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# Effects of Upland Stream Nutrient Restoration on Atlantic Salmon Populations

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MRes, BSc (Hons)



Submitted in fulfilment of the requirements for the Degree of Doctor  
of Philosophy

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*“IN THE GRAVEL OF THE MOORLAND STREAM THE EGGS WERE HATCHING, LITTLE FISH BREAKING FROM CONFINING SKINS TO SEEK LIFE, EACH ONE ALONE, SAVE FOR THE FRIEND OF ALL, THE SPIRIT OF THE WATERS. AND THE STAR-STREAM OF HEAVEN FLOWED WESTWARD TO FAR BEYOND THE OCEAN WHERE SALMON MOVING FROM DEEP WATERS TO THE SHALLOWS OF THE ISLANDS, LEAPT – EAGER FOR IMMORTALITY.”*

*HENRY WILLIAMSON, ‘SALAR THE SALMON’, 1935*

# Abstract

Aquatic biodiversity has experienced severe declines over past decades, with many species requiring conservation interventions in order to preserve and protect threatened populations. However, assessing whether conservation measures work effectively with the intended outcome is important when considering their implementation. One conservation target is the Atlantic salmon (*Salmo salar*), populations of which have declined dramatically since the 1960s. Given that many salmon die during the spawning migration, the reduction in the number of spawning adults has also led to fewer marine-derived nutrients being deposited in upland streams in the form of salmon carcasses. These carcasses fertilise the nursery streams of the salmon, to the potential benefit of the young fish, and so the decline in the number of adult salmon carcasses may have adverse effects on the next generation.

In this thesis, I explore in successive chapters the potential for restoring the nutrients that are normally supplied by returning spawning salmon to upland streams, by using carcass analogue pellets. I examine the impacts of different methods of the application of these pellets, and differing doses and timing of applications, on the growth and performance of juvenile salmon populations. I also assess the effect of the application method on aquatic macroinvertebrate communities. I develop a mathematical model to predict the impact of manipulating the early freshwater growth rate of individual salmon on their life history trajectory, following a cohort of fish through to spawning and egg production; this allows exploration of the effect of nutrient additions on the viability of salmon populations. Finally, I detail an incidental study on the effects of high summer temperatures on the performance of juvenile salmon populations.

Chapter 1 introduces the main issues and the study species and presents the ecological and conservation context for the study. Juvenile Atlantic salmon often reside in upland streams, and these streams may differ to the degree of nutrient limitation that they experience as a result of cultural practices leading to the oligotrophication of these streams. In Chapter 2, I review the sources, retention and fate of nutrients in upland streams, alongside reviewing the impacts of experimental nutrient additions on salmon populations.

In the first experimental chapter (Chapter 3), I present the results of a two-year experiment that compared two methods of nutrient additions using carcass analogue pellets, one via bagged pellets and the second through hand-scattered pellets. I show the differing impacts of these methods on macroinvertebrates and two cohorts of Atlantic salmon populations. The results varied between treatments and between years, but mainly demonstrated increased body size of individual invertebrates in the scattered treatment. Salmon fry (fish in their first summer of growth) in the scattered treatment showed reduced growth but greater densities, whilst fry in the bagged treatment saw no change in density and a positive effect on growth in one year of the study. There was no impact of either treatment on the body size of salmon parr (fish at least one year old).

The impacts of nutrient additions are likely to vary depending on seasonal changes to environmental variables, and the amount of nutrients added is also likely to result in different impacts based on these seasonal changes. These changes are assessed in Chapter 4, where I present the results of an experiment that tested the impact of a single dose applied in early spring against a double dose applied in early spring and early summer. The single dose resulted in increased fry density but reduced growth, whilst the double dose increased both growth and density of Atlantic salmon fry.

No study has assessed the impact of nutrient additions over a single generation of Atlantic salmon, and nutrient additions may have unforeseen and adverse consequences. In Chapter 5, I detail an individual-based model that aims to understand the population impact of manipulating early freshwater growth of Atlantic salmon. I demonstrate that increasing early growth results in increased numbers of fish smolting, even though more precociously mature males are produced. The salmon that smolt tend to do so at a younger age but also larger size; these trends are predicted to translate into increases in offspring produced per cohort and hence increases in the population size of Atlantic salmon.

In Chapter 6, I present an incidental study on the impacts of high summer temperatures on the density and biomass of juvenile Atlantic salmon. High temperatures can result in heat stress in Atlantic salmon, affecting their growth and behaviour. I demonstrate a negative relationship with degree hours exceeding 23°C and the log biomass and log density of juvenile salmon.

In the final chapter, I put into context the results of the previous chapters, and address the utility of carcass analogue application as a potential conservation

tool. Though the impacts of nutrient additions may vary temporally and may be complex, the data I present in this thesis suggests that nutrient additions may be used as a conservation tool with positive impacts on the freshwater growth of salmon, which is positively related to increases in their marine survival and thus increases at the population level.

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# Author's Declaration

I certify that the thesis presented here for examination for a PhD degree of the University of Glasgow is solely my own work other than where I have clearly indicated that it is the work of others (in which case the extent of any work carried out jointly by me and any other person is clearly identified in it), and that the thesis has not been edited by a third party beyond what is permitted by the University's PGR Code of Practice.

A version of Chapter 2 was previously published in the journal *Aquatic Conservation: Marine and Freshwater Ecosystems*. This chapter benefitted from input in the conceptualisation and editing by my co-authors, whilst I was responsible for the writing and research.

