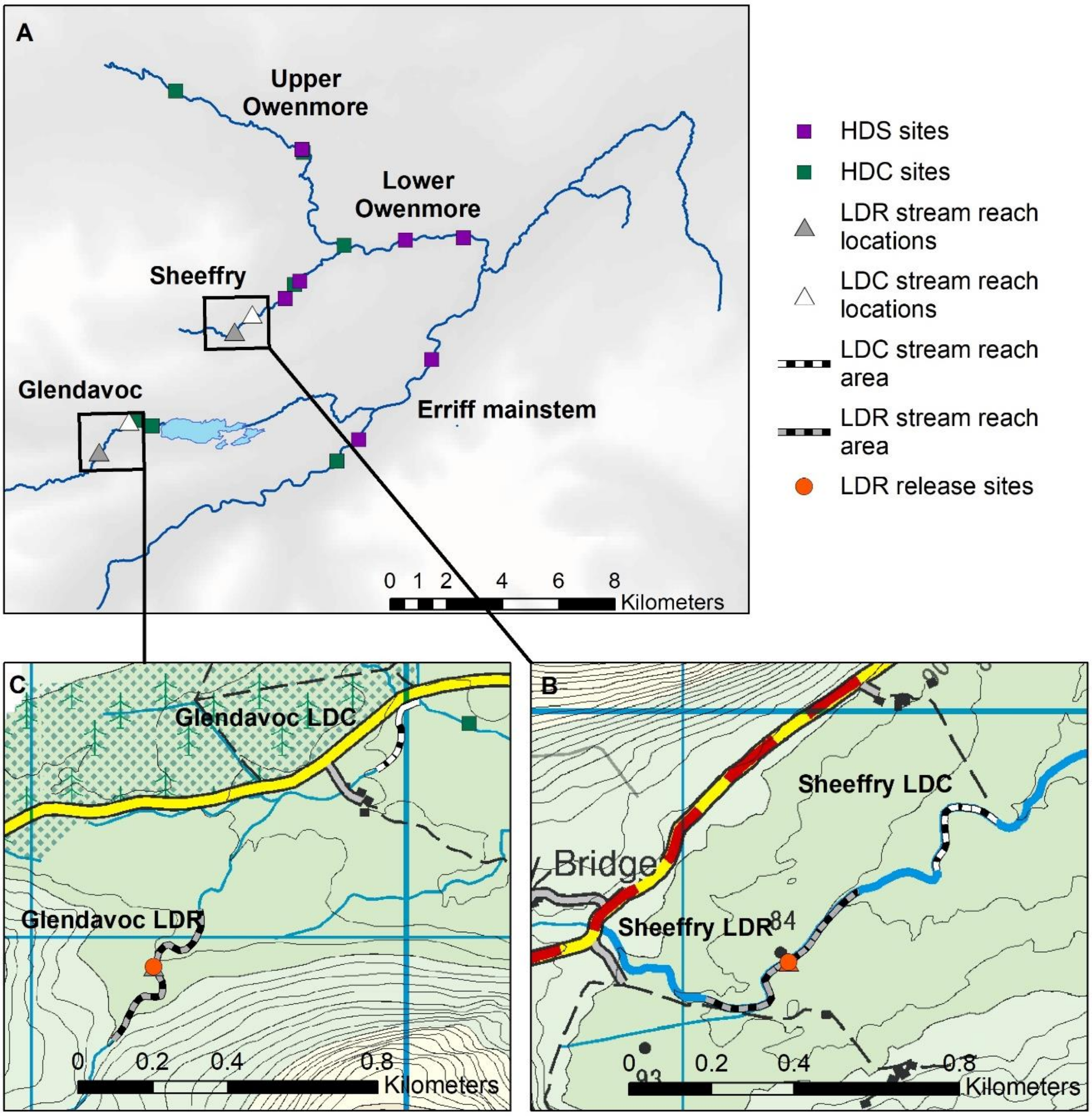

Figure 6.1: Catchment maps showing; A) wider Erriff catchment and tributaries, with high density (HD) site and low density (LD) stream reach locations marked; B) LD stream reaches within the Glendavoc catchment with release site locations marked, and; C) LD stream reaches within the Sheeffry catchment

6.2.2 Experimental design

The experimental design was informed by the two previous experiments (2019 & 2020), with the basic premise of the 2021 experiment remaining the same: being completed in a single year, involving (pre-translocation) post-emergent fry density surveys (June), translocation of salmon fry from high- to low density sites (June), and re-assessment of fry densities through post-translocation surveys at the beginning of autumn (September). However, substantial refinements were made to the experimental design based on review of the previous experiments.

The previous trials indicated that translocation of fry into, and survey of, relatively small low density (LD) areas (40-60 m instream channel length) resulted in the confounding effect of these fry emigrating outside of the surveyed areas (Chapter 5). The design of these trials also made decoupling the effects of emigration and mortality on fry densities challenging. Correspondingly, in the design here, the surveyed area for low density reaches was substantially increased, with low density (LD) reaches consisting of continuous stream reaches of approximately 500 m for low density fry recipient reaches (i.e. where fry were released, hereafter ‘LDR reaches’) and approximately 250 m for low density control (LDC) reaches, which acted as the comparator group to LDR reaches. The greater lengths for LDR reaches were due to the need to ensure that, irrespective of fry dispersal distances, the majority of surviving translocated fry could be recaptured. In the absence of this requirement, LDC reaches could therefore be shorter, with 250 m chosen to ensure rapid sampling could be completed, while also aiming to ensure the area sampled was representative of greater stream lengths.

These LD stream reaches were then divided into individual sites according to habitat type (i.e. predominantly riffle/glide or predominantly pool), with habitat surveys conducted for each individual site. Sites varied in length from 5 to 35 m, according to the length of individual habitat types, with all site lengths set to 5-m increments to aid in site area calculation and habitat surveys. One LDR and one LDC stream reach were included within the upper reaches of both the Glendavoc and Sheeffry rivers, giving a total of four stream reaches (two per treatment) and 62 and 29 individual sites for the LDR and LDC treatment groups respectively (Fig. 6.1). Thus, for the purposes of this experiment, 'stream reach' was defined as the total continuous stream section within each stream assigned to either of the two LD treatments. LD 'sites' were then defined as the individual measured and surveyed habitat units which comprised each stream reach.

High density (HD) sites consisted of 20-m instream length areas of riffle habitat, with these structured as individual and spatially separate units, rather than sub-units of larger stream reaches. HD sites were selected on the basis of knowledge gained in the 2019/20 trials, where this length was used, with most HD sites carried over from these previous experiments. Additionally, the site length chosen corresponded with the length of most sections of suitable spawning habitat within the Erriff catchment (≤ 20 m) and was also suitable in the context of logistical constraints relating to sampling and translocations. HD sites were chosen to be as similar as possible in terms of stream habitat, avoiding inclusion of features such as undercut banks, islands, confluences and split channels wherever possible.

Assignation of sites to the high density (HD) group was informed by data from previous experiments (Chapter 5). Sites with post-emergent fry densities equal to or greater than the upper 80th percentile (70 fish 100 m^{-2}) from all sites fished in the previous two years were assigned as high density. Hence, these sites could be considered to represent the optimum spawning habitat within the catchment, given all potential sites were already selected based both on their suitability for spawning and quality of fry riffle habitat.

HD sites were then split to provide two groups: controls (no manipulation) and treatment (manipulation). In HD treatments, salmon fry were removed and translocated into LDR reaches, these are referred to hereafter as ‘High Density Source’ (HDS) sites, HD control (HDC; i.e. high density sites where no fry were removed) then acted as the comparator group for HDS sites in autumn. The designation of sites to the control or treatment groups was initially done numerically, involving the ranking of sites according to fry density and designation as alternating treatments and controls. This was then adjusted to allow relatively easy ingress/egress and hence rapid removal of fry from HDS sites to reduce the time spent in captivity during translocations. For example, by not using HD sites located over 2 km from areas accessible by vehicle. In total 14 sites were assigned to the HDS and HDC treatments, with this number split evenly between treatments.

6.2.3 Pre-translocation surveys

Pre-translocation surveys were completed between June 9th and 18th 2021. The primary aim of these surveys was to determine densities of post-emergent salmon fry prior to translocation to provide baseline comparative data to post-translocation surveys at the beginning of autumn. However, comparison of pre-translocation versus autumn fry densities indicated that the pre-translocation surveys completed within the fry emergence period, as most LD sites had higher fry densities in autumn than June, while HD site densities were comparable between both survey periods. Notwithstanding, fry densities recorded during the period of fry emergence were considered to be strongly correlated with those which would be obtained post-emergence, and so were considered a strong proxy of actual post-emergence fry densities.

Prospective HD sites were selected both using fry density data from previous experiments and through the completion of preliminary walkover surveys of the lower Owenmore, which was not included in previous experiments, on June 2nd, 2021. Prior to sampling, upstream and downstream boundaries of all sites were marked on both banks using brightly coloured marker posts, which were then photographed *in-situ* after survey completion and geo-referenced to enable their subsequent location without needing permanent site markers. Low density stream reaches were also selected based upon a combination of walkover surveys and data from previous experiments. As with HD sites, individual LD sites were marked, photographed and geo-referenced. The marking, photography and geo-location of these sites was completed between June 3rd and June 8th, 2021, prior to electrofishing. All HD sites were located either within the Erriff mainstem (including the Owenmore) or the lower areas of the Glendavoc and Sheeffry catchments, with the LD stream reaches located near the headwaters of these two smaller tributaries (Fig. 6.1).

Electrofishing equipment consisted of portable Hans Grassl backpack units (model IG600) set between approximately 115 and 200V continuous direct current (DC), as per Chapters 2 and 5. All electrofishing surveys were conducted by the same operator (LC) for standardisation. Prior to fishing, water levels at each site were estimated and categorised as either ‘very low’, ‘low’ or ‘normal’ (higher flow categories were unnecessary as fishing was not completed in such conditions). Fishing was always carried out in an upstream direction without stop-nets, starting from the downstream site boundary, and comprised a single pass. During fishing, captured fish were held in water, with fish observed but not captured also counted by species, with the exception of salmonid fry, which were counted collectively due to difficulties distinguishing between species. Post-fishing, captured salmon and trout fry and parr were identified to species, measured (total length, TL; nearest mm) and then released. Larger trout and any other species captured were counted and released without measurement to enable rapid processing and release of all fish. Any salmonid fry observed but not captured were then assigned as either salmon or trout based on the captured proportions of each species, as in the Autumn surveys of the two previous years (Chapter 5).

6.2.4 Habitat Surveys

To enable density calculations and to account for differences in fry densities between sites and stream reaches related to habitat factors, habitat surveys were conducted for all experimental sites, either during initial site marking (LD sites) or after the completion of pre-translocation surveys (HD sites), between June 3rd and June 18th, 2021. All habitat variables were recorded by the same operator (LC) to reduce bias. Site areas were calculated by setting transects perpendicular to the direction of flow at 5-m intervals along each site, starting at the upstream boundary marker(s) and finishing at the downstream boundary. Wetted width was recorded for each transect, with site area (m^2) being a multiple of the mean width and site length. River depth was recorded at 5 points along each transect (left bankside edge, ¼ width from the left bank, channel centre, ¼ width from the right bank, right bankside edge). These data enabled pre-translocation salmon and trout fry densities to be determined ($n\ 100\ m^{-2}$). Additionally, the proportional area of each site covered by riffle, glide and pool habitats was estimated visually for each site, along with the proportional area with macrophyte cover and proportional area covered by each of the following substrate classes; sand/silt (approximate diameter; $D \leq 2$ mm), gravel ($2 < D \leq 64$mm), cobbles ($64 < D \leq 256$ mm), boulders ($D > 256$ mm) and bedrock. While useful for making rapid observations, visual estimation is a less accurate means to record habitat units and riverbed substrates than more extensive survey techniques, such as grid sampling (Hankin and Reeves, 1988; Latulippe, Lapointe and Talbot, 2001). Therefore, to reduce inaccuracies, repeat surveys for all habitat variables which were visually estimated were conducted in conjunction with post-translocation autumn electrofishing surveys, with mean values from these two observations used for analyses.

6.2.5 Translocations

Translocations were completed in three batches between June 21st and 23rd, 2021. Fry were collected from HDS sites using the same electrofishing method (single upstream pass), equipment and operator as in pre-translocation surveys. To minimise edge effects, such as immigration of fry from upstream and downstream areas of similar density (e.g. where riffles measured over 20 m in length), the area fished consisted of the 20-m site plus any further suitable riffle/glide habitat up to a maximum of 20 m upstream or downstream of the upstream and downstream boundary markers respectively. Most high density sites within this study were situated in riffle-pool-glide type habitat, with large pools between suitable riffles areas. This habitat structure likely serves to at least partially isolate individual riffles, with deeper pools mostly unsuitable for colonisation by post-emergent salmonid fry, primarily due to competition and predation from older salmonids, and particularly brown trout (Kennedy and Strange, 1986; Bardonnet and Heland, 1994; Heggenes, Bagliniere and Cunjak, 1999; Armstrong and Nislow, 2006). Hence, this was considered an effective way of minimising immigration into HDS sites.

To enable identification of translocated versus non-translocated fish in subsequent surveys, all translocated fry were adipose fin clipped, as per Chapter 5. Fish were then transferred to a 60-litre aerated transport tank for transportation. Water temperatures were monitored within the transport tank and maintained at the same approximate temperature as the river water, with bags containing ice prepared for immersion in the transport tank where necessary. These fry were then released into a single riffle section at the centre of each LDR stream reach (hereafter ‘release site’), with fry released in small groups as evenly as possible throughout the entire site. This method enabled assessment of the dispersal abilities of fry both upstream and downstream from the release site, hence informing any possible future use of this method as a management tool (e.g. the spatial segregation of fry release sites within streams subject to translocations).

6.2.6 Autumn surveys

Post-translocation autumn electrofishing surveys were completed between August 31st and September 7th, 2021, using the same method, equipment and operator as pre-translocation surveys. As in June, any salmonid fry observed but not captured were assigned as either salmon or trout based on the captured proportions of each species, with this method also used to assign salmon fry as either non-translocated (i.e. those fish present naturally) or translocated fish. All individual LDR, LDC, HDS and HDC sites were fished within this period, allowing autumn fry densities to be linked to both pre-translocation fry densities and treatment group.

6.2.6 Statistical analyses

Site-level differences in pre-translocation fry densities were initially explored using univariate analyses, with this also enabling testing for sources of treatment bias between treatment groups. Additionally, to account for any habitat-driven differences in autumn fry densities or fry lengths, the habitat data were tested using univariate analyses (Mann Whitney U tests, Welch’s two sample t-tests) before a principal component analysis (PCA) was conducted that incorporated the proportions of each of the 5 substrate classes, macrophyte cover, as well as the combined proportions of riffle and glide habitat, and mean site depth. Riffle and glide proportions were combined due to the relative difficulty in determining between these flow types, particularly in different flow conditions, and subjectivity of these observations. The proportion of pool habitat was excluded to maintain a variable: observation ratio of at least 1:10, and as it was necessarily correlated with the combined riffle and glide proportion, with these summing to 1. The PCA input incorporated all sites within each of the four treatments. Individual habitat variables and PC1 and PC2 scores were then compared between LDR vs. LDC sites and HDS vs. HDC sites. The PCA was run with all covariates scaled so that their means equalled zero and variances equalled one. PCA calculations were then done via singular value decomposition of the centred and scaled data matrix.

6.2.7 Generalised linear models

Generalised linear models (GLMs) were used to investigate the relationship between site-level pre-translocation fry densities, treatments, translocated fry densities and site-level measures of overall salmon fry density, as well as site-level non-translocated fry population change and autumn total lengths, while accounting for habitat variables, including densities of other fish species and age classes.

In all models, bidirectional selection was used to select the additional habitat variables to be included in each model, with these variables used to reduce the level of confounding variation. Specifically, both forward and backward stepwise selection was run on a range of habitat variables, with the Akaike information criterion (AIC) used to evaluate model fit at each stage. In cases where AIC scores were extremely similar between models containing different numbers of predictor variables, Bayesian information criterion scores were also used to inform model selection, thus decreasing the risks of model over-parameterisation. Only variables hypothesised to be of biological relevance were included in the selection process, with these listed for all models in Table 6.1, with correlation matrices and variance inflation factors (VIFs) used to identify any sources of collinearity between predictor variables prior to model selection. Only those variables selected through both forward and backward selection were included in the final model. In all models, a gaussian distribution was used for the response variable, based on QQ plots of model residuals.

Model validation was applied at each stage during model selection and after selection of the final model to verify the underlying assumptions. Specifically, residuals were plotted versus fitted values to assess homogeneity of variance, and residuals versus each covariate to investigate model misfit. Additionally, VIFs were calculated at each stage of model selection to check for multicollinearity. Predictions for each model were then used to visualise the effects of each covariate within the model on a similar and easily interpretable scale, using a range of values from the minimum to the maximum recorded values for the covariate of interest, while all other covariates were fixed at their mean values.

For all models, brown trout age class density variables were simplified to 0+ (fry) and 1+ (i.e. all trout parr, sub-adults and adults) age classes, given the low numbers of 1+ and older brown trout recorded at most experimental sites. The nature of the relationship between all modelled response variables and densities of all age classes of trout over 1+ was also hypothesised to be similar (i.e. negatively correlated due to competition and predation). Additionally, 1+ and 2+ age class salmon parr were not differentiated, as determination between these age classes was extremely difficult, given their overlapping length frequency distributions, and their effect on salmon fry was considered to be similar (i.e. asymmetric competition). Pre-translocation densities for each of these fish density variables were used as these were considered most likely to impact on fry survival immediately post-emergence, with fish larvae most vulnerable to mortality, and particularly predation, at smaller body sizes (Peterson and Wroblewski, 1984; McGurk, 1986; Houde, 1997).

6.2.8 Autumn fry densities

As with pre-translocation fry densities, and in line with (H_1) and (H_2), site level differences in autumn fry densities were first investigated using univariate analyses. To further test (H_2), site level differences within and between the two LD treatments were then analysed using GLMs, to account for additional habitat variation between sites and treatments. The response variable in this case was autumn fry density, inclusive of all captured and missed translocated and non-translocated salmon fry. All models included a linear component for pre-translocation fry density, with a quadratic component included in model selection to account for density-dependence in terms of fry density change (note: 'density change' is used as distinction cannot be made between immigration/emigration and mortality and as site-level fry densities increased over the summer period). Additionally, stream reach was included in model selection, both to account for any variation between stream reaches which could not be accounted for by recorded habitat variables, and to investigate any differences between treatments. Furthermore, following selection of the final model, model residuals were compared for data subsets from the LDR and LDC treatments to further investigate differences between treatments.

In line with H_3, overall autumn fry densities at sites within the two LDR stream reaches were then modelled against both pre-translocation fry densities and autumn translocated fry densities to investigate the relationship between translocated fry density and overall fry density in autumn. An interaction term between these two predictor variables was used to account for differences in the effect of translocated fry density at differing densities of non-translocated fry. As with the previous model, stream reach was included in model selection, to account for any variation between stream reaches which could not be accounted for by the recorded habitat variables.

6.2.9 Autumn non-translocated fry retention

In line with (H_3), to investigate the effect of autumn translocated fry densities on relative site-level non-translocated fry retention, i.e. the relative relationship between densities of non-translocated fry density pre-translocation (density at t_1) and in autumn (density at t_2), the following formula was used as the GLM response variable, including only data from sites within the LDR treatment:

$$\log_n\left(\frac{\text{density } t_2}{\text{density } t_1}\right)$$

This response variable was modelled against pre-translocation, non-translocated fry density, thereby testing for density-dependent effects, as well as autumn translocated fry density. Stream reach was again included in model selection to account for any differences in fry survival and/or net immigration/emigration between stream reaches. It should be noted that the effects of mortality and immigration/emigration of fry could not be distinguished, based on the experimental design. Additionally, as pre-translocation surveys were conducted during fry emergence, all fry retention figures were positive, as recorded fry densities were higher in the autumn surveys than in pre-translocation surveys. However, as noted above, the pre-translocation densities were likely strongly correlated with post-emergent fry densities, and thus can still be used to provide useful information on density-dependence and the effect of translocated fry.

6.2.10 Autumn fry lengths

To investigate the effect of translocated fry on non-translocated fry growth, in line with (H_4), site level autumn non-translocated fry mean TLs (mm) were tested against pre-translocation and autumn non-translocated fry densities and autumn translocated fry densities, with pre-translocation fry mean TL included in all models to account for differences in initial fry size. Thus, measures of translocated and non-translocated fry densities were effectively modelled against the change in non-translocated fry mean total length over the sampling period. It should be noted that mean fry lengths only provide a proxy for fry growth, given the inability to identify individual fish, and thus any significant relationships may equally relate to the effects of immigration or emigration of different size classes of salmon fry. Both LDR stream reaches were fished in either a single day or two consecutive days in both June and September. Therefore, while the sampling interval differed slightly between stream reaches it was similar for all observations within each stream reach. Hence, differences in sampling interval were accounted for by inclusion of stream reach in model selection.

6.3 Results

6.3.1 Translocated fry numbers, recapture rates and dispersal

A total of 3030 Atlantic salmon fry were successfully translocated in 2021, with 1573 and 1457 fish released into the Sheeffry and Glendavoc LDR stream reaches respectively. Of these, a total of 340 fish were recaptured in September, representing a recapture rate of 11.2 %, with an estimated further 234 translocated fry observed but not captured during autumn surveys, giving a total of 574 fry. Assuming all fry within each stream reach stayed within the surveyed area and all were either captured or recorded as missed, this represents an estimated survival rate of 18.9 %. Recapture and estimated survival rates were similar across both stream reaches (Glendavoc; 179 fry recaptured, 291 estimated encountered 20.0 % survival; Sheeffry 160 fry recaptured, 283 estimated encountered, 18.0 % survival). Translocated fry were generally concentrated to specific sites within both stream reaches, with approximately two thirds of the 340 recaptured fry caught from just 13 of the 62 LDR sites.

Dispersal was heavily upstream biased in both stream reaches (Fig. 6.2), with translocated fry captured up to a maximum of approximately 255 m and 250 m upstream of the release sites in the Sheeffry and Glendavoc LDR reaches respectively. Although translocated fry were encountered up to 240 and 252.5 m downstream in the Sheeffry and Glendavoc LDR reaches respectively, these seem to represent isolated individuals, with over 80 % of downstream-dispersing fry encountered less than 100 m from the release sites in both stream reaches (Fig. 6.2).

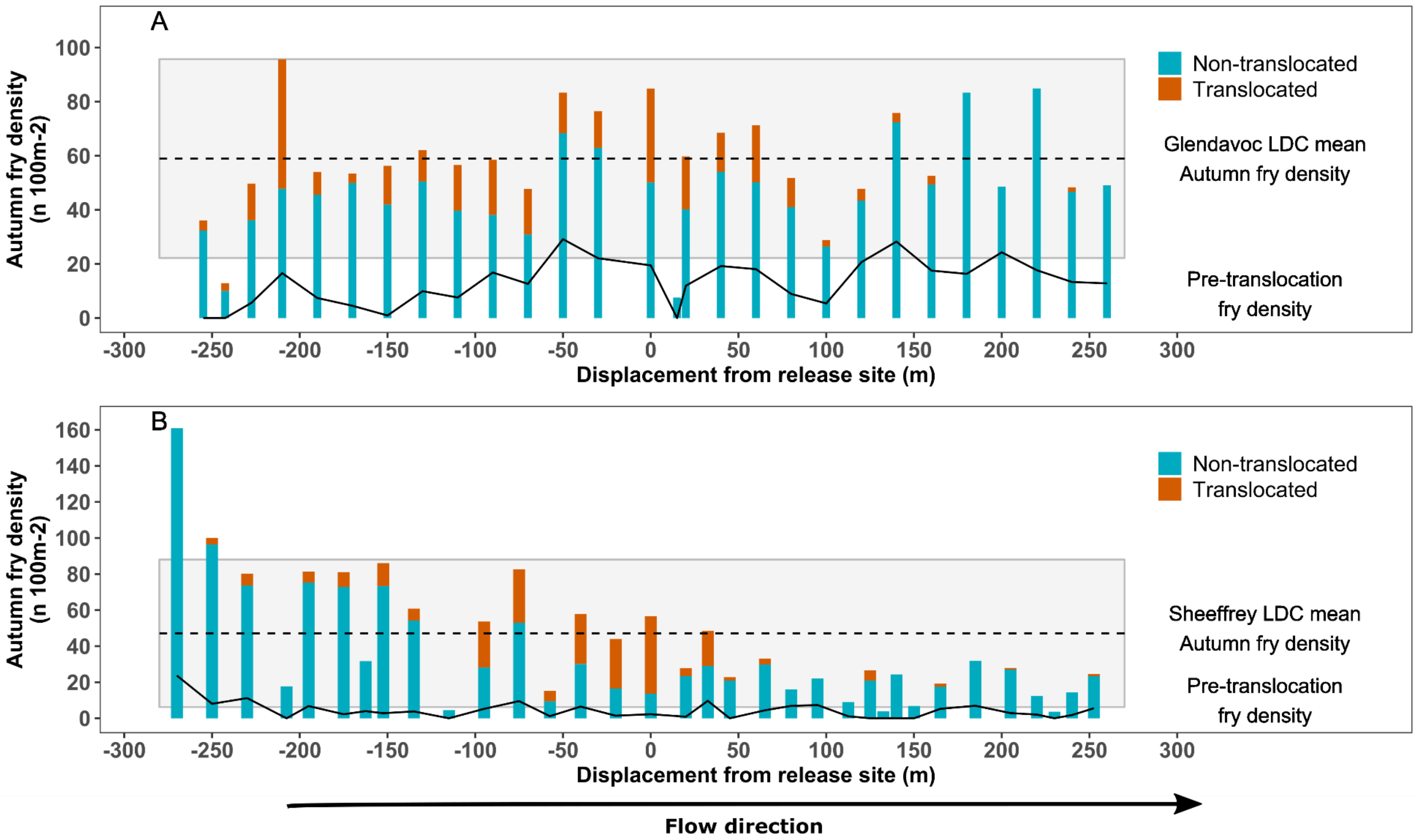

Figure 6.2: Autumn non-translocated & translocated fry densities within the Glendavoc and Sheeffry LDR stream reaches according to displacement distance from the release site. Pre-translocation densities for each site are shown alongside autumn LDC densities within each comparator stream reach

6.3.2 Sources of bias and confounding information

Comparison of habitat data through both univariate analyses and PCA showed no significant differences between the HDS and HDC treatments (Fig. 6.3A; Appendix 5, Table A1). Additionally, pre-translocation fry densities were not significantly different between the two treatments (Welch's two sample t-test; t = 0.9, df = 11.1, p = 0.37), thus showing no significant differences in habitat or pre-translocation fry densities (both potential sources of bias) were present and univariate analyses were sufficient for treatment comparison.

Comparison of habitat data through univariate analysis and PCA showed no significant differences between the LDR and LDC treatments, although very high variation in riffle and glide proportion was seen in both treatments (Fig. 6.3A, 6.3B; Appendix 5, Table A1). However, pre-translocation fry densities were found to be significantly higher in the LDC treatment (Mean LDC ± SD = 15.5 ± 14.9 fish m^{-2}, Mean LDR ± SD = 7.8 ± 7.9 fish m^{-2}, Mann-Whitney u test; U = 634, p = 0.02; Fig. 6.3C, 6.3D). Additionally, while pre-translocation fry densities were comparable to those obtained in the two previous years, autumn fry densities were much higher. In particular, LDR and LDC site densities were approximately 4 times higher than within the same treatment groups from the two previous experiments.

6.3.3 Autumn fry densities

Autumn fry densities did not significantly differ between HDS and HDC sites (Welch's two sample t-test; t = -0.5, df = 10.8, p = 0.62; Fig. 6.3E). Translocated fry were only recorded from approximately 70 % of the LDR sites, with only 32 % of LDR sites having 10 or more translocated fry, while no significant differences in autumn fry densities were seen between treatments (Mann-Whitney u test; U = 825.5, p = 0.53; Fig. 6.3E, 6.3F).

The GLMs indicated further differences between the LDR and LDC treatments, with the significance of the quadratic pre-translocation density variable suggesting density-dependence, which was primarily evident at higher pre-translocation fry densities of approximately 30 fish 100 m^{-2} or more. These densities were only recorded within the LDC treatment due to the overall treatment bias in pre-translocation fry densities, as outlined above (Table 6.1, Equation 1; Fig. 6.4A). While significant differences in autumn fry densities were apparent between stream reaches from this model, once other predictor variables were accounted for, these did not indicate any overall treatment-related difference, with densities highest in the Sheeffry LDR and Glendavoc LDC reaches and lowest in the Glendavoc LDR reach (Table 6.1, Equation 1). The combined proportion of riffle and glide habitat was also found to be positively correlated with autumn fry densities. Additionally, the proportions of gravel and the pre-translocation densities of 1+ salmon, 0+ trout and 1+ trout were found to be negatively correlated with autumn fry densities.

Testing of the autumn fry densities within LDR sites against pre-translocation fry densities and autumn translocated fry densities revealed both variables were significantly and positively correlated with autumn fry density (Table 6.1, Equation 2; Fig. 6.4B). Additionally, an interaction term between these two variables was negative and near-significant ($p = 0.08$), suggesting that at higher pre-translocation fry densities, the effect of increasing autumn translocated fry densities was lower. At the maximum pre-translocation density for LDR sites (29 fish 100 m^{-2}) this effect was negative above autumn translocated fry densities of 20 fish 100 m^{-2} (Fig. 6.4C). The quadratic term for pre-translocation fry densities was excluded during both forward and backward model selection. Cobble proportion was found to be significantly and negatively correlated with autumn fry density, while combined riffle and glide proportion was found to be positively correlated with autumn fry density.

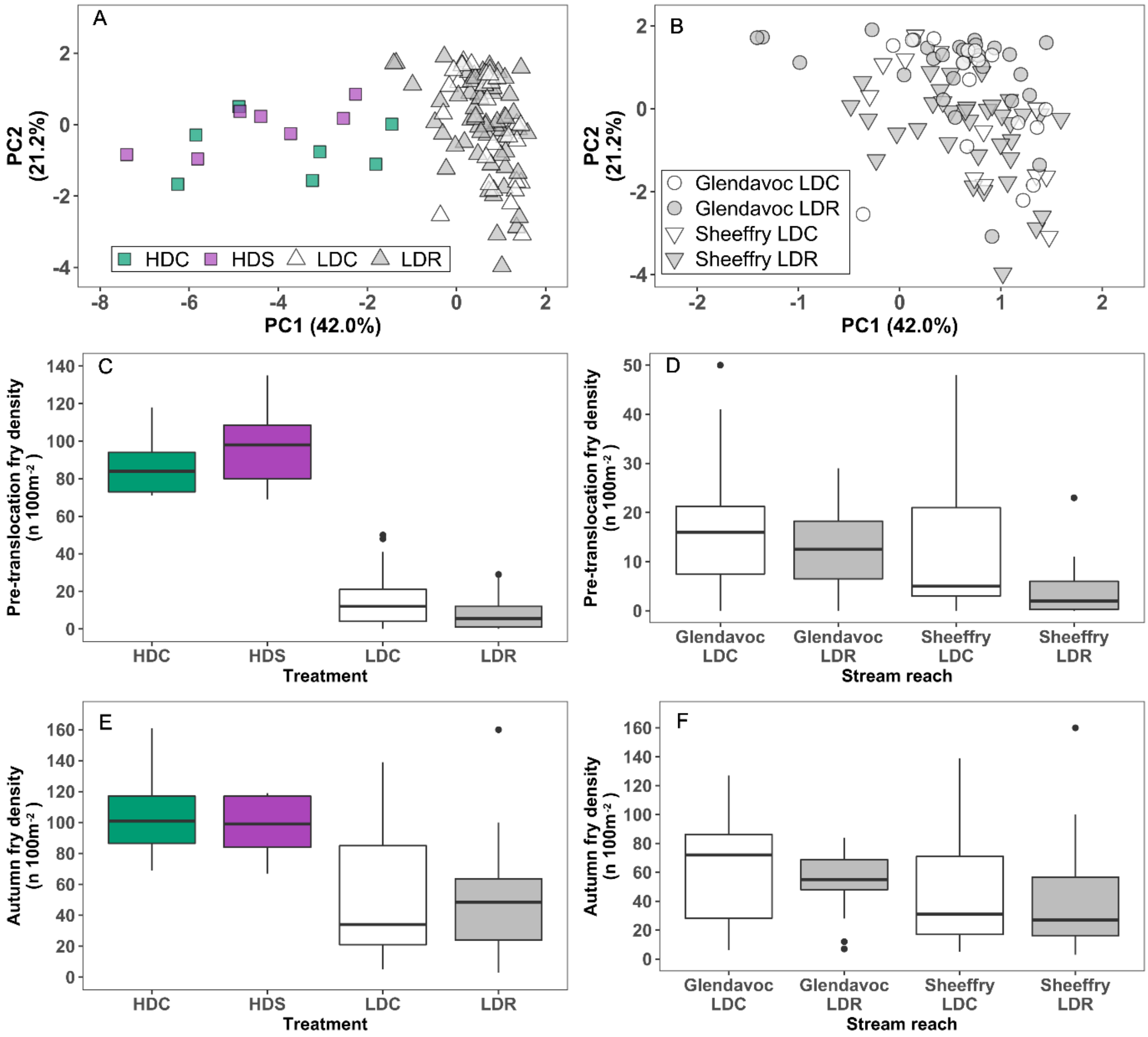

Figure 6.3: Principal Component Analysis of habitat variables for; A) all sites by treatment, and; B) low density sites by treatment. Boxplots showing pre-translocation salmon fry densities for; C) all treatments, and; D) low density stream reaches by treatment. Boxplots showing autumn salmon fry densities for; E) all treatments, and; F) low density stream reaches by treatment.

6.3.4 Non-translocated fry retention

In the GLM testing the effect of September translocated fry density on natural logged site-level retention of non-translocated fry, translocated fry did not have a significant effect in the final model. In contrast, non-translocated fry density was found to be significantly and negatively correlated with fry retention, with this effect size small (Table 6.1, Equation 3; Fig. 6.4D). During backward model selection, autumn translocated fry density was significantly correlated with the response variable, but was not selected during forward selection and was thus excluded from the final model (Appendix 5, Table A4). Gravel proportion was the only other predictor variable included in the final model, with this being significantly and negatively correlated with the response variable (Table 6.1, Equation 3).

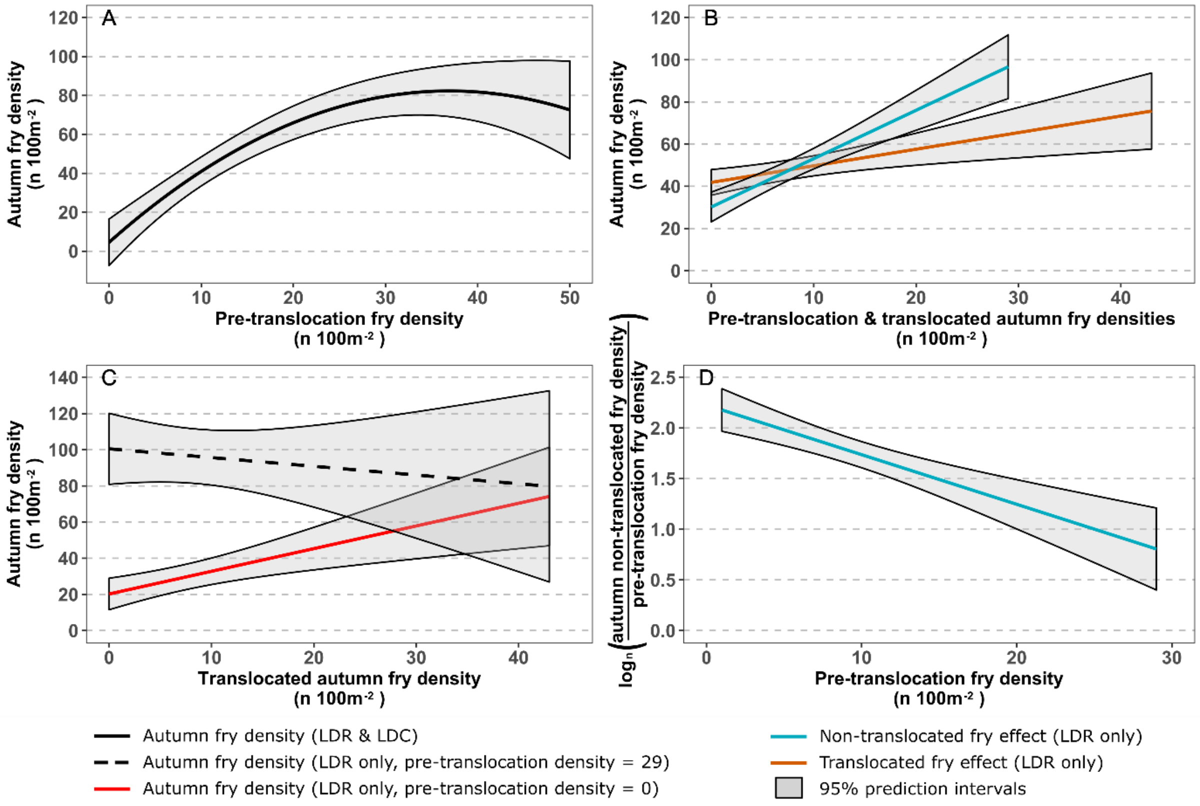

Figure 6.4: Predicted autumn salmon fry density and natural log transformed fry retention values, plotted against variables included in the GLMs in equations 1, 2 and 3 of table 6.1, with all other variables included in the models fixed at their mean values unless otherwise stated; A) Predicted values for autumn salmon fry density plotted against pre-translocation salmon fry density, based upon equation 1; B) predicted values for autumn salmon fry density plotted against pre-translocation salmon fry density (blue) and autumn translocated salmon fry density (orange), based upon equation 2; C) predicted values for autumn salmon fry density plotted against autumn translocated salmon fry density at pre-translocation salmon fry density values of 0 (red) and 29 (black, dashed) fry 100 m^{-2}, based upon equation 2; D) predicted values for log$_n$(fry retention) plotted against pre-translocation salmon fry density. Shaded areas of all plots represent 95 % prediction intervals around the predicted values.

6.3.5 Non-translocated fry growth

Neither pre-translocation, non-translocated fry densities nor autumn translocated fry densities significantly influenced non-translocated fry mean autumn TLs within LDR sites. However, autumn non-translocated fry density had a significant and negative effect on non-translocated fry TLs (Table 6.1, Equation 4; Fig. 6.5A). Substitution of non-translocated fry autumn density for overall autumn fry density within the final model produced models with near-identical AIC scores and effect sizes for the autumn fry density predictor variables, indicating that translocated autumn fry densities had little meaningful effect on non-translocated fry TLs. The final model also contained additional habitat variables, with pre-translocation densities of 1+ age class salmon significantly and positively correlated with non-translocated fry TLs, while riffle and glide proportions were also positively correlated with TLs and near-significant (Table 6.1, Equation 4). The pre-translocation mean TLs of non-translocated fry were also positively correlated with their autumn mean TLs (Fig. 6.5B).

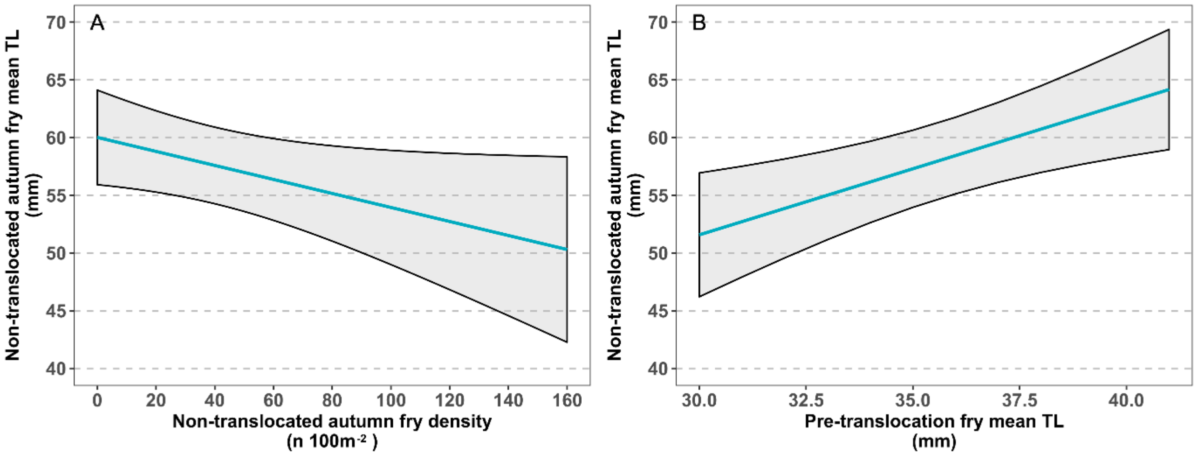

Figure 6.5: Predicted non-translocated fry autumn mean total length (TL) plotted against variables included in the GLM shown in equation 4 of table 6.1, with all other variables included in the model fixed at their mean values; A) non-translocated salmon fry autumn density, and; B) mean non-translocated salmon fry pre-translocation TL. Shaded areas represent 95 % prediction intervals

Table 6.1: Generalised linear model equations (#), statistically significant results are shown in bold

#	Formula	Dataset	N obs.	Variables available for selection	Selection	Covariate(s)	Estimate	Standard error	Z value	P value
1	*Autumn fry density ~ pre-translocation fry density + riffle & glide proportion + pre-translocation fry density^2 + pre-translocation 0^+ trout density + stream reach + pre-translocation 1^+ trout density + gravel proportion +pre-translocation 1^+ salmon density* Response variable distribution = Gaussian	All low density (LD) sites	91	Pre-translocation fry density, Cobble proportion, Riffle & glide proportion, Pre-translocation fry density^2, Gravel proportion, Mean depth, Pre-translocation trout fry density, Pre-translocation 1+ trout density, Pre-translocation 1+ salmon density, Stream reach	Appendix 5: Table A2	Intercept	8.73	7.93	1.10	0.27
						Pre-translocation fry density	4.21	0.58	7.31	**2.60 x 10^{-13}**
						Riffle & glide proportion	35.75	6.63	5.40	**6.87 x 10^{-8}**
						Pre-translocation fry density^2	-0.06	0.01	-4.53	**6.05 x 10^{-6}**
						Pre-translocation 0^+ trout density	-3.84	0.82	-4.67	**3.02 x 10-6**
						Glendavoc LDC stream reach	23.36	6.64	3.52	**0.0004**
						Sheeffry LDR stream reach	23.65	5.92	4.00	**6.45 x 10^{-5}**
						Sheeffry LDC stream reach	10.12	6.50	1.56	0.12
						Pre-translocation 1^+ trout density	-1.85	1.04	-1.79	0.07
						Gravel proportion	-169.67	66.71	-2.54	**0.01**
						Pre-translocation 1^+ salmon density	-0.85	0.41	-2.08	**0.04**
2	*Autumn fry density ~ pre-translocation fry density * translocated autumn fry density + cobble proportion + riffle & glide proportion* Response variable distribution = Gaussian	All low density recipient (LDR) sites	62	Pre-translocation fry density, Translocated autumn fry density, Cobble proportion, Riffle & glide proportion, Pre-translocation fry density^2, Gravel proportion, Mean depth, Pre-translocation trout fry density, Pre-translocation 1+ trout density, Pre-translocation 1+ salmon density, Stream reach	Appendix 5: Table A3	Intercept	25.11	9.26	2.71	**0.007**
						Pre-translocation fry density	2.77	0.44	6.31	**2.89 x 10^{-10}**
						Translocated fry autumn density	1.25	0.37	3.36	**0.0008**
						Cobble proportion	-88.22	32.82	-2.69	**0.007**
						Riffle & glide proportion	19.68	9.05	2.18	**0.03**
						Interaction term	-0.06	0.03	-1.77	0.08
3	*Ln(non-translocated autumn fry density/ pre-translocation fry density) ~ pre-translocation fry density + gravel proportion* Response variable distribution = Gaussian	Low density recipient (LDR) sites where fry were captured in June and autumn	49	Pre-translocation fry density, Cobble proportion, Mean depth, Gravel proportion, Riffle & glide proportion, Translocated autumn fry density, Pre-translocation trout fry density, Pre-translocation 1+ trout density, Pre-translocation 1+ salmon density, Stream reach	Appendix 5: Table A4	Intercept	2.55	0.19	13.60	**< 2 x 10^{-16}**
						Pre-translocation fry density	-0.07	0.01	-6.97	**3.11 x 10^{-12}**
						Gravel proportion	-2.95	1.97	-1.50	0.13
4	*autumn non-translocated fry mean TL ~ pre-translocation mean fry TL + pre-translocation 1^+ salmon density + riffle & glide proportion + non-translocated autumn fry density* Response variable distribution = Gaussian	Low density recipient (LDR) sites where fry were captured in June	51	Pre-translocation mean TL, Pre-translocation 1+ salmon density, Stream reach, Riffle & glide proportion, Non-translocated autumn fry density, Translocated autumn fry density, Pre-translocation fry density, Gravel proportion, Cobble proportion, Mean depth Pre-translocation trout fry density, Pre-translocation 1+ trout density	Appendix 5: Table A5	Intercept	14.30	14.30	1.00	0.32
						Pre-translocation mean fry TL	1.14	0.38	2.99	**0.003**
						Pre-translocation 1^+ salmon density	0.48	0.16	3.02	**0.003**
						Riffle & glide proportion	7.09	3.76	1.89	0.06
						Non-translocated autumn fry density	-0.06	0.03	-1.96	0.05

6.4 Discussion

The results indicate that autumn fry densities of donor sites were not adversely impacted by post-emergent fry removals (consistent with H_1). Although sites that received translocated fry did not have significantly higher fry densities in autumn, contrasting with H_2, total autumn fry densities were positively correlated with autumn translocated fry densities in recipient reaches (as per H_3), with translocated fry also having no significant impacts on non-translocated fry growth or survival/emigration, in line with H_4. These results thus demonstrate that, as a method to enhance autumn fry densities, translocation can successfully increase densities at the stream reach level without impacting fry donor sites, and non-translocated fry growth and survival.

These results are in contrast to Chapter 5, where no impact of translocations on LDR sites was found and relatively few translocated fry were recaptured in autumn surveys. The use of larger continuous stream reaches and translocation of many more fry per stream reach greatly influenced this result, accounting for the high dispersal which was an issue in the two previous years. These positive results are despite the bias in pre-translocation fry densities from LDC and LDR sites, as well as the confounding impacts of extremely high autumn fry densities and uncertainty around post-emergent fry densities. Thus, the results here are enough to suggest that, under more typical conditions in terms of natural fry abundances, and excluding any treatment bias, translocations may also have led to significant overall treatment effect.

This suggests that, compared to alternative enhancement programmes, such as hatchery stocking, translocation may provide a viable conservation tool that avoids negative consequences, such as reduced fitness of wild populations (Araki, Cooper and Blouin, 2007; Christie *et al.*, 2012). Additionally, given the strong link between fry abundances and smolt numbers shown previously (Crozier and Kennedy, 1995), it is likely that larger scale translocations could be used to successfully increase smolt numbers for this, or other, river catchments.

As noted above, the results of this experiment were strongly impacted by extremely high non-translocated autumn fry densities within both LD treatments. Under similar fry densities as those recorded in the two previous experiments, the effect of these translocations may have been much greater, provided the differences in autumn fry densities between years related more to spawning effort than fry survival. As pre-translocation surveys were most likely conducted during the fry emergence period, the true post-emergence fry densities are unknown. However, in the absence of mass fry immigration into LD stream reaches, post-emergent fry densities must have exceeded those recorded in autumn. Thus, post-emergent fry densities likely also greatly exceeded those of previous years. Therefore, there is evidence to suggest that, at lower post-emergent fry densities, a significant difference between LDR and LDC treatments would have been apparent. This is key to the wider applicability of this method, given adult salmon numbers are known to vary widely, both between catchments, and within catchments between years (L'Abée-Lund, Vøllestad and Beldring, 2004; Niemelä *et al.*, 2006). Additionally, inter- and intra-catchment changes in adult age-class structures between years are also common (L'Abée-Lund, Vøllestad and Beldring, 2004; Niemelä *et al.*, 2006), with these also likely to impact on fry densities due to higher fecundity and larger egg sizes of larger females (Thorpe, Miles and Keay, 1984; Heinimaa and Heinimaa, 2004). Variations in egg deposition, and hence post-emergent fry densities, are likely to impact on the potential success of translocations. This hence serves to highlight the need for accurate abundance data at appropriate spatial scales, ideally based upon spawner distribution, such as through redd counts (Gallagher, Hahn and Johnson, 2007), or post-emergent abundances (e.g. through electrofishing surveys), if applying translocation as a conservation tool.

Given the lack of habitat differences between LDR and LDC stream reaches, it is possible that the differences in pre-translocation fry densities may have related to the location of both LDC stream reaches downstream of their comparator LDR reaches. Although results from the two previous experiments indicated that both post-emergent and autumn fry densities within these areas were similar, there was an overall trend towards higher fry densities further downstream. This likely relates to the spawning preferences of Atlantic salmon, which generally tend to spawn in larger streams with relatively higher stream orders than brown trout (Crisp, 2008). This pattern is borne out by long-term population monitoring within the Erriff catchment, which indicates that the highest fry abundances are found within the Erriff mainstem (Inland Fisheries Ireland, unpublished). However, this does not fully explain why pre-translocation densities varied to such an extent at such small geographic scales (≈ 1 km instream length).

The differences in pre-translocation fry densities between the two LD treatments appear to have led to differing population dynamics, as shown by the models from equations 1 and 2. The quadratic term for pre-translocation fry density was found to be significant when modelling all LD sites, producing a dome-shaped stock recruitment curve similar to the Ricker model, as hypothesised by some authors for this species (Schnute and Kronlund, 2002; Honkanen, Boylan, *et al.*, 2018). This was not the case when LDR sites were considered separately, where a linear relationship was found. Predicted autumn fry density values from equation 1 appear to show that density-dependent mortality/emigration was only a major factor in determining autumn fry densities above pre-translocation density values of approximately 30 fish 100 m^{-2}, with many LDC sites exceeding this density, but no LDR sites. The only evidence for density-dependent processes within LDR reaches came from the significance of pre-translocation fry density in equation 3, and the interaction term between this and autumn translocated fry densities from equation 2, with the latter indicating that the effect of translocations was negative at pre-translocation densities of 21 fish 100 m^{-2} or above. While a number of authors have hypothesised about the thresholds for density-dependent mortality in this species (Uusitalo, Kuikka and Romakkaniemi, 2005; Armstrong and Nislow, 2006; Einum, Nislow, Reynolds, *et al.*, 2008), there is little empirical information available on the threshold densities at which density-dependent processes begin to act upon fry survival, with these also likely to vary according to river habitat, and thus carrying capacity (Gibson, Bowlby and Amiro, 2008). This also serves to further highlight the key requirement for translocation success, i.e. that natural fry densities are low relative to the stream carrying capacity, with this likely to be highly variable across rivers (Gibson, Bowlby and Amiro, 2008). Thus, this result serves to further highlight the utility of accurate abundance data at appropriate spatial scales to increase the likelihood of translocations having beneficial impacts

In contrast to the inter-treatment comparison, analysis of the autumn fry densities from within the LDR treatment allowed more robust conclusions to be made regarding H_3 and H_4. The significant and positive effect of autumn translocated fry densities, as shown by the model from equation 2, provides direct support for hypothesis H_3. Additionally, the lack of a significant effect of autumn translocated fry densities on natural logged site retention of non-translocated fry, or on non-translocated fry lengths, provides strong support for H_4. Although the negative interaction term between autumn translocated fry densities and pre-translocation fry densities indicates there is a potential for negative effects at higher fry densities, this was only evident at the unusually high fry densities from this experimental year. Thus, in combination these two results strongly indicate that the overall impact of translocations in LDR stream reaches was positive in terms of fry abundances.

The lack of any significant link between translocated fry and the mean TL of non-translocated fry in autumn also provides robust support for hypothesis H_4. The significant negative effect of autumn non-translocated fry densities on mean TLs suggests some form of density-dependence in fry growth rates, in contrast to Chapter 5. The reason for the significance of this autumn density variable, as opposed to pre-translocation density, may relate to the population dynamics of Atlantic salmon. It has been previously hypothesised that, as dispersal abilities increase, as in larger age classes, the risk of density-dependent mortality decreases, with density-dependence then primarily seen in growth rates (Einum, Sundt-Hansen and Nislow, 2006). Given the high recorded dispersal distances for salmon fry in this experiment, the significance of autumn density may therefore demonstrate that, by the end of the first summer, density-dependence in Atlantic salmon fry is primarily exhibited through reduced growth rates, rather than mortality. While substantial empirical evidence indicates that mortality is the key process impacted by density-dependent processes in the first summer following fry emergence (Nislow, Einum and Folt, 2004; Einum and Nislow, 2005; Honkanen, Boylan, *et al.*, 2018), previous studies have also shown density-dependent growth to occur in this period (Imre, Grant and Cunjak, 2005; Ward, Nislow and Folt, 2009; Einum *et al.*, 2011). Any impact on growth may have further implications on smolt numbers and survival, with early growth potentially linked to age and size at smoltification (Marschall *et al.*, 1998; Strothotte, Chaput and Rosenthal, 2005), while smolt size may affect survival at sea (Kallio-nyberg *et al.*, 2004; Saloniemi *et al.*, 2004).

The effects of other habitat variables within the GLMs were generally in line with expected results, based on known habitat requirements of Atlantic salmon fry and interspecific interactions with brown trout. The negative relationships between autumn fry densities, and pre-translocation densities of both trout age classes, as well as 1+ salmon, may relate to habitat usage, with salmon fry known to utilise shallower and faster flowing areas than older conspecifics and brown trout (Heggenes, 1990; Heggenes, Bagliniere and Cunjak, 1999; Armstrong *et al.*, 2003). These effects may also relate to competition, or, in the case of the older age classes of trout, to intra-guild predation. Competitive interactions between Atlantic salmon and brown trout are well documented (Armstrong *et al.*, 2003; Houde, Wilson and Neff, 2015), while brown trout are also known cannibals and intra-guild predators of other salmonids (Vik, Borgstrøm and Skaala, 2001; Grey *et al.*, 2002; Alvarez and Ward, 2019). The positive correlation between 1+ salmon densities and autumn fry length may provide support for the niche-segregation hypothesis, with larger salmon fry undergoing a shift in habitat usage towards the end of the first summer, thus creating higher habitat overlap with older conspecifics. This effect may equally relate to some measure of primary productivity and/or food availability, with 1+ salmon expected to distribute themselves according to availability of food resources, according to most foraging theories (Hayes, Stark and Shearer, 2000; Heggenes, 2002; Stephens and Krebs, 2019). However, this hypothesis cannot explain the negative correlation between 1+ salmon and salmon fry densities, with this relationship providing support for the niche segregation/overlap hypothesis.

Measures of both cobble and gravel proportions were generally found to be negatively correlated with autumn fry densities and site retention of non-translocated fry. This may indicate that these substrate classes are of lower importance to salmon fry than to spawning adults, and their prevalence may in fact increase salmon fry mortality/emigration. This contrasts with previous research which has shown salmon fry to utilise stream areas with predominantly gravel substrate (Heggenes, 1990; Heggenes, Bagliniere and Cunjak, 1999). However, given the spawning requirements of adult salmon, it may be difficult to disentangle the habitat preferences of salmon fry from their distribution in relation to spawning areas. By accounting for pre-translocation fry densities through GLMs it is possible that more accurate determination of habitat requirements for salmon fry may be made.

It is important to note that the findings of the two previous field experiments showed a positive relationship between both gravel and cobble proportions and autumn fry density (Chapter 5), so the findings here are far from conclusive. It is possible that the negative relationship seen here relates to specific conditions within the 4 experimental stream reaches, which differed from those at most sites in previous years. All stream reaches were characterised by a general lack of overhanging and instream vegetation, woody debris etc., with these known to provide cover for salmonids (Meehan, Swanson and Sedell, 1977; Haury *et al.*, 1995; Roni and Quinn, 2001). Therefore, it is possible that sites predominated by gravel and cobble substrate had a lack of additional cover, as provided by larger substrates, and therefore may have increased fry vulnerability to predation and displacement during high water conditions. Both boulders and interstitial spaces, as provided by larger substrate classes, have been shown to provide additional cover for juvenile salmonids (Haury *et al.*, 1995; Meyer and Griffith, 1997; Finstad *et al.*, 2007). A previous study by Finstad *et al.* (2007) used mean substrate diameters of 194 mm ± 42 SD to create interstitial shelters for Atlantic salmon fry. This substrate size is comparable to the approximate 64-256 mm diameter range used to define cobble substrate here. However, Finstad *et al.* (2007) measured substrate diameters directly, whereas these were only estimated in this study, making direct comparison less accurate. Secondly, Finstad *et al.* (2007) laid individual larger substrate particles onto a bed of finer substrate (mean diameter ± SD = 43 ± 18mm) within artificial stream channels. Thus, the larger substrate particles represented defined shelter structures, given the lack of substrate compaction and disparity in substrate sizes. These conditions might be expected to provide relatively larger and more numerous interstitial spaces than the natural lotic habitats from this study, where individual substrate particles were often embedded with other similarly sized particles.

Irrespective of the mechanism behind this effect, the lack of any positive correlation between gravel or cobble substrate classes and salmon fry densities, retention or total lengths can be seen as a positive indicator for the efficacy of translocations as a management tool, as it indicates that these substrates are not of critical importance to salmon fry. Thus, based on the results of this experiment, salmon fry could theoretically be translocated into areas with low proportions of these substrates, as generally found in areas of low spawning effort, without negatively affecting fry survival or growth.

In contrast to the above substrate measures, the proportion of stream area made up of either riffle or glide flow types was found to be a key positive predictor for determining both autumn fry densities and total lengths, with strong positive correlation seen between combined riffle and glide proportions and each of these response variables. This indicates that, of the various abiotic habitat variables recorded, suitable flow conditions, rather than substrate type, are of greatest importance in ensuring salmon fry performance, as measured through autumn fry densities and lengths. This finding is in line with previous research, as there is substantial evidence showing that shallow, riffle-type habitats are key areas for Atlantic salmon fry (Heggenes, 1990; Armstrong *et al.*, 2003; Koljonen *et al.*, 2013). This finding also has important implications for the application of translocation as a potential management tool for Atlantic salmon, with suitable flow conditions likely to be of considerable importance in determining the overall success of individual translocations in terms of fry survival and growth.

In addition to increasing overall survival and growth of translocated salmon fry, it is likely that availability of suitable flow conditions may also provide a vector for fry dispersal. Maximum fry dispersal distances were much higher than expected in both LDR stream reaches, particularly in the upstream direction, but also differed between streams. The greater dispersal of translocated fry in the Glendavoc, compared to the Sheeffry, may be linked to habitat differences, with the Glendavoc LDR reach consisting of much longer sections of continuous riffle and shorter pool sections than the Sheeffry reach. Deeper pools may serve to partially isolate individual riffles, as they are unsuitable for colonisation by salmon fry, primarily due to competition and predation from older salmonids (Kennedy and Strange, 1986; Bardonnet and Heland, 1994; Heggenes, Bagliniere and Cunjak, 1999; Armstrong and Nislow, 2006). Thus, the higher dispersal in the Glendavoc LDR reach may relate to the relative abundance of riffle habitat, and lack of deeper pools. It should be noted that, within the Glendavoc LDR reach, over 200 m upstream of the release site, a sequence of deep plunge pools and small waterfalls likely hindered fry dispersal. Despite this, over 30 translocated fry were estimated to be present within and above this stream section, suggesting that dispersal through less suitable habitat units is possible.

Even after accounting for the suitability of flow conditions to fry dispersal, the dispersal ability shown by salmon fry in this experiment is in stark contrast to much of the literature on this topic. Previous hypotheses on density-dependent mortality in Atlantic salmon have been largely based upon the premise that fry dispersal is extremely limited following emergence from spawning gravels, and thus fry are effectively ‘trapped’ in areas of high density (Finstad *et al.*, 2010). The results of this experiment show that, where suitable habitat is available and relatively uninterrupted, Atlantic salmon fry will disperse at least as far as 200 m upstream and 100 m downstream from their point of release, even in relatively high gradient streams with small barriers, including waterfalls, present. This highlights the ability of fry translocations to facilitate colonisation on the 200-300 m spatial scale. Equally, this indicates that, where spawning material is abundant but patchy at similar spatial scales, fry may be able to successfully colonise all available stream habitat without the need for translocations. Therefore, the use of translocations as a possible management strategy should be carefully considered in the context of existing environmental factors.

6.5 Conclusions

While there is a clear need for further research under more typical environmental conditions within headwater stream habitats, the results of this study highlight the potential benefits of intra-catchment fry translocations as a management tool for Atlantic salmon and other salmonids. Translocation of Atlantic salmon fry resulted in successful colonisation of extensive sections of stream. Summer survival rates of at least 19 % were higher than those of 1st generation hatchery salmon fry (i.e. wild parents but artificial mate selection) planted out as eggs (Einum and Fleming, 2000). Furthermore, given that it is unlikely that all surviving salmon fry were encountered in autumn, the true fry survival figures may be much higher. Additionally, translocated fry densities were positively correlated with overall densities of autumn fry, with little effect on non-translocated fry survival or growth, demonstrating that translocations had a positive effect on autumn fry numbers in LDR stream reaches. While a significant effect could not be shown in comparison between LDR and LDC treatment groups, there is substantial evidence to suggest that, under more typical environmental conditions, a significant effect would be observed. Thus, intra-catchment translocation shows evident promise as a management and conservation tool for Atlantic salmon.

Chapter 7: Discussion; refining existing monitoring practices and applying novel enhancement strategies to populations of threatened diadromous species

7.1 Population monitoring practices for salmonids

7.1.1 Current issues with population monitoring practices for stream-dwelling salmonids

The common monitoring practice of carrying out time-delineated single pass electrofishing surveys for stream-dwelling salmonids, as discussed in Chapter 2, is likely to lead to very high sampling error, a result of both habitat influences, such as stream wade-ability, and density-dependent error that occurs at higher salmonid densities. It was then demonstrated in Chapter 3 that the current application of these surveys, in failing to account for density-dependent mortality over the summer period, is likely to lead to further inaccuracies in survey results, and poor comparability between surveys conducted at different times during this sampling period. When considered together, these two issues suggest that, in its current form, this monitoring practice must be considered to provide only qualitative data, rather than semi-quantitative data.

As it currently stands, time-delineated single pass surveys are likely only suitable when operating at moderate salmonid densities (i.e. < 69 fish 100 m^{-2}), with observations at higher densities subject to high density-dependent error, as shown in Chapter 2, and as also indicated by Honkanen *et al.* (2018). Thus, this method may be unsuitable for abundance estimation of stream-dwelling salmonids under a number of circumstances, such as where accurate abundance estimates must be obtained across a range of fry densities, diverse or complex habitats, or across relatively broad sampling periods. The results of Chapter 2 are also likely to represent a conservative estimate of the sampling error inherent to this method, given all surveys were conducted within the same catchment under similar flow conditions and with the same operator, with most observations representing repeat surveys of the same sites. Under typical statutory monitoring programmes, where observations are obtained by a number of operators surveying numerous river catchments (e.g. Corcoran *et al.*, 2021; Holmes *et al.*, 2021), these additional sources of error are likely to lead to even further uncertainty around survey results. Given that current population monitoring practices do not commonly take into account any of these sources of error, this may lead to the misappropriation of conservation efforts, which could act against conservation aims for both Atlantic salmon specifically and salmonid fishes generally (e.g. by failing to identify rivers that are below their conservation limits).

7.1.2. Refining current population monitoring methods

In their current form, the electric fishing surveys of Chapters 2 and 3 appear to only be suitable for providing qualitative data on salmonid abundances. However, the results also indicate several ways by which their accuracy and utility can be improved. Inclusion of an area coverage estimate - so enabling density estimations - produced fry density estimates that closely matched those calculated from more rigorous area-delineated single pass electrofishing surveys (Chapter 2). In practice, similar results could potentially be achieved with relative ease by recording a total riffle area measurement in a given year and subsequently estimating the percentage coverage of the riffle during time-delineated surveys. Additionally, given the complexity of juvenile salmonid habitats (Fausch and Northcote, 1992; De Jalón and Gortazar, 2007; Hasegawa and Maekawa, 2008), and the need for representative sampling in population-level studies (Petersen, Minkkinen and Esbensen, 2005), use of variable survey times according to total riffle area would increase the precision and representativeness of survey results. By then incorporating a depletion factor similar to that calculated in Chapter 3, that allows standardisation of results across the survey season, comparison could then be made between surveys conducted across the entire summer sampling period with far greater reliability and precision. Additionally, the ability to generate fry density data would greatly increase the utility of time-delineated survey results in enabling better integration with habitat assessment methods, such as HABSCORE, River2D and PHABSIM (Bourgeois *et al.*, 1996; Milner, Wyatt and Broad, 1998; Gard, 2009). Hence, these data could be used similarly to those obtained from area-delineated methods, while also maintaining their advantage over such methods of more rapid and efficient sampling. Additionally, the use of such refinements would also account for issues presented by survey of different species with variable handling times and the use of differing survey methods, such as using separate electrofishing operators and netters, which are likely to impact on area coverage.

7.1.3 Recommendations for further research on juvenile salmonid surveys by electrofishing

It is assumed above that accurate estimates of area coverage could be obtained by converting percentage coverage of a measured riffle area to an estimated area coverage (in m^2). However, previous studies have indicated that area estimation of substrate types may be subject to some inaccuracy (Hankin and Reeves, 1988; Latulippe, Lapointe and Talbot, 2001). Given the similarities between these methods, albeit substrate composition estimation is likely to be more difficult given the spatial heterogeneity of riverbed substrates, the ability to generate accurate area coverage estimates from such methods should also be tested prior to their implementation.

Given that the depletion factor calculated in Chapter 3 was probably influenced by the nature of the dataset used to create the GLMM (i.e. time-delineated electrofishing surveys), it is likely that depletion factors calculated from the refined time-delineated method described above will differ. The primary difference between the original and the proposed refined method is that the former does not account for area-coverage and/or time spent handling fish, and thus results in a diminishing returns curve for actual fry densities versus the number of fry recorded per 5-minute sample, with high density-dependent error. It was hypothesised in Chapter 3 that this led to a linear model structure being preferred to a quadratic structure, with initial high mortality rates due to density-dependent processes in early summer being obscured by this density-dependent error. By accounting for such error in the refined method, it is likely that the relationship between the results of refined time-delineated surveys and survey sampling date will differ. Thus, it is recommended here that similar depletion factors are calculated from such surveys. Alternatively, given the similarity between true area-delineated survey results and densities calculated from area-estimation during time-delineated surveys in Chapter 2, the results of area-delineated single or multiple pass surveys could be used to develop robust depletion factors which could then be used for all three methods, given the relative accuracy of both area-delineated methods is relatively well known (Temple and Pearsons, 2003; Peterson, Thurow and Guzevich, 2004; Arnason, Antonsson and Einarsson, 2005).

7.2 Inter-catchment translocations of European eel

The results of Chapter 4 indicated that inter-catchment translocation of juvenile European eel can provide a tool for application in conservation programmes for this critically endangered species. However, given the low survival of eels in this study (2.2 % recapture rate), and the effect exerted by a single species (brown trout) on eel survival, the use of such methods should be considered in the context of conservation objectives for eel. Given current EU targets to achieve at least 40 % escapement of silver eel biomass, relative to the best estimate of escapement without anthropogenic influences (European Commission, 2007), then removal of large numbers of glass eels for stocking into areas where their survival may be low might be acting against this objective. Consequently, there remains a salient need to further evaluate this method across a range of habitats and within more speciose ecosystems to determine where the benefits of eel translocations may be greatest. As noted in Chapter 4, the low eel survival rate might have resulted from the harsh lotic environments within the experiment, with eels released into small headwater streams. Previous studies have shown that primary productivity in lotic environments is directly related to stream order (Bott, 1983), with higher stream order rivers also more likely to provide favourable environmental conditions, such as slower flows and higher macroinvertebrate abundance (Strahler, 1957; Rosi-Marshall and Wallace, 2002), particularly when considering the preferred habitat for this species (Lamouroux *et al.*, 1999). However, such habitats are often more speciose, with increasing species richness generally considered to reduce the likelihood of colonisation success via greater competitive and/or predation pressure (Elton, 1958). Thus, translocation success should be tested across a more diverse array of habitats in order to generate robust best-practice guidelines for this conservation method.

7.3 Testing and refining the application of a novel conservation method for Atlantic salmon; intra-catchment translocations

7.3.1 Knowledge gained from three years of salmon translocation experiments within the River Erriff catchment, Ireland.

Although the evaluation of the post-emergence salmon translocations remains in its early stages, the results of translocations within the River Erriff catchment point to a number of conclusions. The first is that the removal of large quantities of post-emergent Atlantic salmon fry from riffles with high fry densities at the beginning of summer can be conducted with minimal impacts on autumn fry densities at those same sites. Therefore, this provides further empirical evidence for the density-dependent mortality and population bottleneck hypotheses of juvenile salmonids proposed by numerous authors (for example, Einum and Nislow, 2005; Imre, Grant and Cunjak, 2005; Einum, Sundt-Hansen and Nislow, 2006; Einum, Nislow, Mckelvey, *et al.*, 2008). Additionally, results from all three experiments suggested that releasing large quantities of salmon fry into low density sites and stream reaches had little effect on either the growth or survival of the resident (i.e. non-translocated) fry.

In combination with the above, the use of intra-catchment translocation also eliminates many of the issues associated with the supplemental stocking of hatchery reared fish, while preserving the social benefits. Specifically, issues of reduced fitness due to non-natural selection processes (Araki, Cooper and Blouin, 2007; Araki *et al.*, 2008) are bypassed, as fry involved in translocations are of wild parentage and not reared in captivity. The only possible example of such artificial selection during translocations relates to stress or anaesthesia tolerance. Given the low mortality experienced in all three years during the translocation process, the relative impact of this is considered negligible, although the possibility that some latent mortality occurred due to cumulative stress effects cannot be excluded, particularly given the well-documented negative effects of stress on fish survival and disease resistance (Wedemeyer, 1970; Pickering and Pottinger, 1989; Petitjean *et al.*, 2019).

The results of all three experiments were less clear regarding the low density treatment comparisons. In all three years, comparison between low density fry recipient and control sites/reaches was impacted by either high fry dispersal (2019 and 2020) or by extremely high natural recruitment and bias in pre-translocation densities (2021). These issues highlight the difficulty in obtaining robust results from non-contained field experiments, in which natural variability in environmental conditions can act as a confounding factor (Fisher, 1992; Osenberg *et al.*, 1994), and where experimental design is critical. Irrespective, the results of all three years experiments, and the differences between these, provide clues as to the impact of fry translocations.

By accounting for high fry dispersal within the experimental design for 2021, estimated fry recapture rates (inclusive of fish missed) were improved from 4.6 % across 2019 and 2020, to approximately 19 % (Chapter 5, 6). Thus, the use of larger experimental units (500 m stream reaches) in 2021 can be considered as key to demonstrating a positive effect of translocations. Additionally, the release of large numbers of fry at each release site in 2021 compared to the two previous years was likely to have greatly increased the likelihood of subsequently recapturing of large numbers of fry, given the relationship between species abundance and recorded numbers is not necessarily linear for rare species (Gotelli and Colwell, 2011), with the translocated fry acting as a species analogue in this case. By increasing the size of the experimental units in 2021, the experimental results provided evidence which is contrary to established hypotheses that dispersal may be extremely limited for this species at this life stage (Finstad *et al.*, 2010), with both upstream and downstream dispersal distances of approximately 250 m noted from both stream reaches, despite relatively high stream gradient and barriers to dispersal, and with numerous fish caught over 200 m upstream of the release sites in both stream reaches.

Even with these amendments, the 2021 experiment was significantly hindered by the later emergence of salmon fry (possibly related to the cold spring), high autumn recruitment (likely due to favourable summer conditions and/or high spawning effort), and pre-translocation fry density that had some bias towards low density control sites. Irrespective of these limitations, the results do indicate that translocations can have a positive effect on fry densities in low density recipient stream reaches, while under more typical fry densities a significant treatment effect may have been evident. It remains to be seen how such increases may translate into increased smolt numbers, and subsequently numbers of adult spawners.

7.3.2 Recommendations for further research

Given the potential of intra-catchment translocations as a conservation strategy for Atlantic salmon, and one that can replace hatchery stocking as a population enhancement tool, there is a need to further test this method on a larger scale. This should aim to determine whether a significant treatment effect can be demonstrated in terms of fry densities. For example, this could involve studies conducted across multiple river catchments and years, with longer stream sections surveyed, and release of salmon fry at multiple points along these, to determine whether translocation can be used to increase autumn fry densities at a scale where observable and significant increases in catchment-level smolt output can potentially also be generated.

Linking translocated fry numbers to smolt output was impossible within the timespan of this project. The 3-year timeframe meant that, of all fry translocated, to date only a proportion of fish translocated in 2019 would have migrated to sea in spring of 2021 as age 2+ year smolts. Given the low numbers of fry translocated in 2019 as part of this project, the ability to determine either the survival rate of fish across this period, or any significant benefit in terms of smolt numbers, is low. However, it should be noted that, of the two translocation batches in 2021, those fish released into the Glendavoc stream which survive until the smolt stage will be recaptured at a downstream smolt trap, thus allowing survival to be estimated from a larger sample size (≈ 1500 fry initially released).

Where typical treatment versus control comparison is required, then the issues of treatment bias from Chapter 6 could be mitigated in future translocations by use of alternating treatment assignations across multiple years. As an additional measure, use of more extensive habitat assessment techniques, such as HABSCORE, River2D or PHABSIM, and completion of redd counts, could be used in the experimental planning phase to test for both habitat suitability and spawning effort (e.g. Gard, 2009), including any potential treatment bias, prior to conducting pre-translocation electrofishing surveys. For 2021, no adjustment to the experimental design could be made after conducting these surveys, due to the limited timeframe within which to conduct translocations. Prior knowledge of spawning effort might therefore have provided an early indication of possible differences in pre-translocation fry densities relative to previous years.

One limitation of these experiments, which was shared with the inter-catchment translocations of European eel, is that both were performed in river systems with a lack of other species. Within the River Erriff catchment, the results of this research indicate that Atlantic salmon represent the dominant species, both by abundance and by biomass, with this likely to have affected the outcome of translocations. As previously noted, increasing species richness is generally considered to reduce the likelihood of colonisation success (Elton, 1958). Thus, there is a pressing need to better understand the impact of other species, such as brown trout, which commonly occur in sympatry with Atlantic salmon, but were only observed at low densities here. Brown trout are of particular importance given the piscivory and aggressive territorial behaviour exhibited by this species (Titus, 1990; Jonsson *et al.*, 1999), with inter-specific competition also considered by some authors to be a driving factor behind the differential habitat use of salmon fry and brown trout (Kennedy and Strange, 1986).

7.3.3 Application of translocation as a management strategy

The field experiments conducted as part of this project provided several key findings that are of high relevance to the future application of the intra-catchment translocation method. The observed dispersal distances from Chapter 6 indicated that the release of fry at approximately 150 to 200 m intervals would allow successful colonisation of large stream areas, although dispersal distances are likely to differ between streams.

The issue of premature pre-translocation surveys in Chapter 6 highlights the narrow window following fry emergence within which translocations must be performed, and the difficulty in matching translocation timing to that of fry emergence, given the logistical difficulties of having survey teams available for application at short notice in relatively remote areas. Most pre-translocation surveys in 2021 were conducted ≈ 1 week earlier than in 2020, but this resulted in sampling prior to the completion of emergence, highlighting the difficulty in accurately predicting this period. The timing of translocations is critical given that the period immediately post-emergence is likely when density-dependent mortality is at its peak, as this is when fry densities are at their highest and dispersal ability at its lowest (Armstrong and Nislow, 2006; Einum, Sundt-Hansen and Nislow, 2006; Einum, Nislow, Reynolds, *et al.*, 2008). The highly significant relationship between Julian day of pre-translocation sampling and fry densities from Chapter 5 provides further evidence of this. Thus, sites must be fished as soon as possible following fry emergence, to ensure that large numbers of fry can be collected without affecting autumn densities (e.g. by reducing fry densities below the stream carrying capacity).

As noted above, use of habitat modelling techniques such as HABSCORE, River2D and PHABSIM (Bourgeois *et al.*, 1996; Milner, Wyatt and Broad, 1998; Gard, 2009), could be used to ensure treatment comparability in translocation experiments. Such methods could also be used in the initial stages of translocation planning to identify areas of potential suitability, and thus avoid the need to electrofish large areas of riffle channel which may be unsuitable for translocations. This could be done, for example, by assessing substrate class variables separately from other recorded habitat variables, so as to identify areas of suitable fry habitat with low spawning potential, as shown by relative abundance of suitable spawning substrate (2-64 mm diameter; Louhi *et al.*, 2008). However, this again represents substantial sampling effort which may be unfeasible, dependent on the scale of such projects.

One potential issue with intra-catchment translocations, which was not considered to be a major factor in this study, but may be important in larger catchments, is the potential for genetically distinct Atlantic salmon populations to exist within single river catchments. For example, intra-catchment genetic variation, and the existence of multiple salmon populations within a single catchment, has been demonstrated for the River Moy, Ireland (Dillane *et al.*, 2008). In the aforementioned study, lakes were found to be the single most important determinant of the observed population structure (Dillane *et al.*, 2008). Additionally, previous research has also found distinct breeding populations to exist within separate tributaries of the same catchment (Vähä *et al.*, 2007), and based on spatial isolation (Primmer *et al.*, 2006). Thus, the movement of salmon fry between major tributaries, or between areas spatially isolated by distance or by major catchment features. such as lakes, would be ill-advised. As a precautionary measure, translocations here were generally carried out between areas separated by the smallest possible instream distance. Additionally, genetic material from adipose fin clips was retained and preserved to allow for future analyses to identify any genetic differentiation between fry captured from different areas of the Erriff catchment.

7.3.4 A holistic approach to the conservation of Atlantic salmon

While inter-catchment translocations show promise as a potential management tool, it is important that this method is viewed holistically and, if shown to be effective in practice, used in combination with other techniques where appropriate. This is also in keeping with previous findings on habitat restoration techniques, where addressing the ultimate cause of habitat degradation is key to their long-term success (Hendry *et al.*, 2003). Thus, in line with Gibson (2017), the primary aim of conservation programmes for this species should be restoring connectivity and habitat quality of river catchments and addressing causes of degradation, to ensure Atlantic salmon populations remain sustainable without requiring continual intervention.

Recognising that the above represents an idealised scenario, and that human intervention is inevitable and sometimes necessary, translocation avoids the issues inherent in the alternative method of hatchery stocking (e.g. Araki, Cooper and Blouin, 2007, 2009; Araki *et al.*, 2008), and thus has greater potential to generate long-term positive outcomes in terms of population supplementation. The effects of translocation are likely to be greatest where suitable spawning material is spatially patchy, and thus natural dispersal is insufficient to allow colonisation of all available stream habitat. Additionally, translocation may act as a powerful tool for reintroducing or supplementing depleted populations within catchment areas where anthropogenic activities have reduced salmonid numbers (e.g. through acute pollution events), or where the causes of historic habitat degradation have been addressed. Thus, introduction of translocated fish could be seen as a means by which to ‘jump-start’ population recovery within stream reaches or entire tributaries, similarly to how hatchery stocking has historically been used (Milner *et al.*, 2008).

The comparison between use of translocation versus hatchery rearing programmes is also of socioeconomic relevance. It has been considered that salmonid hatcheries may provide social benefits to communities beyond the possible conservation contribution to local salmon (Harrison *et al.*, 2018). Hatcheries run on a voluntary basis can be considered as a visible means of environmental stewardship, and are perceived by many operators as an important means for mitigating human obstacles to wild salmon conservation (Harrison *et al.*, 2018). When considered in this context, the controversy surrounding the closure of many hatcheries is perhaps more understandable (Harrison *et al.*, 2018; Harrison, Rybråten and Aas, 2018; Harrison, Hauer, *et al.*, 2019; Harrison, Kochalski, *et al.*, 2019). As noted in Chapter 1, there is a salient need to develop conservation methods that can more effectively sustain declining salmon populations, while allaying concerns of stakeholders over the perceived reduction in recent conservation effort. Intra-catchment translocations meet the above criteria by providing a way by which angling clubs and other groups may partake in environmental stewardship without incurring the detrimental impacts associated with hatcheries. Additionally, while the results from the experiments presented here are mixed, there is evidence to suggest that, if implemented correctly, intra-catchment translocations can be used to provide an overall conservation benefit.

While there remains the potential for intra-catchment translocations to result in negative outcomes, for example through lowering of fry source sites below river carrying capacity, or through poor fry handling resulting in significant mortality, the magnitude of these is likely to be significantly lower than the negative effects associated with hatcheries (e.g. Araki, Cooper and Blouin, 2007, 2009; Araki *et al.*, 2008). This also highlights the need for further research into this method to develop best-practice guidelines to ensure translocations can be carried out with the minimum risk of incurring negative effects. The results here indicate that, as a minimum, this should include density ranges for both fry source and recipient sites, across which translocations are likely to generate positive outcomes, as well as some means by which recipient site habitat suitability can be ensured.

Given the limitations outlined above, the results here are inconclusive as to the suitable density range at fry recipient sites, but with the findings of Chapter 6 indicating that removal of large numbers of fry from riffles with densities of over 70 fish 100 m^{-2} can be carried out with no negative effects in terms of autumn densities. Additionally, given the issue of high density-dependent mortality at fry source sites, the timing of any translocations is likely to be key to their success. Good fish husbandry practices, even over the short captivity period, are also likely to be important, given the potential negative effects of stress (Wedemeyer, 1970; Pickering and Pottinger, 1989; Petitjean *et al.*, 2019), with the results here showing that minimal mortality can be incurred by maintaining dissolved oxygen levels through aeration and water temperatures simply by the use of ice blocks where necessary, even with the additional stress of adipose fin clipping and anaesthesia.

7.4 Conclusions

It is clear that the monitoring practices for salmonids evaluated as part of this research are likely to lead to substantial inaccuracy in abundance estimates for these species, with this likely to lead to mismanagement of declining salmonid populations. The recommendations outlined here could be used to increase both the accuracy and utility of time-delineated electrofishing survey data, thus aiding in the allocation of conservation effort to those populations most at-risk. Additionally, the findings of Chapters 4 to 6 highlight that fish translocations, both intra- and inter-catchment, are feasible tools for enhancing migratory fish numbers within conservation programmes, albeit with some limitations. Given the similarities in the life history strategies and population dynamics between these model species and other salmonids and anguillids globally, there is little to suggest that translocations will not be of similar efficacy. Consequently, these methods should be further tested as a matter of urgency to determine their broader suitability and net conservation benefits for a range of species.

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Appendix 1

Table A1: Model selection process for the model shown by equation 2 of Table 2.1.

Selection	Formula	AIC	BIC	Covariate(s)	Estimate	Standard error	Z value	P value
Forward	*Time-delineated area coverage (m^{2}) ~ Total site area*	2167.0	2177.5	Intercept	39.25	2.40	16.33	**<2 x 10^{-16}**
				Total site area	0.13	0.01	11.29	**<2 x 10^{-16}**
Forward	*Time-delineated area coverage (m^{2}) ~ Total site area + Time-delineated parr density*	2137.8	2151.8	Intercept	49.01	2.83	17.32	**<2 x 10^{-16}**
				Total site area	0.12	0.01	10.38	**<2 x 10^{-16}**
				Time-delineated parr density	-0.51	0.09	-5.73	**2.92 x 10^{-8}**
Forward	*Time-delineated area coverage (m^{2}) ~ Total site area + Time-delineated parr density + Time-delineated fry density*	2061.7	2079.2	Intercept	60.66	2.71	22.38	**<2 x 10^{-16}**
				Total site area	0.12	0.01	12.41	**<2 x 10^{-16}**
				Time-delineated parr density	-0.50	0.08	-6.58	**2.84 x 10^{-10}**
				Time-delineated fry density	-0.36	0.04	-9.51	**<2 x 10^{-16}**
Forward	*Time-delineated area coverage (m^{2}) ~ Total site area + Time-delineated parr density + Time-delineated fry density + Macrophyte proportion*	2043.0	2064.0	Intercept	62.97	2.65	23.74	**<2 x 10^{-16}**
				Total site area	0.08	0.01	7.06	**1.84 x 10^{-11}**
				Time-delineated parr density	-0.53	0.07	-7.17	**9.52 x 10^{-12}**
				Time-delineated fry density	-0.37	0.04	-10.16	**<2 x 10^{-16}**
				Macrophyte proportion	40.44	8.80	4.60	**6.99 x 10^{-6}**
Forward	*Time-delineated area coverage (m^{2}) ~ Total site area + Time-delineated parr density + Time-delineated fry density + Macrophyte proportion + Sampling year*	2030.6	2055.1	Intercept	58.95	2.79	21.15	**<2 x 10^{-16}**
				Total site area	0.09	0.01	7.43	**1.91 x 10^{-12}**
				Time-delineated parr density	-0.47	0.07	-6.50	**4.55 x 10^{-10}**
				Time-delineated fry density	-0.39	0.04	-10.86	**<2 x 10^{-16}**
				Macrophyte proportion	40.94	8.56	4.78	**3.06 x 10^{-6}**
				Sampling year	7.53	1.98	3.81	**0.0002**
Forward	*Time-delineated area coverage (m^{2}) ~ Total site area + Time-delineated parr density + Time-delineated fry density + Macrophyte proportion + Sampling year + Mean depth*	2025.9	2053.9	Intercept	49.75	4.52	11.01	**<2 x 10^{-16}**
				Total site area	0.09	0.01	7.68	**4.12 x 10^{-13}**
				Time-delineated parr density	-0.44	0.07	-6.07	**5.13 x 10^{-9}**
				Time-delineated fry density	-0.39	0.04	-11.10	**<2 x 10^{-16}**
				Macrophyte proportion	35.39	8.74	4.05	**6.93 x 10^{-5}**
				Sampling year	7.74	1.96	3.96	**0.0001**
				Mean depth	54.80	21.33	2.57	**0.01**
Forward	*Time-delineated area coverage (m^{2}) ~ Total site area + Time-delineated parr density + Time-delineated fry density + Macrophyte proportion + Sampling year + Mean depth + Time-delineated trout fry density*	2023.0	2054.5	Intercept	52.31	4.63	11.29	**< 2 x 10^{-16}**
				Total site area	0.08	0.01	7.22	**6.89 x 10^{-12}**
				Time-delineated parr density	-0.45	0.07	-6.13	**3.57 x 10^{-9}**
				Time-delineated fry density	-0.39	0.04	-10.94	**< 2 x 10^{-16}**
				Macrophyte proportion	34.99	8.67	4.04	**7.34 x 10^{-5}**
				Sampling year	6.77	1.99	3.40	**0.001**
				Mean depth	50.63	21.25	2.38	**0.02**
				Time-delineated trout fry density	-0.26	0.12	-2.20	**0.03**
Backward	*Time-delineated area coverage (m^{2}) ~ Total site area + Time-delineated parr density + Time-delineated fry density + Macrophyte proportion + Sampling year + Mean depth + Time-delineated trout fry density + Gravel proportion + Cobble proportion + Boulder proportion + Sampling period + Flow condition*	2023.2	2072.2	Intercept	7.97	56.77	0.14	0.89
				Total site area	0.09	0.01	7.39	**2.67 x 10^{-12}**
				Time-delineated parr density	-0.41	0.08	-4.78	**3.15 x 10^{-6}**
				Time-delineated fry density	-0.39	0.04	-10.49	**< 2 x 10^{-16}**
				Macrophyte proportion	34.67	8.97	3.87	**0.0001**
				Sampling year	5.56	2.10	2.64	**0.01**
				Mean depth	63.90	23.11	2.77	**0.01**
				Time-delineated trout fry density	-0.28	0.12	-2.34	**0.02**
				Gravel proportion	51.50	56.57	0.91	0.36
				Cobble proportion	38.95	55.26	0.71	0.48
				Boulder proportion	56.70	57.97	0.98	0.33
				Sampling period	-4.30	2.17	-1.98	**0.05**
				Flow condition	-5.21	2.36	-2.21	**0.03**
Backward	*Time-delineated area coverage (m^{2}) ~ Total site area + Time-delineated parr density + Time-delineated fry density + Macrophyte proportion + Sampling year + Mean depth + Time-delineated trout fry density + Gravel proportion + Boulder proportion + Sampling period + Flow condition*	2021.7	2067.2	Intercept	47.64	7.43	6.41	**7.80 x 10^{-10}**
				Total site area	0.09	0.01	7.41	**2.31 x 10^{-12}**
				Time-delineated parr density	-0.40	0.08	-4.77	**3.26 x 10^{-6}**
				Time-delineated fry density	-0.39	0.04	-10.50	**< 2 x 10^{-16}**
				Macrophyte proportion	34.02	8.91	3.82	**0.0002**
				Sampling year	5.54	2.10	2.64	**0.01**
				Mean depth	59.01	22.01	2.68	**0.01**
				Time-delineated trout fry density	-0.28	0.12	-2.37	**0.02**
				Gravel proportion	11.96	7.34	1.63	0.10
				Boulder proportion	18.72	21.35	0.88	0.38
				Sampling period	-4.31	2.17	-1.98	**0.05**
				Flow condition	-5.23	2.35	-2.22	**0.03**
Backward	*Time-delineated area coverage (m^{2}) ~ Total site area + Time-delineated parr density + Time-delineated fry density + Macrophyte proportion + Sampling year + Mean depth + Time-delineated trout fry density + Gravel proportion + Sampling period + Flow condition*	2020.5	2062.5	Intercept	50.95	6.39	7.98	**6.72 x 10^{-14}**
				Total site area	0.09	0.01	7.53	**1.08 x 10^{-12}**
				Time-delineated parr density	-0.39	0.08	-4.69	**4.61 x 10^{-6}**
				Time-delineated fry density	-0.39	0.04	-10.75	**< 2 x 10^{-16}**
				Macrophyte proportion	35.98	8.62	4.17	4.22 x 10^{-5}
				Sampling year	5.74	2.09	2.75	**0.01**
				Mean depth	55.08	21.54	2.56	**0.01**
				Time-delineated trout fry density	-0.29	0.12	-2.41	**0.02**
				Gravel proportion	8.87	6.44	1.38	0.17
				Sampling period	-4.25	2.17	-1.96	0.05
				Flow condition	-5.00	2.34	-2.14	**0.03**
Backward	*Time-delineated area coverage (m^{2}) ~ Total site area + Time-delineated parr density + Time-delineated fry density + Macrophyte proportion + Sampling year + Mean depth + Time-delineated trout fry density + Sampling period + Flow condition*	2020.5	2059.0	Intercept	56.53	4.95	11.42	**< 2 x 10^{-16}**
				Total site area	0.09	0.01	7.40	**2.45 x 10^{-12}**
				Time-delineated parr density	-0.44	0.08	-5.78	**2.36 x 10^{-8}**
				Time-delineated fry density	-0.38	0.04	-10.64	**< 2 x 10^{-16}**
				Macrophyte proportion	35.09	8.61	4.07	6.31 x 10^{-5}
				Sampling year	5.34	2.07	2.58	**0.01**
				Mean depth	59.38	21.36	2.78	**0.01**
				Time-delineated trout fry density	-0.26	0.12	-2.21	**0.03**
				Sampling period	-4.05	2.17	-1.87	0.06
				Flow condition	-5.25	2.33	-2.25	**0.03**

Table A2: Model selection process for the model shown by equation 4 of Table 2.1.

Selection	Formula	AIC	BIC	Covariate(s)	Estimate	Standard error	Z value	P value
Forward	|*(Time-delineated fry density/Total fry density -1)*| *~ Time-delineated area coverage (%)*	149.7	160.1	Intercept	0.43	0.06	7.21	**7.7 x 10^{-12}**
				Time-delineated area coverage (%)	-0.003	0.001	-2.001	**0.05**
Forward	|*(Time-delineated fry density/Total fry density -1)*| *~ Time-delineated area coverage (%) + Sampling year*	147.2	161.1	Intercept	0.41	0.06	6.97	**3.28 x 10^{-11}**
				Time-delineated area coverage (%)	-0.003	0.001	-2.47	**0.01**
				Sampling year	0.09	0.04	2.13	**0.03**
Backward	|*(Time-delineated fry density/Total fry density -1)*| *~ Time-delineated area coverage (%) + Sampling year + Time-delineated fry density + Total site area + Sampling period + Flow condition*	152.8	180.5	Intercept	0.60	0.15	3.96	**0.0001**
				Time-delineated area coverage (%)	-0.01	0.002	-2.72	**0.01**
				Sampling year	0.12	0.05	2.39	**0.02**
				Time-delineated fry density	-0.0008	0.0009	-0.87	0.39
				Total site area	-0.0003	0.0003	-1.28	0.20
				Sampling period	-0.03	0.05	-0.62	0.54
				Flow condition	0.01	0.05	0.27	0.78
Backward	|*(Time-delineated fry density/Total fry density -1)*| *~ Time-delineated area coverage (%) + Sampling year + Time-delineated fry density + Total site area + Sampling period*	150.8	175.1	Intercept	0.61	0.15	4.17	**4.37 x 10^{-5}**
				Time-delineated area coverage (%)	-0.01	0.002	-2.71	**0.01**
				Sampling year	0.11	0.05	2.42	**0.02**
				Time-delineated fry density	-0.0008	0.0009	-0.87	0.38
				Total site area	-0.0003	0.0003	-1.26	0.21
				Sampling period	-0.04	0.05	-0.77	0.44
Backward	|*(Time-delineated fry density/Total fry density -1)*| *~ Time-delineated area coverage (%) + Sampling year + Time-delineated fry density + Total site area*	149.5	170.3	Intercept	0.57	0.14	4.16	**4.56 x 10^{-5}**
				Time-delineated area coverage (%)	-0.005	0.002	-2.60	**0.01**
				Sampling year	0.11	0.05	2.40	**0.02**
				Time-delineated fry density	-0.0009	0.0009	-0.94	0.35
				Total site area	-0.0003	0.0003	-1.17	0.24
Backward	|*(Time-delineated fry density/Total fry density -1)*| *~ Time-delineated area coverage (%) + Sampling year + Total site area*	148.4	165.7	Intercept	0.49	0.11	4.67	**5.17 x 10^{-6}**
				Time-delineated area coverage (%)	-0.004	0.002	-2.48	**0.01**
				Sampling year	0.10	0.04	2.23	**0.03**
				Total site area	-0.0002	0.0002	-0.89	0.37
Backward	|*(Time-delineated fry density/Total fry density -1)*| *~ Time-delineated area coverage (%) + Sampling year*	147.2	161.1	Intercept	0.41	0.06	6.97	**3.28 x 10^{-11}**
				Time-delineated area coverage (%)	-0.003	0.001	-2.47	**0.01**
				Sampling year	0.09	0.04	2.13	**0.03**

Appendix 2

Table A1: Model selection process for model shown in table 3.1.

Selection	Formula	AIC	BIC	Model component	Covariate(s)	Estimate	Standard error	Z value	P value
Forward	*Salmon fry number ~ Julian day + (1|River catchment) + (1|Year) + (1|Operator)*	46789.9	46859.4	Conditional model	Intercept	6.10	0.17	35.20	**$< 2 \times 10^{-16}$**
					Julian day	-0.004	0.0007	-6.15	**7.65×10^{-10}**
				Zero-inflation model	Intercept	-3.41	0.69	-4.97	**6.87×10^{-7}**
					Julian day	0.005	0.003	1.74	0.08
Forward	*Salmon fry number ~ Julian day + Stream Order + (1|River catchment) + (1|Year) + (1|Operator)*	46469.1	46551.3	Conditional model	Intercept	5.42	0.18	30.04	**$< 2 \times 10^{-16}$**
					Julian day	-0.005	0.0007	-6.56	**5.57×10^{-11}**
					Stream order	0.19	0.01	13.96	**$< 2 \times 10^{-16}$**
				Zero-inflation model	Intercept	-0.87	0.75	-1.16	0.25
					Julian day	0.004	0.003	1.42	0.16
					Stream order	-0.69	0.06	-10.92	**$< 2 \times 10^{-16}$**
Forward	*Salmon fry number ~ Julian day + Stream Order + Riffle grade + (1|River catchment) + (1|Year) + (1|Operator)*	46117.3	46212.0	Conditional model	Intercept	5.99	0.18	33.01	**$< 2 \times 10^{-16}$**
					Julian day	-0.005	0.0007	-7.05	**1.82×10^{-12}**
					Stream order	0.17	0.01	13.08	**$< 2 \times 10^{-16}$**
					Riffle grade	-0.16	0.009	-16.76	**$< 2 \times 10^{-16}$**
				Zero-inflation model	Intercept	-2.23	0.79	-2.83	**0.005**
					Julian day	0.01	0.003	1.70	0.09
					Stream order	-0.67	0.06	-10.61	**$< 2 \times 10^{-16}$**
					Riffle grade	0.32	0.04	8.05	**8.61×10^{-16}**
Forward	*Salmon fry number ~ Julian day + Stream Order + Riffle grade + Salmon parr number + (1|River catchment) + (1|Year) + (1|Operator)*	45989.0	46096.4	Conditional model	Intercept	5.99	0.18	33.13	**$< 2 \times 10^{-16}$**
					Julian day	-0.005	0.0007	-7.15	**8.50×10^{-13}**
					Stream order	0.16	0.01	12.40	**$< 2 \times 10^{-16}$**
					Riffle grade	-0.16	0.01	-16.81	**$< 2 \times 10^{-16}$**
					Salmon parr n	0.01	0.003	4.31	**1.62×10^{-5}**
				Zero-inflation model	Intercept	-1.99	0.80	-2.50	**0.01**
					Julian day	0.01	0.003	1.79	0.07
					Stream order	-0.59	0.06	-9.10	**$< 2 \times 10^{-16}$**
					Riffle grade	0.31	0.04	7.56	**4.12×10^{-14}**
					Salmon parr n	-0.19	0.02	-9.12	**$< 2 \times 10^{-16}$**
Forward	*Salmon fry number ~ Julian day + Stream Order + Riffle grade + Salmon parr number + Trout parr number + (1|River catchment) + (1|Year) + (1|Operator)*	45890.2	46010.3	Conditional model	Intercept	6.12	0.18	34.20	**$< 2 \times 10^{-16}$**
					Julian day	-0.005	0.0007	-7.10	**1.23×10^{-12}**
					Stream order	0.14	0.01	10.62	**$< 2 \times 10^{-16}$**
					Riffle grade	-0.16	0.009	-16.89	**$< 2 \times 10^{-16}$**
					Salmon parr n	0.01	0.003	5.36	**8.41×10^{-8}**
					Trout parr n	-0.04	0.005	-8.08	**6.47×10^{-16}**
				Zero-inflation model	Intercept	-2.12	0.80	-2.67	**0.01**
					Julian day	0.005	0.003	1.55	0.12
					Stream order	-0.54	0.07	-8.32	**$< 2 \times 10^{-16}$**
					Riffle grade	0.30	0.04	7.34	**2.07×10^{-13}**
					Salmon parr n	-0.21	0.02	-9.44	**$< 2 \times 10^{-16}$**
					Trout parr n	0.09	0.02	5.27	**1.39×10^{-7}**
Forward	*Salmon fry number ~ Julian day + Stream Order + Riffle grade + Salmon parr number + Trout parr number + Trout fry number + (1|River catchment) + (1|Year) + (1|Operator)*	45849.3	45982.0	Conditional model	Intercept	6.24	0.18	34.52	**$< 2 \times 10^{-16}$**
					Julian day	-0.005	0.0007	-7.34	**2.15×10^{-13}**
					Stream order	0.13	0.01	9.37	**$< 2 \times 10^{-16}$**
					Riffle grade	-0.16	0.01	-17.08	**$< 2 \times 10^{-16}$**
					Salmon parr n	0.01	0.003	4.74	**2.10×10^{-6}**
					Trout parr n	-0.04	0.01	-7.77	**7.95×10^{-15}**
					Trout fry n	-0.01	0.002	-3.92	**9.04×10^{-5}**
				Zero-inflation model	Intercept	-3.11	0.83	-3.74	**0.0002**
					Julian day	0.01	0.003	2.08	**0.04**

					Stream order	-0.47	0.07	-7.02	**2.19 x 10^{-12}**
					Riffle grade	0.32	0.04	7.66	**1.81 x 10^{-14}**
					Salmon parr n	-0.19	0.02	-8.99	**< 2 x 10^{-16}**
					Trout parr n	0.08	0.02	4.92	**8.68 x 10^{-7}**
					Trout fry n	0.03	0.01	5.34	**9.20 x 10^{-8}**
Forward	*Salmon fry number ~ Julian day + Stream Order + Riffle grade + Salmon parr number + Trout parr number + Trout fry number + Gravel percentage + (1|River catchment) + (1|Year) + (1|Operator)*	45833.8	45979.1	Conditional model	Intercept	6.04	0.19	32.44	**< 2 x 10^{-16}**
					Julian day	-0.005	0.0007	-7.19	**6.48 x 10^{-13}**
					Stream order	0.12	0.01	9.21	**< 2 x 10^{-16}**
					Riffle grade	-0.14	0.01	-13.75	**< 2 x 10^{-16}**
					Salmon parr n	0.01	0.003	5.35	**9.04 x 10^{-8}**
					Trout parr n	-0.04	0.005	-7.78	**6.99 x 10^{-15}**
					Trout fry n	-0.01	0.002	-3.99	**6.71 x 10^{-5}**
					Gravel percentage	0.003	0.0008	4.31	**1.60 x 10^{-5}**
				Zero-inflation model	Intercept	-2.91	0.85	-3.41	**0.0006**
					Julian day	0.01	0.003	2.07	**0.04**
					Stream order	-0.47	0.07	-7.02	**2.21 x 10^{-12}**
					Riffle grade	0.30	0.04	6.66	**2.84 x 10^{-11}**
					Salmon parr n	-0.20	0.02	-9.02	**< 2 x 10^{-16}**
					Trout parr n	0.08	0.02	4.88	**1.05 x 10^{-6}**
					Trout fry n	0.03	0.01	5.40	**6.83 x 10^{-8}**
					Gravel percentage	-0.004	0.004	-1.09	0.27
Forward	*Salmon fry number ~ Julian day + Stream Order + Riffle grade + Salmon parr number + Trout parr number + Trout fry number + Gravel percentage + Cobble percentage + (1|River catchment) + (1|Year) + (1|Operator)*	45815.1	45973.1	Conditional model	Intercept	5.75	0.20	28.67	**< 2 x 10^{-16}**
					Julian day	-0.005	0.0007	-7.11	**1.20 x 10^{-12}**
					Stream order	0.12	0.01	9.03	**< 2 x 10^{-16}**
					Riffle grade	-0.13	0.01	-12.22	**< 2 x 10^{-16}**
					Salmon parr n	0.01	0.003	5.40	**6.69 x 10^{-8}**
					Trout parr n	-0.04	0.005	-7.67	**1.68 x 10^{-14}**
					Trout fry n	-0.006	0.002	-3.92	**8.23 x 10^{-5}**
					Gravel percentage	0.01	0.001	5.78	**7.37 x 10^{-9}**
					Cobble percentage	0.004	0.001	3.93	**8.69 x 10^{-5}**
				Zero-inflation model	Intercept	-2.04	0.91	-2.24	**0.03**
					Julian day	0.006	0.003	2.04	**0.04**
					Stream order	-0.47	0.07	-7.08	**1.48 x 10^{-12}**
					Riffle grade	0.27	0.05	5.76	**8.50 x 10^{-9}**
					Salmon parr n	-0.19	0.02	-8.95	**< 2 x 10^{-16}**
					Trout parr n	0.08	0.02	4.76	**1.90 x 10^{-6}**
					Trout fry n	0.03	0.01	5.25	**1.56 x 10^{-7}**
					Gravel percentage	-0.01	0.004	-2.37	**0.02**
					Cobble percentage	-0.01	0.005	-2.66	**0.008**
Backward	*Salmon fry number ~ Julian day + Stream Order + Riffle grade + Salmon parr number + Trout parr number + Trout fry number + Gravel percentage + Cobble percentage + Mean depth + Flow condition + (1|River catchment) + (1|Year) + (1|Operator)*	45816.4	45999.7	Conditional model	Intercept	5.73	0.20	28.22	**< 2 x 10^{-16}**
					Julian day	-0.005	0.0007	-7.19	**6.37 x 10^{-13}**
					Stream order	0.12	0.01	8.89	**< 2 x 10^{-16}**
					Riffle grade	-0.13	0.01	-12.25	**< 2 x 10^{-16}**
					Salmon parr n	0.01	0.003	5.35	**8.66 x 10^{-8}**
					Trout parr n	-0.04	0.005	-7.67	**1.68 x 10^{-14}**
					Trout fry n	-0.01	0.002	-3.88	**0.0001**
					Gravel percentage	0.01	0.001	5.83	**5.68 x 10^{-9}**
					Cobble percentage	0.004	0.001	3.95	**7.85 x 10^{-5}**
					Mean depth	-0.0003	0.001	-0.21	0.83
					Flow Condition	0.02	0.01	1.12	0.26
				Zero-inflation model	Intercept	-2.32	0.92	-2.51	**0.01**
					Julian day	0.01	0.003	1.87	0.06
					Stream order	-0.48	0.07	-7.12	**1.09 x 10^{-12}**

					Riffle grade	0.26	0.05	5.67	**1.40 x 10^{-8}**
					Salmon parr n	-0.19	0.02	-8.96	**< 2 x 10^{-16}**
					Trout parr n	0.08	0.02	4.77	**1.89 x 10^{-6}**
					Trout fry n	0.03	0.01	5.32	**1.06 x 10^{-7}**
					Gravel percentage	-0.01	0.004	-2.42	**0.02**
					Cobble percentage	-0.01	0.01	-2.76	**0.01**
					Mean depth	0.01	0.01	2.26	**0.02**
					Flow Condition	0.04	0.06	0.64	0.52
Backward	*Salmon fry number ~ Julian day + Stream Order + Riffle grade + Salmon parr number + Trout parr number + Trout fry number + Gravel percentage + Cobble percentage + Mean depth + (1|River catchment) + (1|Year) + (1|Operator)*	45814.1	45984.7	Conditional model	Intercept	5.75	0.20	28.41	**< 2 x 10^{-16}**
					Julian day	-0.005	0.0007	-7.10	**1.26 x 10^{-12}**
					Stream order	0.12	0.01	9.00	**< 2 x 10^{-16}**
					Riffle grade	-0.13	0.01	-12.22	**< 2 x 10^{-16}**
					Salmon parr n	0.01	0.003	5.40	**6.60 x 10^{-8}**
					Trout parr n	-0.04	0.005	-7.67	**1.70 x 10^{-14}**
					Trout fry n	-0.01	0.002	-3.94	**8.11 x 10^{-5}**
					Gravel percentage	0.01	0.001	5.79	**7.23 x 10^{-9}**
					Cobble percentage	0.004	0.001	3.93	**8.47 x 10^{-5}**
					Mean depth	-0.0003	0.001	-0.22	0.83
				Zero-inflation model	Intercept	-2.28	0.92	-2.48	**0.01**
					Julian day	0.01	0.003	1.98	**0.05**
					Stream order	-0.48	0.07	-7.09	**1.34 x 10^{-12}**
					Riffle grade	0.26	0.05	5.72	**1.08 x 10^{-8}**
					Salmon parr n	-0.19	0.02	-8.95	**< 2 x 10^{-16}**
					Trout parr n	0.08	0.02	4.78	**1.74 x 10^{-6}**
					Trout fry n	0.03	0.01	5.30	**1.16 x 10^{-7}**
					Gravel percentage	-0.01	0.004	-2.43	**0.02**
					Cobble percentage	-0.01	0.005	-2.77	**0.01**
					Mean depth	0.01	0.01	2.25	**0.02**
Backward	*Salmon fry number ~ Julian day + Stream Order + Riffle grade + Salmon parr number + Trout parr number + Trout fry number + Gravel percentage + Cobble percentage + (1|River catchment) + (1|Year) + (1|Operator)*	45815.1	45973.1	Conditional model	Intercept	5.75	0.20	28.67	**< 2 x 10^{-16}**
					Julian day	-0.005	0.0007	-7.11	**1.20 x 10^{-12}**
					Stream order	0.12	0.01	9.03	**< 2 x 10^{-16}**
					Riffle grade	-0.13	0.01	-12.22	**< 2 x 10^{-16}**
					Salmon parr n	0.01	0.003	5.40	**6.69 x 10^{-8}**
					Trout parr n	-0.04	0.005	-7.67	**1.68 x 10^{-14}**
					Trout fry n	-0.006	0.002	-3.92	**8.23 x 10^{-5}**
					Gravel percentage	0.01	0.001	5.78	**7.37 x 10^{-9}**
					Cobble percentage	0.004	0.001	3.93	**8.69 x 10^{-5}**
				Zero-inflation model	Intercept	-2.04	0.91	-2.24	**0.03**
					Julian day	0.006	0.003	2.04	**0.04**
					Stream order	-0.47	0.07	-7.08	**1.48 x 10^{-12}**
					Riffle grade	0.27	0.05	5.76	**8.50 x 10^{-9}**
					Salmon parr n	-0.19	0.02	-8.95	**< 2 x 10^{-16}**
					Trout parr n	0.08	0.02	4.76	**1.90 x 10^{-6}**
					Trout fry n	0.03	0.01	5.25	**1.56 x 10^{-7}**
					Gravel percentage	-0.01	0.004	-2.37	**0.02**
					Cobble percentage	-0.01	0.005	-2.66	**0.008**

Appendix 3

Table A1: Multiple pass electrofishing data used to validate the area-delineated single pass electrofishing method for European eels

Treatment	Stream	Dispersal distance	Pass 1 captured	Pass 1 missed	Pass 2 captured	Pass 2 missed	Pass 3 captured	Pass 3 missed	Pass 1 total captured/missed	Multiple pass total captured/pass 3 missed
Trout-free	TL4	0	23	4	3	1	0	1	27	27
Trout-free	TL7	40	4	0	0	0	0	0	4	4
Trout-free	TL2	80	1	1	1	0	0	0	2	2
Trout-populated	T1	120	8	0	0	0	0	0	8	8
Trout-populated	T4	80	5	1	1	0	0	0	6	6
Total			41	6	5	1	0	1	47	47

Table A2: Summary of stream reach-level means of physical variables calculated from values recorded at either stream reach- or site-level according to treatment, including outputs from principal component analysis. Principal components with weighting absolute values equal to or greater than 0.3 are shown in bold

	Principal component		Level	Variable mean (± SD)		Treatment comparison
	1	2		Trout-populated	Trout-free	
Total variance explained (%)	**40.3**	**27.0**				
Mean depth (cm)	-0.08	**-0.52**	Site	23.85(±3.28)	23.46(±2.48)	Welch's two sample t-test; t = 0.24, p = 0.81, df = 10.8
Mean width (m)	**-0.39**	-0.17	Site	1.68(±0.24)	1.64(±0.46)	Welch's two sample t-test; t = 0.20, p = 0.84, df = 7.2
Percentage riffle	**0.38**	0.04	Site	52.01(±9.38)	46.53(±3.23)	Welch's two sample t-test; t = 1.45, p = 0.19, df = 7.6
Cover Index	0.23	**0.43**	Site	4.72(±0.94)	4.21(±0.48)	Welch's two sample t-test; t = 1.26, p = 0.24, df = 9.1
Stream length (km)	**-0.41**	**0.34**	Stream reach	2.72(±0.64)	2.81(±0.97)	Welch's two sample t-test; t = -0.20, p = 0.84, df = 8.4
Stream Gradient (%)	**0.32**	**-0.46**	Stream reach	7.78(±3.36)	6.00(±3.44)	Welch's two sample t-test; t = 0.94, p = 0.36, df = 10.6
Highest Altitude (m)	**-0.37**	**-0.39**	Stream	421(±60.39)	453(±67.1)	Welch's two sample t-test; t = -0.91, p = 0.37, df = 10.2
Catchment area (km)	**-0.47**	0.17	Stream reach	2.38(±0.52)	2.33(±0.94)	Welch's two sample t-test; t = 0.11, p = 0.91, df = 7.6
Principal component 1	*NA*	*NA*	*NA*	-0.35(±1.52)	0.04(±2.14)	Welch's two sample t-test; t = -0.71, p = 0.49, df = 8.87
Principal component 2	*NA*	*NA*	*NA*	-0.07(±1.77)	0.08(±1.18)	Welch's two sample t-test; t = -0.18, p = 0.86, df = 10.44
SD	1.80	1.47				

Table A3: Summary of chemical variables recorded at stream reach-level according to treatment, including outputs from principal component analysis. Principal components with weighting absolute values equal to or greater than 0.3 are shown in bold

	PCA Component		Variable mean (± SD)		Treatment comparison
	1	2	Trout-populated	Trout-free	
Total variance explained (%)	**34.7**	**28.1**			
pH	0.11	0.22	5.26(±0.94)	5.16(±0.95)	Welch's two sample t-test; t = 0.20, p = 0.84, df = 10.6
Conductivity	**-0.37**	0.21	27.17(±3.81)	29.35(±8.08)	Mann-Whitney U; U = 22, p = 0.94
Mg (mg l^{-1})	0.20	**0.43**	0.69(±0.15)	0.96(±0.66)	Mann-Whitney U; U = 15.5, p = 0.47
Ca (mg l^{-1})	0.07	0.18	0.89(±0.43)	3.77(±6.40)	Mann-Whitney U; U = 18, p = 0.73
Na (mg l^{-1})	**-0.38**	0.04	4.45(±1.24)	4.46(±1.23)	Welch's two sample t-test; t = -0.02, p = 0.98, df = 10.7
K (mg l^{-1})	0.29	**0.36**	0.05(±0.05)	0.07(±180.35)	Welch's two sample t-test; t = -0.52, p = 0.61, df = 10.7
Cl (mg l^{-1})	**-0.42**	0.15	5.89(±3.28)	7.32(±5.80)	Mann-Whitney U; U = 15.5, p = 0.47
NO$_3$ (mg l^{-1})	**0.33**	**0.31**	0.85(±1.07)	2.63(±3.74)	Mann-Whitney U; U = 17, p = 0.60
SO$_4$ (mg l^{-1})	-0.23	**0.37**	2.23(±0.24)	3.18(±1.06)	Welch's two sample t-test; t = -2.15, p = 0.08, df = 5.4
Al (ng l^{-1})	**-0.31**	0.22	91.74(±43.08)	127.51(±45.44)	Welch's two sample t-test; t = -1.44, p = 0.18, df = 10.5
Fe (ng ml^{-1})	-0.20	-0.03	292.04(±187.35)	263.30(±167.25)	Welch's two sample t-test; t = 0.29, p = 0.77, df = 10.9
Zn (ng ml^{-1})	0.16	0.24	35.87(±13.54)	41.52(±29.41)	Mann-Whitney U; U = 22, p = 0.94
Pb (ng ml^{-1})	-0.27	**0.33**	1.26(±0.89)	8.81(±14.96)	Mann-Whitney U; U = 14, p = 0.36
Mn (ng ml^{-1})	0.09	**0.30**	55.1(±36.67)	201.8(±214.32)	Mann-Whitney U; U = 10, p = 0.14
Principal component 1	*NA*	*NA*	-0.12(±1.08)	0.14(±3.19)	Welch's two sample t-test; t = -0.20, p = 0.85, df = 5.98
Principal component 2	*NA*	*NA*	0.95(±0.72)	-1.11(±2.47)	Welch's two sample t-test; t = 1.97, p = 0.10, df = 5.73
SD	2.20	1.98			

Table A4: Model selection process for equation 1 of table 4.1.

Selection	Formula	AIC	BIC	Covariate(s)	Estimate/ *edf*	Standard error/*Ref. df*	Z value/*Chi squared*	P value
Forward	*Eel number ~ s(Dispersal distance) + Treatment, Offset = log$_n$(Site area), random = ~(1|Stream reach)*	348.4	363.3	Intercept	-4.69	0.29	-16.25	**< 2 x 10^{-16}**
				Treatment	0.86	0.28	3.06	**0.002**
				s(Dispersal distance)	*3.48*	*3.48*	*58.90*	***4.59 x 10^{-10}***
Forward	*Eel number ~ s(Dispersal distance) + Treatment + Pool percentage + (1|Stream reach), Offset = log$_n$(Site area)*	346.6	364.6	Intercept	-5.58	0.56	-9.89	**< 2 x 10^{-16}**
				Treatment	0.78	0.29	2.71	**0.007**
				Pool percentage	0.02	0.01	1.85	**0.06**
				s(Dispersal distance)	*3.57*	*3.57*	*57.17*	***5.34 x 10^{-10}***
Backward	*Eel number ~ s(Dispersal distance) + Treatment + Pool percentage + Riffle percentage + Mean depth + Gravel proportion + Cobble proportion + Boulder proportion + Cover index + (1|Stream reach), Offset = log$_n$(Site area)*	354.4	389.6	Intercept	-7.96	2.52	-3.16	**0.002**
				Treatment	0.84	0.33	2.56	**0.01**
				Pool percentage	0.01	0.02	0.81	0.42
				Riffle percentage	-0.01	0.01	-0.81	0.42
				Mean depth	0.01	0.03	0.47	0.64
				Gravel proportion	0.03	0.02	1.20	0.23
				Cobble proportion	0.03	0.02	1.36	0.17
				Boulder proportion	0.02	0.02	0.82	0.41
				Cover index	0.07	0.12	0.58	0.56
				s(Dispersal distance)	*3.56*	*3.56*	*53.69*	***9.23 x 10^{-10}***
Backward	*Eel number ~ s(Dispersal distance) + Treatment + Pool percentage + Riffle percentage + Gravel proportion + Cobble proportion + Boulder proportion + Cover index + (1|Stream reach), Offset = log$_n$(Site area)*	352.6	384.9	Intercept	-7.75	2.41	-3.22	**0.001**
				Treatment	0.86	0.33	2.64	**0.008**
				Pool percentage	0.01	0.02	0.94	0.35
				Riffle percentage	-0.01	0.01	-0.81	0.42
				Gravel proportion	0.03	0.02	1.24	0.22
				Cobble proportion	0.03	0.02	1.36	0.17
				Boulder proportion	0.02	0.02	0.88	0.38
				Cover index	0.07	0.12	0.60	0.55
				s(Dispersal distance)	*3.55*	*3.55*	*53.38*	***1.03 x 10^{-9}***
Backward	*Eel number ~ s(Dispersal distance) + Treatment + Pool percentage + Riffle percentage + Gravel proportion + Cobble proportion + Boulder proportion + (1|Stream reach), Offset = log$_n$(Site area)*	350.9	380.3	Intercept	-7.65	2.40	-3.19	**0.001**
				Treatment	0.84	0.32	2.60	**0.009**
				Pool percentage	0.01	0.02	0.95	0.34
				Riffle percentage	-0.01	0.01	-0.80	0.42
				Gravel proportion	0.03	0.02	1.35	0.18
				Cobble proportion	0.03	0.02	1.54	0.12
				Boulder proportion	0.02	0.02	0.92	0.36
				s(Dispersal distance)	*3.60*	*3.60*	*55.73*	***4.76 x 10^{-10}***
Backward	*Eel number ~ s(Dispersal distance) + Treatment + Pool percentage + Gravel proportion + Cobble proportion + Boulder proportion + (1|Stream reach), Offset = log$_n$(Site area)*	349.6	376.1	Intercept	-8.52	2.17	-3.92	**8.93 x 10^{-5}**
				Treatment	0.84	0.32	2.61	**0.009**
				Pool percentage	0.02	0.01	1.82	0.07
				Gravel proportion	0.03	0.02	1.40	0.16
				Cobble proportion	0.03	0.02	1.51	0.13
				Boulder proportion	0.02	0.02	0.94	0.35
				s(Dispersal distance)	*3.64*	*3.64*	*57.69*	***2.37 x 10^{-10}***
Backward	*Eel number ~ s(Dispersal distance) + Treatment + Pool percentage + Gravel proportion + Cobble proportion + (1|Stream reach), Offset = log$_n$(Site area)*	348.4	372.0	Intercept	-6.69	0.96	-6.96	**3.45 x 10^{-12}**
				Treatment	0.71	0.30	2.40	**0.02**
				Pool percentage	0.02	0.01	1.76	0.08
				Gravel proportion	0.01	0.01	1.04	0.30
				Cobble proportion	0.02	0.01	1.40	0.16
				s(Dispersal distance)	*3.64*	*3.64*	*57.21*	***3.65 x 10^{-10}***
Backward	*Eel number ~ s(Dispersal distance) + Treatment + Pool percentage + Cobble proportion + (1|Stream reach), Offset = log$_n$(Site area)*	347.5	368.2	Intercept	-6.21	0.84	-7.35	**1.94 x 10^{-13}**
				Treatment	0.77	0.29	2.70	**0.007**
				Pool percentage	0.02	0.01	1.92	0.05
				Cobble proportion	0.01	0.01	1.03	0.30
				s(Dispersal distance)	*3.56*	*3.56*	*56.6*	***6.36 x 10^{-10}***
Backward	*Eel number ~ s(Dispersal distance) + Treatment + Pool percentage + (1|Stream reach), Offset = log$_n$(Site area)*	346.6	364.6	Intercept	-5.58	0.56	-9.89	**< 2 x 10^{-16}**
				Treatment	0.78	0.29	2.71	**0.007**
				Pool percentage	0.02	0.01	1.85	0.06
				s(Dispersal distance)	*3.57*	*3.57*	*57.17*	***5.34 x 10^{-10}***

Table A5: Model selection process for equation 2 of table 4.1.

Selection	Formula	AIC	BIC	Covariate(s)	Estimate/ *edf*	Standard error/*Ref. df*	Z value/*Chi squared*	P value
Forward	*Eel number ~ s(Dispersal distance) + (1|Stream reach), Offset = log*$_n$*(Site area)*	163.7	174.5	Intercept	-4.75	0.42	-11.43	**$<2 \times 10^{-16}$**
				s(Dispersal distance)	*2.47*	*2.47*	*13.62*	***0.002***
Forward	*Eel number ~ s(Dispersal distance) + 2^+ trout density + (1|Stream reach), Offset = log*$_n$*(Site area)*	159.1	173.8	Intercept	-4.19	0.41	-10.18	**$<2 \times 10^{-16}$**
				2^+ trout density	-0.20	0.08	-2.39	**0.02**
				s(Dispersal distance)	*2.42*	*2.42*	*11.48*	***0.004***
Backward	*Eel number ~ s(Dispersal distance) + 0^+ trout density + 1^+ trout density + 2^+ trout density + Adult trout density + Riffle percentage + Pool percentage + Mean depth + Gravel proportion + Cobble proportion + Boulder proportion + Cover index + (1|Stream reach), Offset = log*$_n$*(Site area)*	174.1	213.9	Intercept	-6.12	4.58	-1.34	0.18
				0^+ trout density	0.05	0.02	2.01	**0.04**
				1^+ trout density	0.008	0.03	0.25	0.81
				2^+ trout density	-0.24	0.11	-2.29	**0.02**
				Adult trout density	0.04	0.10	0.43	0.67
				Riffle percentage	-0.03	0.02	-1.44	0.15
				Pool percentage	0.01	0.02	0.62	0.53
				Mean depth	0.01	0.05	0.21	0.84
				Gravel proportion	0.02	0.05	0.41	0.68
				Cobble proportion	0.02	0.04	0.46	0.65
				Boulder proportion	0.03	0.04	0.74	0.46
				Cover index	0.14	0.18	0.78	0.44
				s(Dispersal distance)	*1.00*	*1.00*	*9.05*	***0.003***
Backward	*Eel number ~ s(Dispersal distance) + 0^+ trout density + 1^+ trout density + 2^+ trout density + Adult trout density + Riffle percentage + Pool percentage + Gravel proportion + Cobble proportion + Boulder proportion + Cover index + (1|Stream reach), Offset = log*$_n$*(Site area)*	172.2	209.7	Intercept	-5.77	4.24	-1.36	0.17
				0^+ trout density	0.05	0.02	2.04	**0.04**
				1^+ trout density	0.01	0.03	0.32	0.75
				2^+ trout density	-0.24	0.10	-2.29	0.02
				Adult trout density	0.05	0.09	0.51	0.61
				Riffle percentage	-0.04	0.02	-1.46	0.14
				Pool percentage	0.01	0.02	0.64	0.52
				Gravel proportion	0.02	0.05	0.39	0.70
				Cobble proportion	0.02	0.04	0.43	0.67
				Boulder proportion	0.03	0.04	0.73	0.47
				Cover index	0.14	0.18	0.78	0.43
				s(Dispersal distance)	*1.00*	*1.00*	*9.13*	***0.003***
Backward	*Eel number ~ s(Dispersal distance) + 0^+ trout density + 2^+ trout density + Adult trout density + Riffle percentage + Pool percentage + Gravel proportion + Cobble proportion + Boulder proportion + Cover index + (1|Stream reach), Offset = log*$_n$*(Site area)*	170.3	205.9	Intercept	-6.18	4.13	-1.50	0.13
				0^+ trout density	0.04	0.02	2.04	**0.04**
				2^+ trout density	-0.22	0.09	-2.45	**0.01**
				Adult trout density	0.05	0.09	0.53	0.60
				Riffle percentage	-0.03	0.02	-1.53	0.13
				Pool percentage	0.02	0.02	0.66	0.51
				Gravel proportion	0.02	0.05	0.46	0.64
				Cobble proportion	0.02	0.04	0.50	0.62
				Boulder proportion	0.03	0.04	0.78	0.44
				Cover index	0.15	0.18	0.85	0.39
				s(Dispersal distance)	*1.00*	*1.00*	*9.35*	***0.002***
Backward	*Eel number ~ s(Dispersal distance) + 0^+ trout density + 2^+ trout density + Adult trout density + Riffle percentage + Pool percentage + Cobble proportion + Boulder proportion + Cover index + (1|Stream reach), Offset = log*$_n$*(Site area)*	168.5	201.8	Intercept	-4.58	2.22	-2.06	**0.04**
				0^+ trout density	0.04	0.02	2.00	**0.05**
				2^+ trout density	-0.23	0.09	-2.55	**0.01**
				Adult trout density	0.05	0.09	0.59	0.55
				Riffle percentage	-0.03	0.02	-1.54	0.12
				Pool percentage	0.01	0.02	0.63	0.53
				Cobble proportion	0.01	0.02	0.28	0.78
				Boulder proportion	0.01	0.02	0.79	0.43
				Cover index	0.17	0.18	0.95	0.34
				s(Dispersal distance)	*1.00*	*1.00*	*8.86*	***0.003***
Backward	*Eel number ~ s(Dispersal distance) + 0^+ trout density + 2^+ trout density + Adult trout density + Riffle percentage + Pool percentage + Boulder proportion + Cover index + (1|Stream reach), Offset = log*$_n$*(Site area)*	166.5	197.6	Intercept	-4.39	1.96	-2.24	**0.02**
				0^+ trout density	0.04	0.02	1.99	**0.05**
				2^+ trout density	-0.23	0.09	-2.55	**0.01**
				Adult trout density	0.05	0.09	0.55	0.58
				Riffle percentage	-0.03	0.02	-1.45	0.15
				Pool percentage	0.02	0.02	0.67	0.51
				Boulder proportion	0.01	0.01	0.80	0.42
				Cover index	0.18	0.17	1.01	0.31
				s(Dispersal distance)	*1.00*	*1.00*	*9.09*	*0.003*
Backward	*Eel number ~ s(Dispersal distance) + 0^+ trout density + 2^+ trout density + Riffle percentage + Pool percentage + Boulder proportion + Cover index + (1|Stream reach), Offset = log*$_n$*(Site area*	164.9	193.5	Intercept	-4.38	1.94	-2.25	**0.02**
				0^+ trout density	0.04	0.02	2.03	**0.04**
				2^+ trout density	-0.23	0.09	-2.56	**0.01**
				Riffle percentage	-0.03	0.02	-1.41	0.16
				Pool percentage	0.015	0.02	0.64	0.52
				Boulder proportion	0.01	0.01	0.81	0.42
				Cover index	0.18	0.17	1.04	0.30
				s(Dispersal distance)	*1.00*	*1.00*	*8.96*	***0.003***
Backward	*Eel number ~ s(Dispersal distance) + 0^+ trout density + 2^+ trout density + Riffle percentage + Boulder proportion + Cover index + (1|Stream reach), Offset = log*$_n$*(Site area)*	163.3	189.0	Intercept	-3.63	1.38	-2.62	**0.009**
				0^+ trout density	0.04	0.02	1.97	**0.05**
				2^+ trout density	-0.25	0.08	-2.94	**0.003**
				Riffle percentage	-0.04	0.02	-2.13	**0.03**
				Boulder proportion	0.01	0.01	1.05	0.29
				Cover index	0.22	0.17	1.28	0.20
				s(Dispersal distance)	*1 .00*	*1.00*	*8.70*	***0.003***
Backward	*Eel number ~ s(Dispersal distance) + 0^+ trout density + 2^+ trout density + Riffle percentage + Cover index + (1|Stream reach), Offset = log*$_n$*(Site area)*	162.3	184.8	Intercept	-2.74	1.13	-2.43	**0.02**
				0^+ trout density	0.04	0.02	2.06	**0.04**
				2^+ trout density	-0.23	0.08	-2.88	**0.004**
				Riffle percentage	-0.04	0.02	-2.30	**0.022**
				Cover index	0.12	0.15	0.82	0.41
				s(Dispersal distance)	*1.00*	*1.00*	*8.51*	***0.004***
Backward	*Eel number ~ s(Dispersal distance) + 0^+ trout density + 2^+ trout density + Riffle percentage + (1|Stream reach), Offset = log*$_n$*(Site area)*	161.0	181.3	Intercept	-2.03	0.86	-2.37	**0.02**
				0^+ trout density	0.04	0.02	2.17	**0.03**
				2^+ trout density	-0.24	0.08	-2.90	**0.004**
				Riffle percentage	-0.04	0.02	-2.43	**0.02**
				s(Dispersal distance)	*1.00*	*1.00*	*8.37*	***0.004***
Backward	*Eel number ~ s(Dispersal distance) + 2^+ trout density + Riffle percentage +*	159.8	177.5	Intercept	-3.23	0.93	-3.46	**0.0005**
				2^+ trout density	-0.21	0.09	-2.48	**0.01**

	(1|Stream reach), Offset = $\log_n$(Site area)			Riffle percentage	-0.02	0.02	-1.11	0.27
				s(Dispersal distance)	*2.31*	*2.31*	*9.85*	***0.008***
Backward	*Eel number ~ s(Dispersal distance) + 2^+ trout density + (1|Stream reach), Offset = $\log_n$(Site area)*	159.1	173.8	Intercept	-4.19	0.41	-10.18	**<2 x 10^{-16}**
				2^+ trout density	-0.20	0.08	-2.39	**0.02**
				s(Dispersal distance)	*2.42*	*2.42*	*11.48*	***0.004***

Table A6: Model selection process for equation 3 of table 4.1.

Selection	Formula	AIC	BIC	Covariate(s)	Estimate	Standard error	Z value	P value
Forward	*Eel length ~ All 1^+ trout density + (1|Stream reach)*	161.6	166.2	Intercept	79.89	4.75	16.82	**<2 x 10^{-16}**
				All 1^+ trout density	*0.76*	*0.25*	*2.99*	***0.003***
Forward	*Eel length ~ All 1^+ trout density + Mean depth + (1|Stream reach)*	159.1	164.7	Intercept	96.04	8.69	11.05	**< 2 x 10^{-16}**
				All 1^+ trout density	0.87	0.25	3.49	**0.0005**
				Mean depth	-0.76	0.34	-2.22	**0.03**
Forward	*Eel length ~ All 1^+ trout density + Mean depth + Gravel proportion + (1|Stream reach)*	158.8	165.1	Intercept	104.50	10.26	10.18	**< 2 x 10^{-16}**
				All 1^+ trout density	0.76	0.25	3.04	**0.002**
				Mean depth	-0.77	0.32	-2.38	**0.02**
				Gravel proportion	-0.35	0.22	-1.62	**0.10615**
Forward	*Eel length ~ All 1^+ trout density + Mean depth + Gravel proportion + 0^+ trout density + (1|Stream reach)*	157.0	164.4	Intercept	120.00	8.63	13.91	**< 2 x 10^{-16}**
				All 1^+ trout density	0.81	0.19	4.21	**2.61 x 10^{-5}**
				Mean depth	-1.12	0.32	-3.56	**0.0004**
				Gravel proportion	-0.50	0.17	-3.00	**0.003**
				0^+ trout density	-0.39	0.18	-2.16	**0.03**
Backward	*Eel length ~ 0^+ trout density + All 1^+ trout density + Riffle percentage + Pool percentage + Mean depth + Gravel proportion + Cobble proportion + Boulder proportion + Cover index + Eel density + (1|Stream reach)*	157.7	170.2	Intercept	179.31	28.06	6.39	**1.65 x 10^{-10}**
				0^+ trout density	-0.82	0.21	-3.83	**0.0001**
				All 1^+ trout density	1.67	0.17	9.79	**< 2 x 10^{-16}**
				Riffle percentage	-0.20	0.09	-2.31	**0.02**
				Pool percentage	0.63	0.14	4.54	**5.72 x 10^{-6}**
				Mean depth	-2.17	0.36	-6.00	**1.98 x 10^{-9}**
				Gravel proportion	-0.84	0.27	-3.07	**0.002**
				Cobble proportion	-0.40	0.26	-1.57	**0.12**
				Boulder proportion	-0.54	0.25	-2.13	**0.03**
				Cover index	-0.70	1.46	-0.48	0.63
				Eel density	-1.53	0.40	-3.84	**0.0001**
Backward	*Eel length ~ 0^+ trout density + All 1^+ trout density + Riffle percentage + Pool percentage + Mean depth + Gravel proportion + Cobble proportion + Boulder proportion + Cover index + (1|Stream reach)*	156.1	167.8	Intercept	196.22	28.96	6.78	**1.24 x 10^{-11}**
				0^+ trout density	-0.42	0.15	-2.69	**0.007**
				All 1^+ trout density	1.43	0.24	6.06	**1.37 x 10^{-9}**
				Riffle percentage	-0.11	0.13	-0.89	0.38
				Pool percentage	0.42	0.16	2.56	**0.01**
				Mean depth	-1.61	0.31	-5.20	**1.97 x 10^{-7}**
				Gravel proportion	-1.30	0.33	-3.97	**7.34 x 10^{-5}**
				Cobble proportion	-0.60	0.25	-2.36	**0.02**
				Boulder proportion	-0.84	0.28	-3.01	**0.003**
				Cover index	-3.45	1.47	-2.34	**0.02**
Backward	*Eel length ~ 0^+ trout density + All 1^+ trout density + Pool percentage + Mean depth + Gravel proportion + Cobble proportion + Boulder proportion + Cover index + (1|Stream reach)*	154.9	166.8	Intercept	188.31	28.06	6.71	**1.93 x 10^{-11}**
				0^+ trout density	-0.43	0.16	-2.74	**0.006**
				All 1^+ trout density	1.36	0.23	6.00	**2.02 x 10^{-9}**
				Pool percentage	0.45	0.16	2.77	**0.006**
				Mean depth	-1.55	0.31	-5.05	**4.52 x 10^{-7}**
				Gravel proportion	-1.26	0.33	-3.80	**0.0001**
				Cobble proportion	-0.60	0.26	-2.31	**0.02**
				Boulder proportion	-0.82	0.28	-2.91	**0.004**
				Cover index	-3.54	1.50	-2.36	**0.02**

Appendix 4

Table A1: Site and translocation numbers for 2019 and 2020 experiments

Catchment area	2019					2020						
	HDC N=	LDC N=	HDS N=	LDR N=	Total fry translocated	HDC N=	LDC N=	HDS N=	LDR N=	Total fry removed	Total fry added	Source site location(s)
Derrinkee	1	2	2	1	140	1	3	0	1	NA	121	Erriff mainstem (N = 1)
Owenmore	3	3	3	3	206	7	1	3	1	318	156	Owenmore (N = 1)
Glendavoc	3	3	3	3	136	2	5	3	2	187	413	Glendavoc (N = 3), Erriff mainstem (N = 2)
Sheeffry	3	2	3	3	135	2	5	3	3	163	410	Sheeffry (N = 3), Owenmore (N = 2), Erriff mainstem (N = 1)
Erriff mainstem	4	3	4	4	508	3	0	4	NA	443	NA	NA
Derrycraff	1	1	1	1	13							
Total	15	14	16	15	1138	15	14	13	7	1111	1100	

Table A2: Habitat data summary for all assigned sites (HDS, HDC, LDR and LDC) outlining the results of univariate and principal component analyses. Analyses which showed a significant difference between treatments are shown in bold. Principal components with weighting absolute values equal to or greater than 0.3 are also shown in bold

	PCA component		Mean (± SD)		Comparison	Mean (± SD)		Comparison	Mean (± SD)		Comparison
	1	2	HD	LD		HDS	HDC		LDR	LDC	
Total variance explained (%)	36.28	28.06									
Mean site depth (cm)	0.04	**0.48**	0.17 (±0.03)	0.16 (±0.05)	**Mann-Whitney u test; U = 1899.5, p = 0.01**	0.17 (±0.04)	0.17 (±0.03)	Mann-Whitney u test; U = 423.5, p = 0.87	0.17 (±0.06)	0.15 (±0.04)	Mann-Whitney u test; U = 362.5, p = 0.29
Site area (m^2)	**0.33**	**0.43**	187.67 (±119.67)	141.93 (±73.47)	**Mann-Whitney u test; U = 1883, p = 0.01**	192.15 (±111.18)	183.34 (±129.10)	Mann-Whitney u test; U = 495, p = 0.37	149.85 (±87.12)	135.70 (±61.67)	Mann-Whitney u test; U = 325.5, p = 0.74
Sand proportion	-0.08	**0.49**	0.04 (±0.02)	0.008 (±0.02)	**Mann-Whitney u test; U = 1945, p = 0.002**	0.007 (±0.012)	0.02 (±0.02)	**Mann-Whitney u test; U = 213.5, p = 0.0004**	0.01 (±0.03)	0.006 (±0.01)	Mann-Whitney u test; U = 310.5, p = 0.96
Gravel proportion	**-0.58**	0.18	0.60 (±0.14)	0.51 (±0.14)	**Mann-Whitney u test; U = 1943.5, p = 0.004**	0.57 (±0.18)	0.63 (±0.18)	Mann-Whitney u test; U = 372.5, p = 0.35	0.49 (±0.10)	0.53 (±0.17)	Mann-Whitney u test; U = 288, p = 0.70
Cobble proportion	**0.56**	-0.13	0.36 (±0.17)	0.41 (±0.12)	**Mann-Whitney u test; U = 1083, p = 0.02**	0.38 (±0.16)	0.33 (±0.17)	Mann-Whitney u test; U = 469.5, p = 0.61	0.44 (±0.09)	0.39 (±0.13)	Mann-Whitney u test; U = 365, p = 0.27
Boulder proportion	**0.31**	**-0.33**	0.03 (±0.06)	0.07 (±0.06)	**Mann-Whitney u test; U = 753, p = 7.57 x 10^{-6}**	0.04 (±0.07)	0.02 (±0.04)	Mann-Whitney u test; U = 511.5, p = 0.21	0.07 (±0.05)	0.08 (±0.07)	Mann-Whitney u test; U = 303, p = 0.93
Macrophyte cover proportion	**0.37**	**0.42**	0.15 (±0.17)	0.06 (±0.13)	**Mann-Whitney u test; U = 2028, p = 0.0005**	0.16 (±0.19)	0.14 (±0.15)	Mann-Whitney u test; U = 424, p = 0.87	0.09 (±0.14)	0.05 (±0.11)	Mann-Whitney u test; U = 338, p = 0.53
Median substrate size (mm)	NA	NA	64.88 (±23.67)	78.33 (±25.49)	**Mann-Whitney u test; U = 1061, p = 0.009**	69.21 (±23.21)	60.70 (±23.73)	Mann-Whitney u test; U = 514.5, p = 0.21	77.43 (±20.75)	79.03 (±29.03)	Mann-Whitney u test; U = 313, p = 0.93
PC1			0.28 (±1.69)	-0.09 (±1.19)	**Mann-Whitney u test; U = 1802, p = 0.05**	-0.03 (±1.81)	0.58 (±1.53)	Mann-Whitney u test; U = 384, p = 0.44	-0.31 (±1.06)	0.09 (±1.27)	Mann-Whitney u test; U = 264.5, p = 0.40
PC2			-0.20 (±1.09)	0.83 (±1.36)	**Mann-Whitney u test; U = 796, p = 3.7 x 10^{-5}**	0.04 (±1.11)	-0.44 (±1.03)	Welch's two sample t-test; t = 1.75, df = 56.4, p = 0.09	0.58 (±1.57)	1.04 (±1.16)	Welch's two sample t-test; t = -1.15, df = 37.5, p = 0.26

Table A3: Comparison of 0+ fry densities by treatment group for the Spring and autumn sampling periods, statistically significant results are shown in bold

	Mean (± SD)		Comparison	Mean (± SD)		Comparison	Mean (± SD)		Comparison
Sampling period	HD	LD		HDS	HDC		LDR	LDC	
Spring 2019	0.62 (±0.18)	0.15 (±0.13)	**Welch's two sample t-test; t = 9.6, df = 35.7, p = 2.0 x 10^{-11}**	0.63 (±0.20)	0.60 (±0.17)	Welch's two sample t-test; t = 0.34, df = 18.9, p = 0.74	0.14 (±0.14)	0.15 (±0.12)	Welch's two sample t-test; t = -0.05, df = 17.0, p = 0.96
Spring 2020	0.72 (±0.16)	0.18 (±0.09)	**Mann-Whitney U test; U = 176, p = 1.5 x 10^{-5}**	0.64 (±0.13)	0.78 (±0.16)	Mann-Whitney U test; U = 9, p = 0.31	0.20 (±0.07)	0.17 (±0.10)	Mann-Whitney U test; U = 36, p = 0.36
Combined	0.65 (±0.18)	0.16 (±0.11)	**Welch's two sample t-test; t = 13.3, df = 51.3, p < 2.2 x 10^{-16}**	0.63 (±0.18)	0.67 (±0.19)	Welch's two sample t-test; t = -0.59, df = 29.9, p = 0.56	0.16 (±0.12)	0.16 (±0.11)	Welch's two sample t-test; t = 0.13, df = 28.0, p = 0.90
Autumn 2019	0.34 (±0.17)	0.15 (±0.13)	**Welch's two sample t-test; t = 4.1, df = 36.8, p = 0.00023**	0.31 (±0.14)	0.38 (±0.20)	Welch's two sample t-test; t = -0.85, df = 15.8, p-value = 0.41	0.15 (±0.15)	0.15 (±0.11)	Welch's two sample t-test; t = -0.05, df = 16.5, p-value = 0.96
Autumn 2020	0.34 (±0.16)	0.09 (±0.06)	**Mann-Whitney U test; U = 173, p = 3.0 x 10^{-5}**	0.31 (±0.09)	0.37 (±0.21)	Mann-Whitney U test; U = 15.5, p = 1	0.10 (±0.05)	0.09 (±0.06)	Welch's two sample t-test; t = 0.38, df = 8.9, p-value = 0.72
Combined	0.34 (±0.17)	0.12 (±0.10)	**Mann-Whitney U test; U = 1004.5, p = 2.5 x 10^{-8}**	0.31 (±0.12)	0.37 (±0.20)	Mann-Whitney U test; U = 114.5, p = 0.62	0.13 (±0.12)	0.13 (±0.09)	Mann-Whitney U test; U = 148, p = 0.96
Combined Table 5.1 Equation 3 residuals	-0.82 (±11.56)	0.007 (±7.25)	Mann-Whitney U test; U = 1313, p = 0.33	-3.92 (±8.96)	2.19 (±13.07)	Mann-Whitney U test; U = 326, p = 0.10	0.26 (±8.49)	-0.19 (±6.27)	Welch's two sample t-test; t = 0.14, df = 21, p = 0.89

Table A4: Comparison of spring fry density by catchment area and sampling year. Statistically significant results are shown in bold

Catchment area	Sampling period	Spring mean fry density (fish 100 m^{-2} ± SD)	Inter-year	Derrycraff	Derrinkee	Owenmore	Erriff	Glendavoc	Sheeffry
Sheeffry	2019	55(±28.14)	Mann-Whitney u test; U = 106, p = 0.13	**Welch's two sample t-test; t = 3.29, df = 15.13, p = 0.005**	Welch's two sample t-test; t = 0.95, df = 10.11, p = 0.37	Welch's two sample t-test; t = 0.87, df = 23.00, p = 0.39	**Welch's two sample t-test; t = 2.75, df = 15.01, p = 0.01**	**Mann-Whitney u test; U = 115, p-value = 0.05**	
	2020	38.08(±34.35)		*NA*	Mann-Whitney u test; U = 45.5, p = 1	**Mann-Whitney u test; U = 45.5, p-value = 0.05**	Mann-Whitney u test; U = 62, p = 0.40	Mann-Whitney u test; U = 71, p-value = 0.5	
	Combined	46.20(±32.05)		*NA*	Mann-Whitney u test; U = 212.5, p = 0.28	Mann-Whitney u test; U = 266, p-value = 0.27	Mann-Whitney u test; U = 572.5, p = 0.24	Mann-Whitney u test; U = 388.5, p-value = 0.24	
Glendavoc	2019	29.77(±31.55)	Mann-Whitney u test; U = 55, p = 0.14	Mann-Whitney u test; U = 41.5, p = 0.86	Mann-Whitney u test; U = 38, p = 0.58	Mann-Whitney u test; U = 50, p-value = 0.08	Mann-Whitney u test; U = 143, p = 0.36		
	2020	45.15(±36.68)		*NA*	Mann-Whitney u test; U = 54, p = 0.53	Mann-Whitney u test; U = 55.5, p = 0.14	Mann-Whitney u test; U = 73, p = 0.81		
	Combined	37.46(±34.42)		*NA*	Mann-Whitney u test; U = 181.5, p = 1	Welch's two sample t-test; t = -1.91, df = 48.05, p = 0.06	Mann-Whitney u test; U = 468, p = 0.61		
Erriff	2019	30.78(±17.70)	Welch's two sample t-test; t = -1.89, df = 21.263, p = 0.07	Welch's two sample t-test; t = 1.41, df = 7.60, p = 0.20	Welch's two sample t-test; t = -0.62, df = 6.73, p = 0.56	Welch's two sample t-test; t = -1.55, df = 16.09, p = 0.14			
	2020	42.33(±17.63)		*NA*	Welch's two sample t-test; t = 1.43, df = 12.75, p = 0.18	**Welch's two sample t-test; t = -2.55, df = 22.20, p = 0.02**			
	Combined	34.33(±18.26)		*NA*	Mann-Whitney u test; U = 281.5, p = 0.87	Mann-Whitney u test; U = 301.5, p = 0.006			
Owenmore	2019	44.85(±30.23)	Welch's two sample t-test; t = -1.74, df = 22.53, p = 0.09	**Welch's two sample t-test; t = 2.29, df = 156.00, p = 0.04**	Welch's two sample t-test; t = 0.31, df = 10.42, p = 0.76				
	2020	63.31(±23.28)		*NA*	**Welch's two sample t-test; t = 3.56, df = 15.72, p = 0.003**				
	Combined	54.08(±28.06)		*NA*	**Mann-Whitney u test; U = 253.5, p = 0.04**				
Derrinkee	2019	39.71(±36.99)	Welch's two sample t-test; t = 0.60, df = 8.56, p = 0.56	Welch's two sample t-test; t = 1.27, df = 8.70, p = 0.24					
	2020	30.43(±17.52)		*NA*					
	Combined	35.07(±28.22)		*NA*					
Derrycraff	2019	19.83(±17.05)	*NA*						
	2020	*NA*							
	Combined	*NA*							
Entire Catchment	2019	36.64(±27.36)	Mann-Whitney u test; U = 1873.5, p = 0.09						
	2020	45.28(±29.21)							
	Combined	40.32(±28.38)							

Table A5: Comparison of spring and autumn non-translocated fry mean TLs between treatment groups and by sampling year. Statistically significant results are shown in bold

	Mean (± SD)		Comparison	Mean (± SD)		Comparison	Mean (± SD)		Comparison
Sampling period	HD	LD		HDS	HDC		LDR	LDC	
Spring 2019	45.77±4.82	48.27±4.65	Welch's two sample t-test; t = -1.97, df = 52.26, p = 0.05	46.34±4.83	45.18±4.92	Welch's two sample t-test; t = 0.66, df = 28.79, p = 0.5	48.39±3.80	48.14±5.60	Welch's two sample t-test; t = 0.13, df = 19.14, p = 0.90
Spring 2020	37.17±2.34	39.10±3.89	**Mann-Whitney u test; U = 161, p = 0.007**	37.27±2.34	37.08±2.41	Mann-Whitney u test; U = 94, p = 0.89	38.39±3.54	39.46±4.13	Welch's two sample t-test; t = -0.62, df = 13.94, p = 0.55
Combined	41.69±5.78	44.09±6.29	**Mann-Whitney u test; U = 988.5, p = 0.02**	42.27±5.99	41.13±5.61	Welch's two sample t-test; t = 0.76, df = 56.43, p = 0.45	44.89±6.09	43.47±6.50	Mann-Whitney u test; U = 299, p = 0.39
Inter-year comparison	**Welch's two sample t-test; t = 8.85, df = 44.27, p = 2.39 x 10^{-11}**	**Mann-Whitney u test; U = 493, p = 3.93 x 10^{-7}**		**Welch's two sample t-test; t = 6.62, df = 22.56, p = 1.04 x 10^{-6}**	**Mann-Whitney u test; U = 215, p = 1.79 x 10^{-6}**		**Welch's two sample t-test; t = 5.87, df = 13.18, p = 5.18 x 10^{-5}**	**Welch's two sample t-test; t = 4.44, df = 19.96, p = 0.0003**	
Autumn 2019	57.21±4.87	60.53±6.72	**Welch's two sample t-test; t = -2.12, df = 46.76, p = 0.04**	57.89±4.07	56.49±5.66	Welch's two sample t-test; t = 0.79, df = 25.30, p = 0.44	60.62±6.53	60.43±7.18	Mann-Whitney u test; U = 87, p = 0.88
Autumn 2020	54.08±3.57	53.53±12.84	Mann-Whitney u test; U = 233.5, p = 0.23	54.54±3.18	53.68±3.93	Mann-Whitney u test; U = 97, p = 1	55.13±4.63	52.73±15.55	Mann-Whitney u test; U = 52.5, p = 0.82
Combined	55.73±4.55	57.47±10.37	**Mann-Whitney u test; U = 1061.5, p = 0.03**	56.39±4.01	55.09±5.00	Mann-Whitney u test; U = 520, p = 0.20	58.79±6.42	56.44±12.65	Mann-Whitney u test; U = 301.5, p = 0.72
Combined equation 5 residuals	0.16±2.43	-0.20±1.87	Welch's two sample t-test; t = 0.55, df = 18.32, p = 0.59	0.59±2.47	-0.24±2.37	Welch's two sample t-test; t = 1.21, df = 47.28, p = 0.23	-0.87±1.10	0.35±2.28	Welch's two sample t-test; t = -1.16, df = 7.45, p = 0.28
Inter-year comparison	**Mann-Whitney u test; U = 602, p = 0.01**	**Welch's two sample t-test; t = 2.27, df = 28.42, p = 0.03**		**Welch's two sample t-test; t = 2.49, df = 26.98, p = 0.02**	Mann-Whitney u test; U = 136, p = 0.34		Mann-Whitney u test; U = 68, p = 0.17	Mann-Whitney u test; U = 128, p = 0.08	

Table A6: Comparison of spring mean TL by catchment area and sampling year. Statistically significant results are shown in bold

Catchment area	Sampling period	Spring mean TL (mm ± SD)	Inter-year	Derrycraff	Derrinkee	Owenmore	Erriff	Glendavoc	Sheeffry
Sheeffry	2019	42.6±3.2	**Welch's two sample t-test; t = 2.43, df = 22.40, p = 0.02**	Welch's two sample t-test; t = -12.70, df = 14.04, p = 4.37 x 10^{-9}	Welch's two sample t-test; t = -0.37, df = 7.98, p = 0.72	**Welch's two sample t-test; t = -7.63, df = 17.98, p = 4.84 x 10^{-7}**	**Mann-Whitney u test; U = 41, p = 8.99 x 10^{-5}**	**Welch's two sample t-test; t = -2.60, df = 15.94, p = 0.02**	
	2020	39.0±4.1		*NA*	**Mann-Whitney u test; U = 86, p = 0.0005**	Welch's two sample t-test; t = -0.09, df = 16.51, p = 0.93	Welch's two sample t-test; t = 0.44, df = 16.06, p = 0.66	Welch's two sample t-test; t = 1.00, df = 17.18, p = 0.33	
	Combined	40.8±4.0		*NA*	Mann-Whitney u test; U = 223, p = 0.06	**Mann-Whitney u test; U = 219, p = 0.05**	**Mann-Whitney u test; U = 276, p = 0.003**	Mann-Whitney u test; U = 284, p-value = 0.76	
Glendavoc	2019	47.4±5.4	**Welch's two sample t-test; t = 5.63, df = 12.21, p = 0.0001**	**Welch's two sample t-test;t = -4.68, df = 11.08, p = 0.0007**	Welch's two sample t-test; t = 1.75, df = 12.83, p = 0.10	Welch's two sample t-test; t = -1.92, df = 12.22, p = 0.08	Mann-Whitney u test; U = 138, p = 0.75		
	2020	37.8±1.9		*NA*	Mann-Whitney u test; U = 85.5, p = 0.002	Welch's two sample t-test; t = -1.86, df = 23.86, p = 0.08	Welch's two sample t-test; t = -0.99, df = 22.85, p = 0.33		
	Combined	42.2±6.2		*NA*	**Mann-Whitney u test; U = 218.5, p = 0.05**	Mann-Whitney u test; U = 237, p = 0.15	**Mann-Whitney u test; U = 328, p = 0.05**		
Erriff	2019	47.7±3.2	**Mann-Whitney u test; U = 320, p = 6.14 x 10^{-9}**	**Mann-Whitney u test; U = 0, p = 0.0005**	**Mann-Whitney u test; U = 134, p = 0.01**	**Mann-Whitney u test; U = 75, p = 0.004**			
	2020	38.5±1.7		*NA*	**Mann-Whitney u test; U = 82, p = 0.0002**	Welch's two sample t-test;t = -0.95, df = 23.00, p = 0.35			
	Combined	44.9±5.1		*NA*	**Mann-Whitney u test; U = 415, p = 0.0004**	Mann-Whitney u test; U = 477, p = 0.69			
Owenmore	2019	50.7±2.0	**Welch's two sample t-test; t = 15.67, df = 23.86, p = 4.66 x 10^{-14}**	**Welch's two sample t-test; t = -6.80, df = 15.36, p = 5.30 x 10^{-6}**	**Welch's two sample t-test; t = 4.13, df = 6.02, p = 0.006**				
	2020	39.2±1.8		*NA*	**Mann-Whitney u test; U = 90, p = 5.16 x 10^{-5}**				
	Combined	44.9±6.2		*NA*	**Mann-Whitney u test; U = 274, p = 0.002**				
Derrinkee	2019	43.3±4.2	**Mann-Whitney u test; U = 42, p = 0.001**	**Welch's two sample t-test; t = -6.80, df = 5.51, p = 0.0007**					
	2020	32.1±2.4		*NA*					
	Combined	37.3±6.6		*NA*					
Derrycraff	2019	55.2±0.9							
	2020	*NA*							
	Combined	*NA*							
Entire Catchment	2019	47.5±4.7	**Mann-Whitney u test; U = 4091, p < 2.2 x 10^{-16}**						
	2020	37.8±3.3							
	Combined	43.1±6.3							

Table A7: Comparison of autumn fry density by catchment area and sampling year. Statistically significant results are shown in bold

Catchment area	Sampling period	Autumn mean fry density (fish 100 m^{-2} ± SD)	Inter-year	Derrycraff	Derrinkee	Owenmore	**Erriff**	Glendavoc	Sheeffry
Sheeffry	2019	30.83±9.80	**Mann-Whitney u test; U = 115.5, p = 0.04**	**Mann-Whitney u test; U = 65, p = 0.007**	Mann-Whitney u test; U = 33.5, p = 0.50	Mann-Whitney u test; U = 99.5, p = 0.25	**Mann-Whitney u test; U = 248, p = 0.009**	**Mann-Whitney u test; U = 116, p = 0.04**	
	2020	17.92±15.78		*NA*	Welch's two sample t-test; t = -0.23, df = 14.92, p = 0.82	Mann-Whitney u test; U = 51, p = 0.09	Welch's two sample t-test; t = -1.17, df = 20.07, p = 0.25	Welch's two sample t-test; t = 0.65, df = 21.55, p = 0.52	
	Combined	24.12±14.55		*NA*	Mann-Whitney u test; U = 158.5, p = 0.64	Mann-Whitney u test; U = 316, p = 0.87	Mann-Whitney u test; U = 538, p = 0.49	**Mann-Whitney u test; U = 434.5, p = 0.04**	
Glendavoc	2019	20.69±24.31	Mann-Whitney u test; U = 85.5, p = 0.98	Mann-Whitney u test; U = 33, p = 0.63	Mann-Whitney u test; U = 25, p = 0.11	Mann-Whitney u test; U = 65, p = 0.33	Mann-Whitney u test; U = 120.5, p = 0.12		
	2020	14.46±11.10		*NA*	Welch's two sample t-test; t = -0.87, df = 10.99, p = 0.40	**Mann-Whitney u test; U = 31, p = 0.006**	**Welch's two sample t-test; t = -2.30, df = 22.92, p = 0.03**		
	Combined	17.58±18.79		*NA*	**Mann-Whitney u test; U = 112, p = 0.05**	**Mann-Whitney u test; U = 200.5, p = 0.01**	**Mann-Whitney u test; U = 319.5, p = 0.01**		
Erriff	2019	21.26±8.27	Welch's two sample t-test; t = -0.86, df = 18.56, p = 0.40	Welch's two sample t-test; t = 2.07, df = 8.99, p = 0.07	Welch's two sample t-test; t = -1.74, df = 6.42, p = 0.13	Welch's two sample t-test; t = -0.38, df = 15.10, p = 0.71			
	2020	24.00±9.63		*NA*	Welch's two sample t-test; t = 0.82, df = 10.06, p = 0.43	Mann-Whitney u test; U = 59.5, p = 0.33			
	Combined	22.10±8.68		*NA*	Mann-Whitney u test; U = 266, p = 0.90	Welch's two sample t-test; t = -1.19, df = 34.08, p = 0.24			
Owenmore	2019	23.08±16.19	Mann-Whitney u test; U = 70, p = 0.47	Welch's two sample t-test; t = 1.58, df = 16.91, p = 0.13	Welch's two sample t-test; t = -1.38, df = 9.38, p = 0.20				
	2020	29.62±17.20		*NA*	Mann-Whitney u test; U = 64, p = 0.15				
	Combined	26.35±16.70		*NA*	Mann-Whitney u test; U = 179, p = 0.94				
Derrinkee	2019	36.43±22.73	Welch's two sample t-test; t = 1.7262, df = 9.43, p = 0.12	**t = 2.40, df = 7.13, p = 0.05**					
	2020	19.43±12.74		*NA*					
	Combined	27.93±19.78		*NA*					
Derrycraff	2019	14.83±6.52	*NA*						
	2020	*NA*							
	Combined	*NA*							
Entire Catchment	2019	23.81±15.66	Mann-Whitney u test; U = 2478.5, p = 0.34						
	2020	21.21±14.37							
	Combined	22.70±15.13							

Table A8: Comparison of autumn mean TL of non-translocated fry by catchment area and sampling year. Statistically significant results are shown in bold.

Catchment area	Sampling period	Mean TL (mm ± SD)	Inter-year	Derrycraff	Derrinkee	Owenmore	Erriff	Glendavoc	Sheeffry
Sheeffry	2019	53.65±2.96	Mann-Whitney u test; U = 48, p = 0.11	**Welch's two sample t-test; t = -9.70, df = 8.15, p = 9.32 x 10^{-6}**	Welch's two sample t-test; t = -1.99, df = 10.39, p = 0.07	**Welch's two sample t-test; t = -7.37, df = 22.00, p = 2.24 x 10^{-7}**	**Mann-Whitney u test; U = 83.5, p = 0.02**	**Welch's two sample t-test; t = -4.60, df = 17.76, p = 0.0002**	
	2020	56.54±6.46		*NA*	**Mann-Whitney u test; U = 86, p = 0.0005**	Mann-Whitney u test; U = 80, p = 0.84	Mann-Whitney u test; U = 97, p = 0.32	Mann-Whitney u test; U = 103.5, p = 0.34	
	Combined	55.15±5.20		*NA*	Mann-Whitney u test; U = 225, p = 0.15	**Mann-Whitney u test; U = 145, p = 0.001**	Mann-Whitney u test; U = 395.5, p = 0.27	Mann-Whitney u test; U = 213.5, p = 0.06	
Glendavoc	2019	61.43±5.06	**Mann-Whitney u test; U = 141, p = 0.0007**	**Welch's two sample t-test; t = -4.42, df = 13.09, p = 0.0007**	**Welch's two sample t-test; t = 2.20, df = 15.77, p = 0.04**	Welch's two sample t-test; t = -0.64, df = 17.62, p = 0.53	**Mann-Whitney u test; U = 241, p = 0.007**		
	2020	51.08±14.39		*NA*	**Mann-Whitney u test; U = 79, p = 0.009**	Mann-Whitney u test; U = 60, p = 0.22	Mann-Whitney u test; U = 89.5, p = 0.55		
	Combined	56.05±11.96		*NA*	**Mann-Whitney u test; U = 257, p = 0.02**	Mann-Whitney u test; U = 244, p = 0.19	Mann-Whitney u test; U = 572.5, p = 0.17		
Erriff	2019	56.13±3.57	Mann-Whitney u test; U = 218, p = 0.05	**Mann-Whitney u test; U = 0, p = 2.21 x 10^{-6}**	Mann-Whitney u test; U = 94, p = 0.91	**Mann-Whitney u test; U = 17, p = 8.76 x 10^{-7}**			
	2020	54.48±2.75		*NA*	**Welch's two sample t-test; t = 4.09, df = 9.33, p = 0.003**	Welch's two sample t-test; t = -1.08, df = 23, p = 0.29			
	Combined	55.61±3.38		*NA*	**Welch's two sample t-test; t = 1.95, df = 15.96, p = 0.07**	**Welch's two sample t-test; t = -3.19, df = 41.31, p = 0.003**			
Owenmore	2019	62.51±2.93	Welch's two sample t-test; t = 5.73, df = 22.92, p = 7.89 x 10^{-6}	**Welch's two sample t-test; t = -4.72, df = 8.07, p = 0.001**	**Welch's two sample t-test; t = 3.36, df = 10.29, p = 0.007**				
	2020	55.72±3.00		*NA*	**Welch's two sample t-test; t = 4.76, df = 9.69, p = 0.0008**				
	Combined	59.98±4.52		*NA*	**Welch's two sample t-test; t = 3.59, df = 20.92, p = 0.002**				
Derrinkee	2019	56.95±3.76	**Welch's two sample t-test; t = 4.56, df = 11.94, p = 0.0007**	**Welch's two sample t-test; t = -6.61, df = 10.65, p = 4.46 x 10^{-5}**					
	2020	47.46±4.03		*NA*					
	Combined	52.21±6.19		*NA*					
Derrycraff	2019	70.87±3.81	*NA*						
	2020	*NA*							
	Combined	*NA*							
Entire Catchment	2019	58.86±5.92	**Mann-Whitney u test; U = 3183, p = 4.85 x 10^{-6}**						
	2020	53.61±8.17							
	Combined	56.57±7.44							

Table A9: Model selection process for equation 1 of table 5.1.

Selection	Formula	AIC	BIC	Covariate(s)	Estimate	Standard error	Z value	P value
Forward	*Spring fry density ~ gravel prop + (1|catchment area) + (1|year)*	1277.8	1292.3	Intercept	18.68	8.74	2.14	**0.033**
				Gravel proportion	38.24	13.72	2.79	**0.005**
Forward	*Spring fry density ~ gravel prop. + macrophyte cover + (1|catchment area) + (1|year)*	1271.2	1288.6	Intercept	5.08	10.20	0.50	0.62
				Gravel proportion	49.06	13.74	3.57	**0.0004**
				Macrophyte cover	64.75	23.49	2.76	**0.006**
Forward	*Spring fry density ~ gravel prop. + macrophyte cover + Julian day + (1|catchment area) + (1|year)*	1268.1	1288.3	Intercept	169.29	69.55	2.43	**0.02**
				Gravel proportion	48.89	13.46	3.63	**0.0003**
				Macrophyte cover	65.91	22.93	2.88	**0.004**
				Julian day	-0.93	0.39	-2.39	**0.02**
Forward	*Spring fry density ~ gravel prop. + macrophyte cover + Julian day + cobble prop. + (1|catchment area) + (1|year)*	1265.9	1289.0	Intercept	59.34	86.24	0.69	0.49
				Gravel proportion	132.63	42.22	3.14	**0.002**
				Macrophyte cover	73.99	22.73	3.26	**0.001**
				Julian day	-0.80	0.39	-2.07	**0.04**
				Cobble proportion	101.29	48.62	2.08	**0.04**
Backward	*Spring fry density ~ gravel prop. + macrophyte cover + Julian day + cobble prop. + mean depth + 1^+ trout + 0^+ trout + 1^+ salmon+ (1|catchment area) + (1|year)*	1272.7	1307.5	Intercept	51.90	90.58	0.57	0.57
				Gravel proportion	142.85	50.34	2.84	**0.005**
				Macrophyte cover	73.25	22.20	3.30	**0.001**
				Julian day	-0.77	0.41	-1.88	**0.06**
				Cobble proportion	114.92	53.94	2.13	**0.03**
				Mean depth	-46.84	58.02	-0.81	0.42
				1^+ trout	0.88	1.53	0.57	0.57
				0^+ trout	0.07	0.30	0.22	0.82
				1^+ salmon	-0.10	0.24	-0.42	0.67
Backward	*Spring fry density ~ gravel prop. + macrophyte cover + Julian day + cobble prop. + mean depth + 1^+ trout + 0^+ trout+ (1|catchment area) + (1|year)*	1270.9	1302.8	Intercept	52.81	90.76	0.58	0.56
				Gravel proportion	149.35	48.02	3.11	**0.002**
				Macrophyte cover	73.53	22.18	3.31	**0.0009**
				Julian day	-0.82	0.39	-2.07	**0.04**
				Cobble proportion	118.09	53.51	2.21	**0.03**
				Mean depth	-40.24	55.69	-0.72	0.47
				1^+ trout	0.83	1.53	0.54	0.59
				0^+ trout	0.06	0.30	0.20	0.84
Backward	*Spring fry density ~ gravel prop. + macrophyte cover + Julian day + cobble prop. + mean depth + 1^+ trout+ (1|catchment area) + (1|year)*	1268.9	1297.9	Intercept	49.36	89.10	0.55	0.8
				Gravel proportion	150.40	47.75	3.15	**0.02**
				Macrophyte cover	73.33	22.16	3.31	**0.001**
				Julian day	-0.80	0.38	-2.08	**0.04**
				Cobble proportion	118.51	53.50	2.22	**0.03**
				Mean depth	-41.21	55.41	-0.74	0.46
				1^+ trout	0.88	1.51	0.58	0.56
Backward	*Spring fry density ~ gravel prop. + macrophyte cover + Julian day + cobble prop. + mean depth+ (1|catchment area) + (1|year)*	1267.3	1293.4	Intercept	62.52	86.22	0.73	0.47
				Gravel proportion	138.09	42.80	3.23	**0.001**
				Macrophyte cover	73.15	22.31	3.28	**0.001**
				Julian day	-0.80	0.38	-2.09	**0.04**
				Cobble proportion	106.05	49.00	2.16	**0.03**
				Mean depth	-42.50	55.56	-0.77	0.44
Backward	*Spring fry density ~ gravel prop. + macrophyte cover + Julian day + cobble prop.+ (1|catchment area) + (1|year)*	1265.9	1289.0	Intercept	59.34	86.24	0.69	0.49
				Gravel proportion	132.63	42.22	3.14	**0.002**
				Macrophyte cover	73.99	22.73	3.26	**0.001**
				Julian day	-0.80	0.39	-2.07	**0.04**
				Cobble proportion	101.29	48.62	2.08	**0.04**

Table A10: Model selection process for equation 2 of table 5.1.

Selection	Formula	AIC	BIC	Covariate(s)	Estimate	Standard error	Z value	P value
Forward	*Spring mean TL ~ Spring fry density+ (1|catchment area) + (1|year)*	507.4	520.4	Intercept	44.10	3.79	11.63	**$< 2 \times 10^{-16}$**
				Spring fry density	-0.04	0.01	-3.02	**0.003**
Forward	*Spring mean TL ~ Spring fry density + gravel prop.+ (1|catchment area) + (1|year)*	487.9	503.6	Intercept	48.14	4.06	11.85	**$< 2 \times 10^{-16}$**
				Spring fry density	-0.03	0.01	-2.98	**0.003**
				Gravel proportion	-6.61	1.34	-4.94	**7.83×10^{-7}**
Forward	*Spring mean TL ~ Spring fry density + gravel prop. + macrophyte cover+ (1|catchment area) + (1|year)*	481.1	499.3	Intercept	46.92	4.03	11.63	**$< 2 \times 10^{-16}$**
				Spring fry density	-0.04	0.01	-3.61	**0.0003**
				Gravel proportion	-5.27	1.35	-3.90	**9.51×10^{-5}**
				Macrophyte cover	6.90	2.27	3.04	**0.002**
Backward	*Spring mean TL ~ Spring fry density + gravel prop. + macrophyte cover + cobble prop. + mean depth + 0^+ trout + 1^+ trout + 1^+ salmon+ (1|catchment area) + (1|year)*	487.3	518.6	Intercept	43.61	7.57	5.76	**8.43×10^{-9}**
				Spring fry density	-0.04	0.01	-4.03	**5.48×10^{-5}**
				Gravel proportion	-0.30	6.40	-0.05	0.96
				Macrophyte cover	6.34	2.30	2.75	**0.006**
				Cobble proportion	5.33	6.53	0.82	0.41
				Mean depth	-7.40	6.71	-1.10	0.27
				0^+ trout density	-0.04	0.08	-0.47	0.64
				1^+ trout density	-0.16	0.19	-0.85	0.40
				1^+ salmon density	0.02	0.03	0.56	0.58
Backward	*Spring mean TL ~ Spring fry density + gravel prop. + macrophyte cover + cobble prop. + mean depth + 1^+ trout + 1^+ salmon+ (1|catchment area) + (1|year)*	485.6	514.2	Intercept	43.89	7.53	5.83	**5.72×10^{-9}**
				Spring fry density	-0.04	0.01	-4.03	**5.62×10^{-5}**
				Gravel proportion	-0.70	6.36	-0.11	0.91
				Macrophyte cover	6.39	2.30	2.77	**0.006**
				Cobble proportion	5.00	6.51	0.77	0.44
				Mean depth	-7.64	6.71	-1.14	0.25
				1^+ trout density	-0.16	0.19	-0.82	0.42
				1^+ salmon density	0.01	0.03	0.45	0.65
Backward	*Spring mean TL ~ Spring fry density + gravel prop. + macrophyte cover + cobble prop. + mean depth + 1^+ trout+ (1|catchment area) + (1|year)*	483.8	509.8	Intercept	45.43	6.71	6.77	**1.30×10^{-11}**
				Spring fry density	-0.04	0.01	-4.01	**6.06×10^{-5}**
				Gravel proportion	-2.02	5.63	-0.36	0.72
				Macrophyte cover	6.29	2.30	2.74	**0.006**
				Cobble proportion	3.90	6.04	0.65	0.52
				Mean depth	-8.73	6.26	-1.39	0.16
				1^+ trout density	-0.14	0.19	-0.76	0.45
Backward	*Spring mean TL ~ Spring fry density + gravel prop. + macrophyte cover + cobble prop. + mean depth+ (1|catchment area) + (1|year)*	482.3	505.8	Intercept	43.28	6.09	7.11	**1.17×10^{-12}**
				Spring fry density	-0.04	0.01	-3.98	**6.90×10^{-5}**
				Gravel proportion	0.16	4.85	0.03	0.97
				Macrophyte cover	6.35	2.30	2.76	**0.006**
				Cobble proportion	6.00	5.37	1.12	0.26
				Mean depth	-9.08	6.26	-1.45	0.15
Backward	*Spring mean TL ~ Spring fry density + gravel prop. + macrophyte cover + mean depth+ (1|catchment area) + (1|year)*	481.6	502.4	Intercept	48.22	4.16	11.60	**$< 2 \times 10^{-16}$**
				Spring fry density	-0.04	0.01	-3.82	**0.0001**
				Gravel proportion	-5.04	1.35	-3.72	**0.002**
				Macrophyte cover	6.22	2.31	2.69	**0.007**
				Mean depth	-7.57	6.16	-1.23	0.22
Backward	*Spring mean TL ~ Spring fry density + gravel prop. + macrophyte cover+ (1|catchment area) + (1|year)*	481.1	499.3	Intercept	46.92	4.03	11.63	**$< 2 \times 10^{-16}$**
				Spring fry density	-0.04	0.01	-3.61	**0.0003**
				Gravel proportion	-5.27	1.35	-3.90	**9.51×10^{-5}**
				Macrophyte cover	6.90	2.27	3.04	**0.002**

Table A11: Model selection process for equation 3 of table 5.1.

Selection	Formula	AIC	BIC	Covariate(s)	Estimate	Standard error	Z value	P value
Forward	_Autumn fry density* ~ Spring fry density + (Spring fry density)^2 + (1|Year)_	1023.5	1037.9	Intercept	2.12	2.97	0.72	0.47
				Spring fry density	0.71	0.11	6.42	**1.38 x 10^{-10}**
				Spring fry density^2	-0.0035	0.001	-3.19	**0.001**
Forward	_Autumn fry density* ~ Spring fry density + (Spring fry density)^2 + cobble prop. + (1|Year)_	1019.2	1036.6	Intercept	-4.59	3.98	-1.15	0.25
				Spring fry density	0.74	0.11	6.80	**1.03 x 10^{-11}**
				Spring fry density^2	-0.004	0.001	-3.37	**0.0007**
				Cobble proportion	15.06	5.93	2.54	**0.01**
Forward	_Autumn fry density* ~ Spring fry density + (Spring fry density)^2 + cobble prop. + Julian day of spring sampling + (1|Year)_	1014.8	1035.0	Intercept	-102.70	28.2	-3.65	**0.0003**
				Spring fry density	0.75	0.11	6.98	**2.99 x 10^{-12}**
				Spring fry density^2	-0.004	0.0011	-3.46	**0.0005**
				Cobble proportion	17.59	5.93	2.96	**0.003**
				Julian day spring	0.55	0.15	3.56	**0.0004**
Forward	_Autumn fry density* ~ Spring fry density + (Spring fry density)^2 + cobble prop. + Julian day of spring sampling + gravel prop. + (1|Year)_	1010.0	1033.1	Intercept	-153.00	33.42	-4.58	**4.67 x 10^{-6}**
				Spring fry density	0.71	0.11	6.73	**1.73 x 10^{-11}**
				Spring fry density^2	-0.003	0.001	-3.24	**0.001**
				Cobble proportion	60.58	17.27	3.51	**0.0005**
				Julian day spring	0.62	0.15	4.04	**5.38 x 10^{-5}**
				Gravel proportion	40.42	15.30	2.64	**0.008**
Forward	_Autumn fry density* ~ Spring fry density + (Spring fry density)^2 + cobble prop. + Julian day of spring sampling + gravel prop. + mean site depth + (1|Year)_	1008.7	1034.8	Intercept	-147.70	33.14	-4.46	**8.36 x 10^{-6}**
				Spring fry density	0.75	0.11	7.04	**2.00 x 10^{-12}**
				Spring fry density^2	-0.004	0.001	-3.58	**0.0003**
				Cobble proportion	61.28	17.1	3.59	**0.0003**
				Julian day spring	0.61	0.15	4.04	**5.34 x 10^{-5}**
				Gravel proportion	41.64	15.13	2.75	**0.006**
				Mean site depth	-33.89	18.59	-1.82	0.07
Forward	_Autumn fry density* ~ Spring fry density + (Spring fry density)^2 + cobble prop. + Julian day of Spring sampling + gravel prop. + mean site depth + 1^+ trout + (1|Year)_	1007.5	1036.5	Intercept	-0.013	34.16	-3.81	**0.0001**
				Spring fry density	0.75	011	7.15	**8.87 x 10^{-13}**
				Spring fry density^2	-0.004	0.001	-3.61	**0.0003**
				Cobble proportion	44.54	19.26	2.31	**0.02**
				Julian day spring	0.61	0.15	4.07	**4.78 x 10^{-5}**
				Gravel proportion	25.84	17.33	1.49	0.14
				Mean site depth	-39.08	18.59	-2.10	**0.04**
				1^+ trout density	-0.96	053	-1.80	0.07
Forward	_Autumn fry density* ~ Spring fry density + (Spring fry density)^2 + cobble prop. + Julian day of Spring sampling + gravel prop. + mean site depth + 1^+ trout + 1^+ salmon + (1|Year)_	1006.7	1038.6	Intercept	-130.30	33.85	-3.85	**0.0001**
				Spring fry density	0.75	0.10	7.21	**5.53 x 10^{-13}**
				Spring fry density^2	-0.004	0.001	-3.67	**0.0002**
				Cobble proportion	53.86	19.87	2.71	**0.007**
				Julian day spring	0.53	0.15	3.44	**0.0006**
				Gravel proportion	37.90	18.62	2.04	**0.04**
				Mean site depth	-32.47	18.83	-1.72	0.08
				1^+ trout density	-1.12	0.54	-2.08	**0.04**
				1^+ salmon density	0.13	0.08	1.67	0.10
Backward	_Autumn fry density* ~ Spring fry density + (Spring fry density)^2 + cobble prop. + Julian day of Spring sampling + gravel prop. + mean site depth + 1^+ trout + 1^+ salmon + macrophyte cover + Julian day of autumn sampling + 0^+ trout + (1|Year)_	1011.8	1052.4	Intercept	-173.50	59.36	-2.92	**0.00**
				Spring fry density	0.75	0.11	6.79	**1.14 x 10^{-11}**
				Spring fry density^2	-0.004	0.0011	-3.47	**0.0005**
				Cobble proportion	51.02	20.89	2.44	**0.01**
				Julian day spring	0.41	0.20	2.10	**0.04**
				Gravel proportion	35.95	20.19	1.78	0.07
				Mean site depth	-29.34	19.80	-1.48	0.14
				1^+ trout density	-1.16	0.6	-2.08	**0.04**
				1^+ salmon density	0.15	0.08	1.87	0.06
				Macrophyte cover	-0.21	6.93	-0.03	0.98
				Julian day autumn	0.03	0.9	0.91	0.36
				0^+ trout density	0.03	0.11	0.28	0.78
Backward		1009.8	1047.5	Intercept	-173.00	57.40	-3.02	**0.003**

	Autumn fry density ~ Spring fry density + (Spring fry density)^2 + cobble prop. + Julian day of Spring sampling + gravel prop. + mean site depth + 1^+ trout + 1^+ salmon + Julian day of autumn sampling + 0^+ trout + (1|Year)*			Spring fry density	0.75	0.10	7.22	**5.31 x 10^{-13}**
				Spring fry density^2	-0.003	0.001	-3.59	**0.0003**
				Cobble proportion	51.20	20.01	2.56	**0.01**
				Julian day spring	0.41	0.20	2.12	**0.03**
				Gravel proportion	36.18	18.79	1.93	**0.05**
				Mean site depth	-29.48	19.28	-1.53	0.13
				1^+ trout density	-1.16	0.54	-2.14	**0.03**
				1^+ salmon density	0.15	0.08	1.88	0.06
				Julian day autumn	0.26	0.27	0.96	0.34
				0^+ trout density	0.03	0.11	0.28	0.78
Backward	*Autumn fry density* ~ Spring fry density + (Spring fry density)^2 + cobble prop. + Julian day of Spring sampling + gravel prop. + mean site depth + 1^+ trout + 1^+ salmon + Julian day of autumn sampling + (1|Year)*	1007.9	1042.6	Intercept	-173.30	57.41	-3.02	**0.003**
				Spring fry density	0.75	0.10	7.24	**4.51 x 10^{-13}**
				Spring fry density^2	-0.004	0.001	-3.62	**0.0003**
				Cobble proportion	51.71	19.94	2.59	**0.009**
				Julian day spring	0.43	0.19	2.28	**0.02**
				Gravel proportion	36.96	18.59	1.99	**0.05**
				Mean site depth	-30.59	18.88	-1.62	0.11
				1^+ trout density	-1.12	0.54	-2.12	**0.03**
				1^+ salmon density	0.15	0.08	1.87	0.06
				Julian day autumn	0.25	0.27	0.93	0.35
Backward	*Autumn fry density* ~ Spring fry density + (Spring fry density)^2 + cobble prop. + Julian day of Spring sampling + gravel prop. + mean site depth + 1^+ trout + 1^+ salmon + (1|Year)*	1006.7	1038.6	Intercept	-130.30	33.85	-3.85	**0.0001**
				Spring fry density	0.75	0.10	7.21	**5.53 x 10^{-13}**
				Spring fry density^2	-0.004	0.001	-3.67	**0.0002**
				Cobble proportion	53.86	19.87	2.71	**0.007**
				Julian day spring	0.53	0.15	3.44	**0.0006**
				Gravel proportion	37.90	18.62	2.04	**0.04**
				Mean site depth	-32.47	18.83	-1.72	0.08
				1^+ trout density	-1.12	0.54	-2.08	**0.04**
				1^+ salmon density	0.13	0.08	1.67	0.10

Table A12: Model selection process for equation 4 of table 5.1

Selection	Formula	AIC	BIC	Covariate(s)	Estimate	Standard error	Z value	P value
Forward	Autumn fry density* ~ Spring fry density by = treatment/control + (Spring fry density)^2 by = treatment/control + (1|Year)	844.7	866.3	Intercept	0.12	3.4	0.03	0.98
				Spring fry density	0.80	0.1	4.89	**1.01 x 10^{-6}**
				Treatment/control; treatment	5.11	4.88	1.05	0.29
				Spring fry density^2	-0.004	0.002	-2.46	**0.01**
				Spring fry density: treatment/control; treatment	-0.32	0.24	-1.37	0.17
				Spring fry density^2: treatment/control; treatment	0.03	0.002	1.08	0.28
Forward	Autumn fry density* ~ Spring fry density by = treatment/control + (Spring fry density)^2 by = treatment/control + Julian day of spring sampling + (1|Year)	841.0	865.2	Intercept	-106.70	32.51	-3.28	**0.001**
				Spring fry density	0.82	0.16	5.05	**4.52 x `10^{-7}**
				Treatment/control; treatment	5.84	4.82	1.21	0.23
				Spring fry density^2	-0.004	0.002	-2.52	**0.01**
				Julian day spring	0.60	0.18	3.32	**0.0009**
				Spring fry density: treatment/control; treatment	-0.35	0.24	-1.48	0.14
				Spring fry density^2: treatment/control; treatment	0.003	0.002	1.16	0.25
Forward	Autumn fry density* ~ Spring fry density by = treatment/control + (Spring fry density)^2 by = treatment/control + Julian day of spring sampling + cobble prop. + (1|Year)	834.4	861.3	Intercept	-133.10	32.48	-4.10	**4.14 x 10^{-5}**
				Spring fry density	0.87	0.16	5.58	**2.48 x 10^{-8}**
				Treatment/control; treatment	4.33	4.67	0.93	0.35
				Spring fry density^2	-0.005	0.002	-2.92	**0.004**
				Julian day spring	0.70	0.18	3.96	**7.52 x 10^{-5}**
				Cobble proportion	21.14	7.07	2.99	**0.003**
				Spring fry density: treatment/control; treatment	-0.37	0.23	-1.65	0.10
				Spring fry density^2: treatment/control; treatment	0.003	0.002	1.44	0.15
Forward	Autumn fry density* ~ Spring fry density by = treatment/control + (Spring fry density)^2 by = treatment/control + Julian day of spring sampling + cobble prop. + 1$^+$ trout + (1|Year)	830.0	859.6	Intercept	-0.01	31.60	-4.36	**1.28 x 10^{-5}**
				Spring fry density	0.81	0.15	5.22	**1.81 x 10^{-7}**
				Treatment/control; treatment	1.16	4.70	0.25	0.80
				Spring fry density^2	-0.004	0.002	-2.61	**0.009**
				Julian day spring	0.74	0.17	4.30	**1.72 x 10^{-5}**
				Cobble proportion	23.07	6.91	3.34	**0.0008**
				1$^+$ trout density	-1.29	0.50	-2.56	**0.01**
				Spring fry density: treatment/control; treatment	-0.27	0.22	-1.21	0.23
				Spring fry density^2: treatment/control; treatment	0.002	0.002	1.10	0.27
Forward	Autumn fry density* ~ Spring fry density by = treatment/control + (Spring fry density)^2 by = treatment/control + Julian day of spring sampling + cobble prop. + 1$^+$ trout + site mean depth + (1|Year)	826.6	858.9	Intercept	-133.20	30.89	-4.31	**1.62 x 10^{-5}**
				Spring fry density	8.60	0.15	5.64	**1.71 x 10^{-8}**
				Treatment/control; treatment	2.46	4.62	0.53	0.59
				Spring fry density^2	-0.004	0.002	-2.91	**0.004**
				Julian day spring	0.76	0.17	4.52	**6.23 x 10^{-6}**
				Cobble proportion	20.47	6.83	3.00	**0.003**
				1$^+$ trout density	-1.44	0.50	-2.90	**0.004**
				Site mean depth	-52.39	22.25	-2.36	**0.02**
				Spring fry density: treatment/control; treatment	-0.27	0.22	-1.24	0.22
				Spring fry density^2: treatment/control; treatment	0.002	0.002	0.98	0.33
Backward	Autumn fry density* ~ Spring fry density by = treatment/control + (Spring fry density)^2 by = treatment/control + Julian day of spring sampling + cobble prop. + 1$^+$ trout + site mean depth + gravel prop + macrophyte cover + Julian day of autumn sampling + 0$^+$ trout + 1$^+$ salmon + (1|Year)	831.4	877.1	Intercept	-206.30	NA	NA	NA
				Spring fry density	0.87	NA	NA	NA
				Treatment/control; treatment	3.44	NA	NA	NA
				Spring fry density^2	-0.004	NA	NA	NA
				Julian day spring	0.59	NA	NA	NA
				Cobble proportion	48.92	NA	NA	NA
				1$^+$ trout density	-1.27	NA	NA	NA
				Site mean depth	-41.20	NA	NA	NA
				Gravel proportion	32.27	NA	NA	NA
				Macrophyte cover	0.20	NA	NA	NA
				Julian day autumn	0.28	NA	NA	NA
				0$^+$ trout density	0.02	NA	NA	NA

				1^+ salmon density	0.17	NA	NA	NA
				Spring fry density: treatment/control; treatment	-0.32	NA	NA	NA
				Spring fry density^2: treatment/control; treatment	0.002	NA	NA	NA
Backward	_Autumn fry density* ~ Spring fry density by = treatment/control + (Spring fry density)^2 by = treatment/control + Julian day of spring sampling + cobble prop. + 1^+ trout + site mean depth + gravel prop + Julian day of autumn sampling + 0^+ trout + 1^+ salmon + (1|Year)_	829.4	872.4	Intercept	-206.70	NA	NA	NA
				Spring fry density	0.87	NA	NA	NA
				Treatment/control; treatment	3.43	NA	NA	NA
				Spring fry density^2	-0.004	NA	NA	NA
				Julian day spring	0.59	NA	NA	NA
				Cobble proportion	48.75	NA	NA	NA
				1^+ trout density	-1.27	NA	NA	NA
				Site mean depth	-41.06	NA	NA	NA
				Gravel proportion	32.06	NA	NA	NA
				Julian day autumn	0.28	NA	NA	NA
				0^+ trout density	0.02	NA	NA	NA
				1^+ salmon density	0.17	NA	NA	NA
				Spring fry density: treatment/control; treatment	-0.32	NA	NA	NA
				Spring fry density^2: treatment/control; treatment	0.002	NA	NA	NA
Backward	_Autumn fry density* ~ Spring fry density by = treatment/control + (Spring fry density)^2 by = treatment/control + Julian day of spring sampling + cobble prop. + 1^+ trout + site mean depth + gravel prop + Julian day of autumn sampling + 1^+ salmon + (1|Year)_	827.4	867.8	Intercept	-206.70	70.54	-2.93	**0.003**
				Spring fry density	0.88	0.15	5.87	**4.49 x 10^{-9}**
				Treatment/control; treatment	3.46	4.53	0.76	0.45
				Spring fry density^2	-0.004	0.002	-3.04	**0.002**
				Julian day spring	0.60	0.22	2.76	**0.006**
				Cobble proportion	49.32	22.13	2.23	**0.03**
				1^+ trout density	-1.25	0.57	-2.19	**0.03**
				Site mean depth	-42.24	22.30	-1.89	0.06
				Gravel proportion	32.90	20.59	1.60	0.11
				Julian day autumn	0.27	0.36	0.77	0.44
				1^+ salmon density	0.17	0.09	1.95	0.05
				Spring fry density: treatment/control; treatment	-0.32	0.21	-1.50	0.13
				Spring fry density^2: treatment/control; treatment	0.002	0.002	1.18	0.24
Backward	_Autumn fry density* ~ Spring fry density by = treatment/control + (Spring fry density)^2 by = treatment/control + Julian day of spring sampling + cobble prop. + 1^+ trout + site mean depth + gravel prop + 1^+ salmon + (1|Year)_	826.0	863.7	Intercept	-160.90	37.76	-4.26	**2.04 x 10^{-5}**
				Spring fry density	0.88	0.15	5.87	**4.43 x 10^{-9}**
				Treatment/control; treatment	3.53	4.55	0.78	0.44
				Spring fry density^2	-0.005	0.001	-3.09	**0.002**
				Julian day spring	0.70	0.17	4.05	5.14 x 10^{-5}
				Cobble proportion	53.95	21.35	2.53	**0.01**
				1^+ trout density	-1.19	0.57	-2.10	**0.04**
				Site mean depth	-45.12	22.04	-2.05	**0.04**
				Gravel proportion	36.60	20.08	1.82	0.07
				1^+ salmon density	0.16	0.09	1.85	0.06
				Spring fry density: treatment/control; treatment	-0.32	0.21	-1.50	0.13
				Spring fry density^2: treatment/control; treatment	0.003	0.002	1.19	0.23

Table A13: Model selection process for equation 5 of table 3.

Selection	Formula	AIC	BIC	Covariate(s)	Estimate	Standard error	Z value	P value
Forward	*Autumn mean TL ~ Spring mean TL + sampling interval + (1|Year)*	396.7	408.7	Intercept	40.91	5.71	7.16	**8.02×10^{-13}**
				Spring mean TL	0.68	0.08	8.53	**$< 2.00 \times 10^{-16}$**
				Sampling interval	-0.20	0.06	-3.46	**0.0005**
Backward	*Autumn mean TL ~ Spring mean TL + sampling interval + cobble prop. + macrophyte cover + spring fry density + post-translocation fry density + autumn fry density + gravel prop. + site mean depth + 0^+ trout + 1^+ trout + 1^+ salmon + (1|Year)*	409.2	445.3	Intercept	33.30	11.95	2.79	**0.005**
				Spring mean TL	0.75	0.14	5.48	**4.30×10^{-8}**
				Sampling interval	-0.16	0.08	-1.88	0.06
				Cobble proportion	-2.10	8.48	-0.25	0.80
				Macrophyte cover	1.42	2.57	0.55	0.58
				Spring fry density	0.02	0.02	1.03	0.30
				Post-translocation fry density	-0.02	0.02	-1.07	0.29
				Autumn fry density	0.02	0.03	0.80	0.42
				Gravel proportion	0.34	8.43	0.04	0.97
				Site mean depth	7.74	7.75	1.00	0.32
				0^+ trout density	0.09	0.09	0.97	0.33
				1^+ trout density	0.06	0.23	0.27	0.79
				1^+ salmon density	-0.02	0.03	-0.71	0.48
Backward	*Autumn mean TL ~ Spring mean TL + sampling interval + cobble prop. + macrophyte cover + spring fry density + post-translocation fry density + autumn fry density + site mean depth + 0^+ trout + 1^+ trout + 1^+ salmon + (1|Year)*	407.2	440.9	Intercept	33.58	9.85	3.41	**0.0006**
				Spring mean TL	0.75	0.14	5.48	**4.30×10^{-8}**
				Sampling interval	-0.16	0.08	-1.95	0.05
				Cobble proportion	-2.43	2.06	-1.18	0.24
				Macrophyte cover	1.39	2.47	0.56	0.57
				Spring fry density	0.02	0.02	1.03	0.30
				Post-translocation fry density	-0.02	0.02	-1.07	0.29
				Autumn fry density	0.02	0.03	0.82	0.41
				Site mean depth	7.73	7.74	1.00	0.32
				0^+ trout density	0.09	0.09	0.98	0.33
				1^+ trout density	0.06	0.22	0.27	0.79
				1^+ salmon density	-0.03	0.03	-0.86	0.39
Backward	*Autumn mean TL ~ Spring mean TL + sampling interval + cobble prop. + macrophyte cover + spring fry density + post-translocation fry density + autumn fry density + site mean depth + 0^+ trout + 1^+ salmon + (1|Year)*	405.3	436.6	Intercept	33.79	9.83	3.44	**0.0006**
				Spring mean TL	0.74	0.14	5.50	**3.91×10^{-8}**
				Sampling interval	-0.16	0.08	-1.96	0.05
				Cobble proportion	-2.39	2.06	-1.16	0.25
				Macrophyte cover	1.43	2.47	0.58	0.56
				Spring fry density	0.02	0.02	1.05	0.29
				Post-translocation fry density	-0.02	0.02	-1.04	0.30
				Autumn fry density	0.02	0.03	0.77	0.44
				Site mean depth	8.10	7.63	1.06	0.29
				0^+ trout density	0.09	0.09	0.99	0.32
				1^+ salmon density	-0.02	0.03	-0.84	0.40
Backward	*Autumn mean TL ~ Spring mean TL + sampling interval + cobble prop. + spring fry density + post-translocation fry density + autumn fry density + site mean depth + 0^+ trout + 1^+ salmon + (1|Year)*	403.6	432.5	Intercept	31.10	8.67	3.59	**0.0003**
				Spring mean TL	0.79	0.10	7.71	**1.25×10^{-14}**
				Sampling interval	-0.15	0.08	-1.87	0.06
				Cobble proportion	-2.57	2.03	-1.27	0.21
				Spring fry density	0.02	0.02	1.13	0.26
				Post-translocation fry density	-0.02	0.02	-1.16	0.25
				Autumn fry density	0.02	0.03	0.89	0.37
				Site mean depth	7.97	7.62	1.05	0.30
				0^+ trout density	0.08	0.09	0.89	0.37
				1^+ salmon density	-0.02	0.03	-0.84	0.40
Backward	*Autumn mean TL ~ Spring mean TL + sampling interval + cobble prop. + spring fry density + post-translocation fry density + autumn fry density + site mean depth + 0^+ trout + (1|Year)*	402.3	428.8	Intercept	29.72	8.55	3.48	**0.0005**
				Spring mean TL	0.78	0.10	7.63	**2.30×10^{-14}**
				Sampling interval	-0.13	0.07	-1.68	0.09
				Cobble proportion	-2.90	2.00	-1.45	0.15
				Spring fry density	0.017	0.02	1.02	0.31

				Post-translocation fry density	-0.02	0.02	-1.06	0.29
				Autumn fry density	0.026	0.03	0.96	0.34
				Site mean depth	10.69	6.95	1.54	0.12
				0^{+} trout density	0.06	0.09	0.73	0.47
Backward	*Autumn mean TL ~ Spring mean TL + sampling interval + cobble prop. + spring fry density + post-translocation fry density + autumn fry density + site mean depth + (1|Year)*	400.9	424.9	Intercept	32.21	7.87	4.09	**4.27 x 10^{-5}**
				Spring mean TL	0.75	0.10	7.82	**5.32 x 10^{-15}**
				Sampling interval	-0.15	0.07	-2.10	**0.04**
				Cobble proportion	-2.74	2.00	-1.37	0.17
				Spring fry density	0.016	0.02	0.97	0.33
				Post-translocation fry density	-0.02	0.02	-1.07	0.28
				Autumn fry density	0.03	0.03	1.14	0.25
				Site mean depth	10.83	6.97	1.55	0.12
Backward	*Autumn mean TL ~ Spring mean TL + sampling interval + cobble prop. + post-translocation fry density + autumn fry density + site mean depth + (1|Year)*	399.8	421.5	Intercept	33.11	7.86	4.21	**2.54 10^{-5}**
				Spring mean TL	0.75	0.10	7.76	**8.58 x 10^{-15}**
				Sampling interval	-0.15	0.07	-2.19	**0.03**
				Cobble proportion	-2.90	2.00	-1.45	0.15
				Post-translocation fry density	-0.008	0.01	-0.58	0.56
				Autumn fry density	0.035	0.03	1.34	0.18
				Site mean depth	10.47	7.00	1.50	0.13
Backward	*Autumn mean TL ~ Spring mean TL + sampling interval + cobble prop. + autumn fry density + site mean depth + (1|Year)*	398.1	417.4	Intercept	32.08	7.67	4.18	**2.88 x 10^{-5}**
				Spring mean TL	0.75	0.10	7.81	**5.54 x 10^{-15}**
				Sampling interval	-0.15	0.07	-2.12	**0.03**
				Cobble proportion	-2.78	2.00	-1.39	0.16
				Autumn fry density	0.03	0.02	1.21	0.23
				Site mean depth	10.96	6.97	1.57	0.12
Backward	*Autumn mean TL ~ Spring mean TL + sampling interval + cobble prop. + site mean depth + (1|Year)*	397.6	414.4	Intercept	37.95	6.00	6.33	**2.54 x 10^{-10}**
				Spring mean TL	0.71	0.09	7.75	**9.14 x 10^{-15}**
				Sampling interval	-0.19	0.06	-3.21	**0.001**
				Cobble proportion	-2.19	1.96	-1.12	0.26
				Site mean depth	8.66	6.78	1.28	0.20
Backward	*Autumn mean TL ~ Spring mean TL + sampling interval + site mean depth + (1|Year)*	396.8	411.2	Intercept	40.28	5.66	7.12	**1.10 x 10^{-12}**
				Spring mean TL	0.66	0.08	8.23	**< 2.00 x 10^{-16}**
				Sampling interval	-0.20	0.06	-3.54	**0.0004**
				Site mean depth	9.32	6.82	1.37	0.17
Backward	*Autumn mean TL ~ Spring mean TL + sampling interval + (1|Year)*	396.7	408.7	Intercept	40.91	5.71	7.16	**8.02 x 10^{-13}**
				Spring mean TL	0.68	0.08	8.53	**< 2.00 x 10^{-16}**
				Sampling interval	-0.20	0.06	-3.46	**0.0005**

Appendix 5

Table A1: Habitat data summary and comparison between treatments, outlining the results of univariate and principal component analyses. Principal components with weighting absolute values equal to or greater than 0.3 are shown in bold

	PCA component		Mean (± SD)		Comparison	Mean (± SD)		Comparison
	1	2	HDS	HDC		LDR	LDC	
Total variance explained (%)	42.0	21.2						
Mean site depth (cm)	-0.11	**0.67**	0.14 (±0.03)	0.17 (±0.03)	Welch’s two sample t-test; $t = -1.88$, $df = 11.99$, $p = 0.08$	0.17 (±0.05)	0.16 (±0.05)	Mann-Whitney u test; $U = 998.5$, $p = 0.40$
Sand/silt proportion	**0.41**	0.17	0.02 (±0.01)	0.04 (±0.03)	Mann-Whitney u test; $U = 12.5$, $p = 0.07$	0.0004 (±0.003)	0.0009 (±0.005)	Mann-Whitney u test; $U = 882.5$, $p = 0.59$
Gravel proportion	**0.46**	0.22	0.28 (±0.19)	0.20 (±0.09)	Welch’s two sample t-test; $t = 1.00$, $df = 8.54$, $p = 0.34$	0.07 (±0.04)	0.08 (±0.03)	Mann-Whitney u test; $U = 700.5$, $p = 0.08$
Cobble proportion	**0.46**	-0.15	0.49 (±0.11)	0.42 (±0.14)	Welch’s two sample t-test; $t = 1.00$, $df = 11.12$, $p = 0.34$	0.22 (±0.08)	0.20 (±0.05)	Mann-Whitney u test; $U = 1001$, $p = 0.38$
Boulder proportion	**-0.50**	-0.14	0.23 (±0.20)	0.31 (±0.20)	Welch’s two sample t-test; $t = -0.79$, $df = 12$, $p = 0.44$	0.67 (±0.09)	0.69 (±0.07)	Mann-Whitney u test; $U = 838.5$, $p = 0.61$
Bedrock proportion	-0.13	**0.33**	0 (±0)	0.02 (±0.06)	Mann-Whitney u test; $U = 21$, $p = 0.39$	0.04 (±0.07)	0.04 (±0.09)	Mann-Whitney u test; $U = 972.5$, $p = 0.48$
Macrophyte cover proportion	**0.34**	0.08	0.27 (±0.26)	0.19 (±0.23)	Welch’s two sample t-test; $t = 0.60$, $df = 11.78$, $p = 0.56$	0 (±0)	0 (±0)	NA
Riffle & glide proportion	0.15	**-0.57**	0.95 (±0.10)	0.86 (±0.15)	Mann-Whitney u test; $U = 39$, $p = 0.07$	0.75 (±0.30)	0.63 (±0.43)	Mann-Whitney u test; $U = 1005.5$, $p = 0.36$
June 1^+ salmon density (fish 100 m^{-2})	N/A	N/A	10.14 (±3.72)	17.29 (±17.34)	Welch’s two sample t-test; $t = -1.07$, $df = 6.55$, $p = 0.32$	8.95 (±5.66)	11.0 (±6.81)	Mann-Whitney u test; $U = 721.5$, $p = 0.13$
June 0^+ trout density (fish 100 m^{-2})	N/A	N/A	1.29 (±1.80)	2.71 (±3.73)	Mann-Whitney u test; $U = 21$, $p = 0.69$	1.60 (±2.08)	2.76 (±3.73)	Mann-Whitney u test; $U = 808$, $p = 0.42$
June 1^+-adult trout density (fish 100 m^{-2})	N/A	N/A	0 (±0)	0.43 (±1.13)	Mann-Whitney u test; $U = 21$, $p = 0.39$	1.21 (±2.22)	1.0 (±1.41)	Mann-Whitney u test; $U = 887$, $p = 0.91$
PC1			-4.43 (±1.81)	-3.79 (±1.90)	Welch’s two sample t-test; $t = -0.64$, $df = 11.97$, $p = 0.53$	0.60 (±0.63)	0.70 (±0.56)	Mann-Whitney u test; $U = 844$, $p = 0.64$
PC2			-0.06 (±0.66)	-0.70 (±0.82)	Welch’s two sample t-test; $t = 1.60$, $df = 11.50$, $p = 0.14$	0.10 (±1.31)	0.03 (±1.48)	Mann-Whitney u test; $U = 926$, $p = 0.82$

Table A2: Model selection process for the model shown by equation 1 of Table 6.2

Selection	Formula	AIC	BIC	Covariate(s)	Estimate	Standard error	Z value	P value
Forward	*Autumn fry density ~ pre-translocation fry density*	856.8	864.3	Intercept	31.14	3.71	8.40	**$< 2 \times 10^{-16}$**
				Pre-translocation fry density	1.76	0.25	7.15	**8.93×10^{-13}**
Forward	*Autumn fry density ~ pre-translocation fry density + riffle & glide proportion*	824.9	834.9	Intercept	3.80	5.26	0.72	0.47
				Pre-translocation fry density	1.40	0.21	6.63	**3.27×10^{-11}**
				Riffle & glide proportion	43.58	6.79	6.42	**1.40×10^{-10}**
Forward	*Autumn fry density ~ pre-translocation fry density + riffle & glide proportion + pre-translocation fry density^2*	817.3	829.9	Intercept	1.26	5.05	0.25	0.80
				Pre-translocation fry density	3.02	0.55	5.51	**3.66×10^{-8}**
				Riffle & glide proportion	37.24	6.75	5.52	**3.40×10^{-8}**
				Pre-translocation density^2	-0.04	0.01	-3.17	**0.002**
Forward	*Autumn fry density ~ pre-translocation fry density + riffle & glide proportion + pre-translocation fry density^2 + pre-translocation trout fry density*	812.8	827.9	Intercept	3.38	4.94	0.69	0.49
				Pre-translocation fry density	3.17	0.53	5.96	**2.52×10^{-9}**
				Riffle & glide proportion	37.50	6.51	5.76	**8.47×10^{-9}**
				Pre-translocation density^2	-0.04	0.01	-3.16	**0.002**
				Pre-translocation trout fry density	-2.15	0.83	-2.60	**0.009**
Forward	*Autumn fry density ~ pre-translocation fry density + riffle & glide proportion + pre-translocation fry density^2 + pre-translocation trout fry density + stream reach*	811.6	834.2	Intercept	-7.16	6.50	-1.10	0.27
				Pre-translocation fry density	3.69	0.59	6.24	**4.50×10^{-10}**
				Riffle & glide proportion	38.33	6.57	5.84	**5.29×10^{-9}**
				Pre-translocation density^2	-0.05	0.01	-3.70	**0.0002**
				Pre-translocation trout fry density	-2.91	0.85	-3.42	**0.0006**
				Glendavoc LDC reach	13.23	6.57	2.02	**0.04**
				Sheeffry LDR reach	13.71	5.68	2.41	**0.02**
				Sheeffry LDC reach	5.33	6.71	0.79	0.43
Forward	*Autumn fry density ~ pre-translocation fry density + riffle & glide proportion + pre-translocation fry density^2 + pre-translocation trout fry density + stream reach + pre-translocation 1^+ trout density*	807.5	832.6	Intercept	-5.55	6.32	-0.88	0.38
				Pre-translocation fry density	3.82	0.57	6.64	**3.16×10^{-11}**
				Riffle & glide proportion	37.51	6.36	5.90	**3.65×10^{-9}**
				Pre-translocation density^2	-0.05	0.01	-3.99	**6.53×10^{-5}**
				Pre-translocation trout fry density	-3.42	0.85	-4.04	**5.46×10^{-5}**
				Glendavoc LDC reach	16.43	6.48	2.54	**0.01**
				Sheeffry LDR reach	17.94	5.75	3.12	**0.002**
				Sheeffry LDC reach	6.06	6.50	0.93	0.35
				Pre-translocation 1^+ trout density	-2.63	1.05	-2.51	**0.01**
Forward	*Autumn fry density ~ pre-translocation fry density + riffle & glide proportion + pre-translocation fry density^2 + pre-translocation trout fry density + stream reach + pre-translocation 1^+ trout density + gravel proportion*	805.5	833.1	Intercept	4.13	7.80	0.53	0.60
				Pre-translocation fry density	3.85	0.56	6.85	**7.23×10^{-12}**
				Riffle & glide proportion	32.83	6.63	4.95	**7.27×10^{-7}**
				Pre-translocation density^2	-0.05	0.01	-4.14	**3.55×10^{-5}**
				Pre-translocation trout fry density	-3.62	0.83	-4.33	**1.46×10^{-5}**
				Glendavoc LDC reach	19.26	6.48	2.97	**0.003**
				Sheeffry LDR reach	22.34	6.02	3.71	**0.0003**
				Sheeffry LDC reach	10.08	6.65	1.51	0.13
				Pre-translocation 1^+ trout density	-2.29	1.04	-2.21	**0.03**
				Gravel proportion	-134.48	66.03	-2.04	**0.04**
Forward	*Autumn fry density ~ pre-translocation fry density + riffle & glide proportion + pre-translocation fry density^2 + pre-translocation trout fry density + stream reach + pre-translocation 1^+ trout density + gravel proportion +pre-translocation 1^+ salmon density*	803.2	833.4	Intercept	8.73	7.93	1.10	0.27
				Pre-translocation fry density	4.21	0.58	7.31	**2.60×10^{-13}**
				Riffle & glide proportion	35.75	6.63	5.40	**6.87×10^{-8}**
				Pre-translocation density^2	-0.06	0.01	-4.53	**6.05×10^{-6}**
				Pre-translocation trout fry density	-3.84	0.82	-4.67	**3.02×10^{-6}**
				Glendavoc LDC reach	23.36	6.64	3.52	**0.0004**
				Sheeffry LDR reach	23.65	5.92	4.00	**6.45×10^{-5}**
				Sheeffry LDC reach	10.12	6.50	1.56	0.12
				Pre-translocation 1^+ trout density	-1.85	1.04	-1.79	0.07
				Gravel proportion	-169.67	66.71	-2.54	**0.01**
				Pre-translocation 1^+ salmon density	-0.85	0.41	-2.08	**0.04**
Backward	*Autumn fry density ~ pre-translocation fry density + riffle & glide proportion + pre-translocation fry density^2 + pre-translocation trout fry density + stream reach + pre-translocation 1^+ trout density + gravel proportion +pre-translocation 1^+ salmon density + cobble proportion + mean depth*	806.5	841.7	Intercept	21.29	17.84	1.19	0.23
				Pre-translocation fry density	4.23	0.58	7.34	**2.20×10^{-13}**
				Riffle & glide proportion	32.86	8.12	4.05	**5.16×10^{-5}**
				Pre-translocation density^2	-0.06	0.01	-4.59	**4.50×10^{-6}**
				Pre-translocation trout fry density	-3.83	0.82	-4.66	**3.10×10^{-6}**
				Glendavoc LDC reach	22.81	7.03	3.25	**0.001**
				Sheeffry LDR reach	25.38	7.19	3.53	**0.0004**
				Sheeffry LDC reach	9.97	6.87	1.45	0.15
				Pre-translocation 1^+ trout density	-2.01	1.05	-1.92	0.06
				Gravel proportion	-162.96	68.19	-2.39	0.02
				Pre-translocation 1^+ salmon density	-0.85	0.41	-2.06	0.04
				Cobble proportion	-20.69	29.46	-0.70	0.48
				Mean depth	-42.34	66.70	-0.64	0.53
Backward	*Autumn fry density ~ pre-translocation fry density + riffle & glide proportion + pre-translocation fry density^2 + pre-translocation trout fry density + stream reach + pre-translocation 1^+ trout*	804.9	837.6	Intercept	11.68	9.46	1.23	0.22
				Pre-translocation fry density	4.24	0.58	7.35	**2.02×10^{-13}**
				Riffle & glide proportion	35.85	6.62	5.42	**6.03×10^{-8}**
				Pre-translocation density^2	-0.06	0.01	-4.55	**5.43×10^{-6}**

	density + gravel proportion +pre-translocation 1$^+$ salmon density + cobble proportion			Pre-translocation trout fry density	-3.82	0.82	-4.65	**3.37 x 10^{-6}**
				Glendavoc LDC reach	22.13	6.96	3.18	**0.001**
				Sheeffry LDR reach	22.90	6.05	3.78	**0.0002**
				Sheeffry LDC reach	9.08	6.74	1.35	0.18
				Pre-translocation 1$^+$ trout density	-1.92	1.04	-1.85	0.06
				Gravel proportion	-161.10	68.28	-2.36	**0.02**
				Pre-translocation 1$^+$ salmon density	-0.81	0.41	-1.98	**0.05**
				Cobble proportion	-16.31	28.70	-0.57	0.57
Backward	*Autumn fry density ~ pre-translocation fry density + riffle & glide proportion + pre-translocation fry density^2 + pre-translocation trout fry density + stream reach + pre-translocation 1$^+$ trout density + gravel proportion +pre-translocation 1$^+$ salmon density*	803.2	833.4	Intercept	8.73	7.93	1.10	0.27
				Pre-translocation fry density	4.21	0.58	7.31	**2.60 x 10^{-13}**
				Riffle & glide proportion	35.74641	6.63	5.40	**6.87 x 10^{-8}**
				Pre-translocation density^2	-0.06	0.01	-4.53	**6.05 x 10^{-6}**
				Pre-translocation trout fry density	-3.84	0.82	-4.67	**3.02 x 10^{-6}**
				Glendavoc LDC reach	23.36	6.64	3.52	**0.0004**
				Sheeffry LDR reach	23.65	5.92	4.00	**6.45 x 10^{-5}**
				Sheeffry LDC reach	10.12	6.50	1.56	0.12
				Pre-translocation 1$^+$ trout density	1.85	1.04	-1.79	0.07
				Gravel proportion	-169.67	66.71	-2.54	**0.01**
				Pre-translocation 1$^+$ salmon density	-0.85	0.41	-2.08	**0.04**

Table A3: Model selection process for the model shown by equation 2 of Table 6.2

Selection	Formula	AIC	BIC	Covariate(s)	Estimate	Standard error	Z value	P value
Forward	*Autumn fry density ~ pre-translocation fry density * autumn translocated fry density*	558.7	569.3	Intercept	19.47	4.31	4.52	**6.15 x 10^{-6}**
				Pre-translocation fry density	2.90	0.43	6.72	**1.83 x 10^{-11}**
				Translocated autumn fry density	1.47	0.39	3.81	**0.0001**
				Interaction term	-0.09	0.03	-2.39	**0.02**
Forward	*Autumn fry density ~ pre-translocation fry density * autumn translocated fry density + cobble proportion*	553.2	566.0	Intercept	37.48	7.59	4.94	**7.78 x 10^{-7}**
				Pre-translocation fry density	3.15	0.42	7.57	**3.71 x 10^{-14}**
				Translocated autumn fry density	1.53	0.37	4.18	**2.97 x 10^{-5}**
				Cobble proportion	-95.20	33.88	-2.81	**0.005**
				Interaction term	-0.08	0.03	-2.21	**0.03**
Forward	*Autumn fry density ~ pre-translocation fry density * autumn translocated fry density + cobble proportion + riffle & glide proportion*	550.7	565.6	Intercept	25.11	9.26	2.71	**0.007**
				Pre-translocation fry density	2.77	0.44	6.31	**2.89 x 10^{-10}**
				Translocated autumn fry density	1.25	0.37	3.36	**0.0008**
				Cobble proportion	-88.22	32.82	-2.69	**0.007**
				Riffle & glide proportion	19.68	9.05	2.18	**0.03**
				Interaction term	-0.06	0.03	-1.77	0.08
Backward	*Autumn fry density ~ pre-translocation fry density * autumn translocated fry density + cobble proportion + riffle & glide proportion + pre-translocation fry density^{2} + gravel proportion + mean depth + pre-translocation trout fry density + pre-translocation 1^{+} trout density + pre-translocation 1^{+} salmon density + stream reach*	549.1	578.9	Intercept	31.52	20.42	1.54	0.12
				Pre-translocation fry density	5.10	1.09	4.67	**2.96 x 10^{-6}**
				Translocated autumn fry density	0.83	0.35	2.40	**0.02**
				Cobble proportion	-54.34	31.64	-1.72	0.09
				Riffle & glide proportion	17.07	11.25	1.52	0.13
				Pre-translocation fry density^{2}	-0.06	0.04	-1.60	0.11
				Gravel proportion	-220.15	76.27	-2.89	0.004
				Mean depth	-9.46	75.05	-0.13	0.90
				Pre-translocation trout fry density	-2.61	1.21	-2.17	**0.03**
				Pre-translocation 1^{+} trout density	-1.35	1.11	-1.21	0.22
				Pre-translocation 1^{+} salmon density	-1.03	0.53	-1.94	0.05
				Sheeffry LDR reach	22.20	8.28	2.68	**0.007**
				Interaction term	-0.07	0.03	-2.11	**0.03**
Backward	*Autumn fry density ~ pre-translocation fry density * autumn translocated fry density + cobble proportion + riffle & glide proportion + pre-translocation fry density^{2} + gravel proportionpre-translocation trout fry density + pre-translocation 1^{+} trout density + pre-translocation 1^{+} salmon density + stream reach*	547.1	574.8	Intercept	29.32	10.62	2.76	**0.006**
				Pre-translocation fry density	5.11	1.09	4.71	**2.44 x 10^{-6}**
				Translocated autumn fry density	0.83	0.35	2.40	**0.02**
				Cobble proportion	-53.52	30.97	-1.73	0.08
				Riffle & glide proportion	17.84	9.47	1.88	0.06
				Pre-translocation fry density^{2}	-0.06	0.04	-1.64	0.10
				Gravel proportion	-218.61	75.29	-2.90	**0.004**
				Pre-translocation trout fry density	-2.60	1.20	-2.17	**0.03**
				Pre-translocation 1^{+} trout density	-1.33	1.10	-1.21	0.23
				Pre-translocation 1^{+} salmon density	-1.03	0.53	-1.94	0.05
				Sheeffry LDR reach	21.57	6.60	3.27	**0.001**
				Interaction term	-0.07	0.03	-2.11	**0.03**
Backward	*Autumn fry density ~ pre-translocation fry density * autumn translocated fry density + cobble proportion + riffle & glide proportion + pre-translocation fry density^{2} + gravel proportionpre-translocation trout fry density + pre-translocation 1^{+} salmon density + stream reach*	546.6	572.1	Intercept	30.26	10.71	2.83	**0.005**
				Pre-translocation fry density	4.93	1.09	4.53	**5.79 x 10^{-6}**
				Translocated autumn fry density	0.90	0.35	2.61	**0.01**
				Cobble proportion	-51.90	31.31	-1.66	0.10
				Riffle & glide proportion	16.78	9.54	1.76	0.08
				Pre-translocation fry density^{2}	-0.06	0.04	-1.51	0.13
				Gravel proportion	-238.02	74.42	-3.20	**0.001**
				Pre-translocation trout fry density	-2.31	1.19	-1.94	0.05
				Pre-translocation 1^{+} salmon density	-1.04	0.54	-1.94	0.05
				Sheeffry LDR reach	19.84	6.52	3.04	**0.002**
				Interaction term	-0.06	0.03	-2.04	**0.04**

Table A4: Model selection process for the model shown by equation 3 of Table 6.2

Selection	Formula	AIC	BIC	Covariate(s)	Estimate	Standard error	Z value	P value
Forward	*Log$_n$(non-translocated salmon fry autumn density/ pre-translocation salmon fry density) ~ pre-translocation salmon fry density*	77.3	85.1	Intercept	2.33	0.12	19.75	**< 2 x 10^{-16}**
				Pre-translocation fry density	-0.06	0.01	-6.67	**2.58 x 10^{-11}**
Forward	*Log$_n$(non-translocated salmon fry autumn density/ pre-translocation salmon fry density) ~ pre-translocation salmon fry density + cobble proportion*	73.8	86.7	Intercept	2.73	0.20	13.66	**<2 x 10^{-16}**
				Pre-translocation fry density	-0.06	0.01	-5.82	**6.05e-09**
				Cobble proportion	-2.06	0.86	-2.41	**0.02**
Forward	*Log$_n$(non-translocated salmon fry autumn density/ pre-translocation salmon fry density) ~ pre-translocation salmon fry density + cobble proportion + mean depth*	73.7	87.1	Intercept	2.17	0.43	5.01	**5.41 x 10^{-7}**
				Pre-translocation fry density	-0.05	0.01	-4.52	**6.13 x 10^{-7}**
				Cobble proportion	-1.70	0.88	-1.94	**0.05**
				Mean depth	2.59	1.80	1.44	0.15
Forward	*Log$_n$(non-translocated salmon fry autumn density/ pre-translocation salmon fry density) ~ pre-translocation salmon fry density + cobble proportion + mean depth + gravel proportion*	72.5	83.8	Intercept	2.24	0.42	5.32	**1.03 x 10^{-7}**
				Pre-translocation fry density	-0.05	0.01	-4.89	**1.02 x 10^{-6}**
				Cobble proportion	-1.47	0.86	-1.72	0.09
				Mean depth	3.37	1.79	1.88	0.06
				Gravel proportion	-3.43	1.86	-1.84	0.07
Backward	*Log$_n$(non-translocated salmon fry autumn density/ pre-translocation salmon fry density) ~ pre-translocation salmon fry density + cobble proportion + mean depth + gravel proportion + riffle & glide proportion + translocated autumn fry density + pre-translocation trout fry density + pre-translocation 1^+ trout density + pre-translocation 1^+ salmon density + stream reach*	76.6	92.2	Intercept	2.19	0.65	3.39	**0.0007**
				Pre-translocation fry density	-0.04	0.01	-3.57	**0.0004**
				Cobble proportion	-0.81	0.86	-0.95	0.34
				Mean depth	2.72	2.65	1.03	0.31
				Gravel proportion	-4.69	2.39	-1.96	**0.05**
				Riffle & glide proportion	0.34	0.35	0.96	0.34
				Translocated autumn fry density	-0.01	0.01	-1.93	**0.05**
				Pre-translocation trout fry density	-0.06	0.03	-2.01	**0.04**
				Pre-translocation 1^+ trout density	-0.04	0.03	-1.17	0.24
				Pre-translocation 1^+ salmon density	-0.02	0.01	-1.40	0.16
				Sheeffry LDR reach	0.31	0.28	1.11	0.27
Backward	*Log$_n$(non-translocated salmon fry autumn density/ pre-translocation salmon fry density) ~ pre-translocation salmon fry density + mean depth + gravel proportion + riffle & glide proportion + translocated autumn fry density + pre-translocation trout fry density + pre-translocation 1^+ trout density + pre-translocation 1^+ salmon density + stream reach*	75.5	96.3	Intercept	1.98	0.61	3.23	**0.001**
				Pre-translocation fry density	-0.04	0.01	-3.64	**0.0003**
				Mean depth	3.19	2.63	1.21	0.22
				Gravel proportion	-5.26	2.34	-2.25	**0.02**
				Riffle & glide proportion	0.37	0.36	1.04	0.30
				Translocated autumn fry density	-0.01	0.01	-2.23	**0.03**
				Pre-translocation trout fry density	-0.07	0.03	-2.23	**0.03**
				Pre-translocation 1^+ trout density	-0.03	0.03	-1.04	0.30
				Pre-translocation 1^+ salmon density	-0.02	0.01	-1.57	0.12
				Sheeffry LDR reach	0.32	0.28	1.15	0.25
Backward	*Log$_n$(non-translocated salmon fry autumn density/ pre-translocation salmon fry density) ~ pre-translocation salmon fry density + mean depth + gravel proportion + riffle & glide proportion + translocated autumn fry density + pre-translocation trout fry density + pre-translocation 1^+ salmon density + stream reach*	74.5	93.4	Intercept	2.07	0.61	3.37	**0.0008**
				Pre-translocation fry density	-0.04	0.01	-3.78	**0.0002**
				Mean depth	2.97	2.65	1.12	0.26
				Gravel proportion	-6.05	2.23	-2.71	**0.01**
				Riffle & glide proportion	0.31	0.36	0.89	0.38
				Translocated autumn fry density	-0.01	0.01	-2.00	**0.05**
				Pre-translocation trout fry density	-0.06	0.03	-2.04	**0.04**
				Pre-translocation 1^+ salmon density	-0.02	0.01	-1.54	0.12
				Sheeffry LDR reach	0.30	0.28	1.08	0.278674
Backward	*Log$_n$(non-translocated salmon fry autumn density/ pre-translocation salmon fry density) ~ pre-translocation salmon fry density + mean depth + gravel proportion + translocated autumn fry density + pre-translocation trout fry density + pre-translocation 1^+ salmon density + stream reach*	73.3	90.3	Intercept	2.46	0.43	5.65	1.59e-08
				Pre-translocation fry density	-0.04	0.01	-3.67	0.000248
				Mean depth	1.85	2.35	0.79	0.429680
				Gravel proportion	-6.87	2.05	-3.35	0.000815
				Translocated autumn fry density	-0.01	0.01	-1.93	0.053957
				Pre-translocation trout fry density	-0.07	0.03	-2.23	0.025963
				Pre-translocation 1^+ salmon density	-0.02	0.01	-1.36	0.172652
				Sheeffry LDR reach	0.42	0.25	1.68	0.092504
Backward	*Log$_n$(non-translocated salmon fry autumn density/ pre-translocation salmon fry density) ~ pre-translocation salmon fry density + gravel proportion + translocated autumn fry density + pre-translocation trout fry density + pre-translocation 1^+ salmon density + stream reach*	71.9	87.1	Intercept	2.73	0.27	10.12	< 2e-16
				Pre-translocation fry density	-0.04	0.01	-3.65	0.000260
				Gravel proportion	-7.11	2.04	-3.49	0.000491
				Translocated autumn fry density	-0.01	0.01	-2.10	0.036066
				Pre-translocation trout fry density	-0.07	0.03	-2.26	0.023651
				Pre-translocation 1^+ salmon density	-0.02	0.01	-1.60	0.108909
				Sheeffry LDR reach	0.56	0.18	3.08	0.002069

Table A5: Model selection process for the model shown by equation 4 of Table 6.2

Selection	Formula	AIC	BIC	Covariate(s)	Estimate	Standard error	Z value	P value
Forward	*Autumn mean non-translocated fry TL ~ pre-translocation fry TL*	342.9	348.7	Intercept	35.50	14.79	**2.40**	**0.02**
				Pre-translocation mean TL	0.76	0.42	1.79	0.07
Forward	*Autumn mean non-translocated fry TL ~ pre-translocation fry TL + pre-translocation 1^+ salmon density*	334.4	342.1	Intercept	15.92	14.50	1.10	0.27
				Pre-translocation mean TL	1.17	0.40	2.92	**0.004**
				Pre-translocation 1^+ salmon density	0.54	0.16	3.43	**0.0006**
Forward	*Autumn mean non-translocated fry TL ~ pre-translocation fry TL + pre-translocation 1^+ salmon density + stream reach*	333.4	343.1	Intercept	10.45	14.44	0.72	0.47
				Pre-translocation mean TL	1.27	0.39	3.22	**0.001**
				Pre-translocation 1^+ salmon density	0.61	0.16	3.87	**0.0001**
				Sheeffry LDR reach	2.91	1.68	1.74	0.08
Forward	*Autumn mean non-translocated fry TL ~ pre-translocation fry TL + pre-translocation 1^+ salmon density + stream reach + riffle & glide proportion*	332.8	344.4	Intercept	4.12	14.58	0.28	0.78
				Pre-translocation mean TL	1.33	0.39	3.44	**0.0006**
				Pre-translocation 1^+ salmon density	0.52	0.16	3.18	**0.001**
				Sheeffry LDR reach	3.09	1.64	1.89	0.06
				Riffle & glide proportion	6.13	3.71	1.65	0.10
Forward	*Autumn mean non-translocated fry TL ~ pre-translocation fry TL + pre-translocation 1^+ salmon density + stream reach + riffle & glide proportion + non-translocated autumn fry density*	331.8	345.4	Intercept	8.42	14.38	0.59	0.56
				Pre-translocation mean TL	1.24	0.38	3.30	**0.001**
				Pre-translocation 1^+ salmon density	0.54	0.16	3.38	**0.0007**
				Sheeffry LDR reach	2.66	1.61	1.65	0.10
				Riffle & glide proportion	7.30	3.67	1.99	0.05
				Non-translocated autumn fry density	-0.05	0.03	-1.74	0.08
Backward	*Autumn mean non-translocated fry TL ~ pre-translocation fry TL + pre-translocation 1^+ salmon density + stream reach + riffle & glide proportion + non-translocated autumn fry density + translocated autumn fry density + pre-translocation fry density + gravel proportion + cobble proportion + mean depth + pre-translocation trout fry density + pre-translocation 1^+ trout density*	339.7	366.8	Intercept	25.56	17.52	1.46	0.14
				Pre-translocation mean TL	0.99	0.45	2.20	**0.03**
				Pre-translocation 1^+ salmon density	0.58	0.16	3.55	**0.0004**
				Sheeffry LDR reach	2.40	3.75	0.64	0.52
				Riffle & glide proportion	5.51	4.24	1.30	0.19
				Non-translocated autumn fry density	-0.05	0.04	-1.31	0.19
				Translocated autumn fry density	0.06	0.10	0.67	0.50
				Pre-translocation fry density	-0.03	0.18	-0.17	0.87
				Gravel proportion	26.67	32.14	0.83	0.41
				Cobble proportion	-23.91	11.74	-2.04	0.04
				Mean depth	-28.39	33.92	-0.84	0.40
				Pre-translocation trout fry density	0.56	0.41	1.36	0.17
				Pre-translocation 1^+ trout density	-0.29	0.41	-0.72	0.47
Backward	*Autumn mean non-translocated fry TL ~ pre-translocation fry TL + pre-translocation 1^+ salmon density + riffle & glide proportion + non-translocated autumn fry density + translocated autumn fry density + pre-translocation fry density + gravel proportion + cobble proportion + mean depth + pre-translocation trout fry density + pre-translocation 1^+ trout density*	338.1	363.2	Intercept	27.37	17.36	1.58	0.11
				Pre-translocation mean TL	0.87	0.41	2.13	**0.03**
				Pre-translocation 1^+ salmon density	0.59	0.16	3.62	**0.0003**
				Riffle & glide proportion	6.37	4.04	1.58	0.11
				Non-translocated autumn fry density	-0.05	0.04	-1.19	0.23
				Translocated autumn fry density	0.08	0.09	0.93	0.35
				Pre-translocation fry density	-0.09	0.15	-0.58	0.56
				Gravel proportion	37.46	27.49	1.36	0.17
				Cobble proportion	-24.96	11.67	-2.12	**0.03**
				Mean depth	-12.42	23.12	-0.54	0.59
				Pre-translocation trout fry density	0.66	0.38	1.74	0.08
				Pre-translocation 1^+ trout density	-0.28	0.41	-0.69	0.49
Backward	*Autumn mean non-translocated fry TL ~ pre-translocation fry TL + pre-translocation 1^+ salmon density + riffle & glide proportion + non-translocated autumn fry density + translocated autumn fry density + pre-translocation fry density + gravel proportion + cobble proportion + pre-translocation trout fry density + pre-translocation 1^+ trout density*	336.4	359.6	Intercept	24.73	16.70	1.48	0.14
				Pre-translocation mean TL	0.87	0.41	2.13	**0.03**
				Pre-translocation 1^+ salmon density	0.59	0.16	3.59	**0.0003**
				Riffle & glide proportion	7.04	3.85	1.83	0.07
				Non-translocated autumn fry density	-0.05	0.04	-1.41	0.16
				Translocated autumn fry density	0.08	0.09	0.86	0.39
				Pre-translocation fry density	-0.05	0.13	-0.36	0.72
				Gravel proportion	34.63	27.06	1.28	0.20
				Cobble proportion	-23.39	11.33	-2.06	**0.04**
				Pre-translocation trout fry density	0.59	0.36	1.65	0.10
				Pre-translocation 1^+ trout density	-0.31	0.40	-0.78	0.44
Backward	*Autumn mean non-translocated fry TL ~ pre-translocation fry TL + pre-translocation 1^+ salmon density + riffle & glide proportion + non-translocated autumn fry density + translocated autumn fry density + gravel proportion + cobble proportion + pre-translocation trout fry density + pre-translocation 1^+ trout density*	334.5	355.8	Intercept	25.41	16.61	1.53	**0.3**
				Pre-translocation mean TL	0.86	0.41	2.12	**0.03**
				Pre-translocation 1^+ salmon density	0.58	0.16	3.59	**0.0003**
				Riffle & glide proportion	7.07	3.86	1.83	0.07
				Non-translocated autumn fry density	-0.06	0.03	-2.00	**0.05**
				Translocated autumn fry density	0.07	0.09	0.82	0.41
				Gravel proportion	34.88	27.09	1.29	0.20
				Cobble proportion	-24.99	10.44	-2.39	**0.02**
				Pre-translocation trout fry density	0.57	0.35	1.61	0.11
				Pre-translocation 1^+ trout density	-0.33	0.40	-0.81	0.42
Backward		333.2	352.5	Intercept	24.27	16.66	1.46	0.15

	Autumn mean non-translocated fry TL ~ pre-translocation fry TL + pre-translocation 1^+ salmon density + riffle & glide proportion + non-translocated autumn fry density + translocated autumn fry density + gravel proportion + cobble proportion + pre-translocation trout fry density			Pre-translocation mean TL	0.90	0.41	2.19	**0.03**
				Pre-translocation 1^+ salmon density	0.57	0.16	3.54	**0.0004**
				Riffle & glide proportion	6.70	3.86	1.74	0.08
				Non-translocated autumn fry density	-0.06	0.03	-2.00	0.05
				Translocated autumn fry density	0.08	0.09	0.96	0.34
				Gravel proportion	25.54	24.70	1.03	0.30
				Cobble proportion	-23.35	10.31	-2.27	**0.02**
				Pre-translocation trout fry density	0.60	0.35	1.71	0.09
Backward	*Autumn mean non-translocated fry TL ~ pre-translocation fry TL + pre-translocation 1^+ salmon density + riffle & glide proportion + non-translocated autumn fry density + gravel proportion + cobble proportion + pre-translocation trout fry density*	332.1	349.5	Intercept	19.91	16.17	1.23	0.22
				Pre-translocation mean TL	1.03	0.39	2.66	**0.01**
				Pre-translocation 1^+ salmon density	0.52	0.15	3.39	**0.0007**
				Riffle & glide proportion	7.72	3.74	2.07	**0.04**
				Non-translocated autumn fry density	-0.07	0.03	-2.13	**0.03**
				Gravel proportion	18.81	23.89	0.79	0.43
				Cobble proportion	-19.76	9.69	-2.04	**0.04**
				Pre-translocation trout fry density	0.57	0.35	1.62	0.11
	Autumn mean non-translocated fry TL ~ pre-translocation fry TL + pre-translocation 1^+ salmon density + riffle & glide proportion + non-translocated autumn fry density + cobble proportion + pre-translocation trout fry density	330.7	346.2	Intercept	24.12	15.35	1.57	0.12
				Pre-translocation mean TL	0.99	0.39	2.55	**0.01**
				Pre-translocation 1^+ salmon density	0.50	0.15	3.29	**0.001**
				Riffle & glide proportion	6.78	3.56	1.90	0.06
				Non-translocated autumn fry density	-0.07	0.03	-2.40	**0.02**
				Cobble proportion	-20.08	9.74	-2.06	**0.04**
				Pre-translocation trout fry density	0.52	0.35	1.49	0.14