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# Chapter 1 | Introduction

## 1.1 Declines in aquatic biodiversity

Globally, aquatic systems face a multitude of threats, with substantial declines in the biodiversity of both marine and freshwater species apparent over recent decades (Dudgeon *et al.*, 2006; Sala & Knowlton, 2006). These declines in biodiversity span all levels of biological organisation. For example, the exploitation of commercially important marine fish may be driving genetic diversity in these species to be more homogenous, ultimately resulting in losses in genetic diversity for these species (Gandra *et al.*, 2021). On an organismal and population level, the number of individuals is estimated to have declined dramatically. For instance, 90% of large pelagic fish studied have experienced range contractions resulting in local extinctions (McCauley *et al.*, 2015), whilst the number of individuals in many populations has also fallen - for example, silvertip shark (*Carcharhinus albimarginatus*) numbers in the Chagos Islands in the Indian Ocean are estimated to have declined to just 7% of their baseline population level (Ferretti *et al.*, 2018). Such declines in aquatic species, particularly in apex predators, can result in further losses to aquatic diversity such as disturbance to entire ecosystems as a result of trophic cascades (Heithaus *et al.*, 2008).

Pressures on aquatic systems are not only pervasive across the different levels of biological organisation, but widely affect many kinds of aquatic systems. For instance, estuaries, which are a conduit between freshwater and marine systems, are especially vulnerable. Declines in the species richness of estuarine fish assemblages have been observed when comparing current to historical data (Smith *et al.*, 2008). Estuaries and other coastal systems contribute vital ecosystem services, such as providing nursery habitats for fish, but the loss of estuarine and coastal habitats are estimated to have reduced the area of nursery habitat by 69% (Barbier *et al.*, 2011; Worm *et al.*, 2006). Declines in biodiversity have also been observed in other aquatic systems, such as lakes, as a result of multiple stressors. For example, climate change has resulted in reductions in benthic habitat and fish production in Lake Tanganyika, which may impact the populations of commercially important fish (Cohen *et al.*, 2016). Fish are not the

only aquatic taxa experiencing declines in biodiversity. Major threats, particularly habitat loss, have resulted in declines for many amphibian species due to a reduction in the number of ponds that they require for breeding (e.g. Arntzen *et al.*, 2017).

Fresh waters contain immense biodiversity: one third of all vertebrate species reside in fresh water, despite it only occupying 0.8% of the Earth's surface (Dudgeon *et al.*, 2006). However, the declines observed in freshwater biodiversity are of a greater magnitude than those observed in either marine or terrestrial systems. According to the World Wide Fund for Nature (WWF) Living Planet Index of vertebrate species, freshwater vertebrate biodiversity fell from a benchmark of 100 in 1970 to lower than 20 in 2012, whereas the corresponding biodiversity measure for both terrestrial and marine systems declined to around 70 over the same period (Reid *et al.*, 2019; WWF, 2016). Efforts to restore freshwater biodiversity appear to have plateaued, with freshwater invertebrate communities in Europe, which were seeing increases in taxon richness, appearing to have declined since 2010 and their recovery halted since 2013 (Haase *et al.*, 2023). Major stressors continue to threaten the vast biodiversity of freshwater systems. Dudgeon *et al.* (2006) suggested that freshwater diversity is imperilled by five main threats: overexploitation, water pollution, flow modification, habitat destruction/degradation, and invasive species.

These threats are exacerbated by the fact that fresh waters are inherently linked to terrestrial systems, and are thus at greater risk of pollution or nutrient inputs as runoff from terrestrial sources (Blann *et al.*, 2009). For instance, the salting of roads to prevent ice has been shown to impact freshwaters through salinisation from runoff, negatively affecting all trophic levels and multiple levels of biological organisation (Hintz & Relyea, 2019). Runoff from roads can also present other issues, with a chemical component of vehicle tyres causing mortality prior to breeding in adult coho salmon (*Oncorhynchus kisutch*) during stormwater exposure events, with up to 90% of fish dying before reproducing (Tian *et al.*, 2021). Nutrient inputs to fresh water from agricultural practices or through water treatment plants can also play a role in altering freshwater ecosystems, and may result in eutrophication (Smith, 2003). This in turn can result in a host of adverse impacts, from increased growth of algae to reductions in oxygen concentrations, potentially resulting in the mortality of fish species (Smith, 2003). Even what may be imagined as pristine ecosystems, such as groundwater cave habitats, are at risk

of excess nutrient inputs. For example, caves containing populations of the threatened Ozark cavefish (*Amblyopsis rosae*) show nutrient concentrations which exceed local limits alongside high concentrations of faecal bacteria from sewage treatment plants and nearby pastoral farming activities (Graening & Brown, 2003). Other inputs to fresh water from terrestrial systems include suspended sediment, which may alter important habitats if not managed correctly. For example, the spawning habitats of fish may become areas in which fish are prone to gill damage as a result of high levels of suspended sediment (Lazar *et al.*, 2010).

## 1.2 Freshwater habitat management

Where populations or habitats are threatened, effective management can result in recovery. For instance, the Gila trout (*Oncorhynchus gilae*) native to Arizona and New Mexico, USA, have historically faced a range of threats, most significantly competition and predation pressures from introduced species, hybridisation with closely related species, and changes in habitat and water quality (Propst *et al.*, 1992). Since 1923, conservation efforts have been made to increase the population size whilst maintaining genetic diversity (Propst *et al.*, 1992). Management of habitats has included treating streams chemically to remove introduced rainbow trout (*Oncorhynchus mykiss*), which Gila trout were at risk of hybridisation from, closure to anglers and construction of barriers to prevent invasive species, as well as the introduction of Gila trout to other areas of suitable habitat (Propst *et al.*, 1992; Wares *et al.*, 2004). These efforts appear to have been successful in maintaining the genetic integrity of the species, with no lineages showing evidence of hybridisation, and the population has recovered to a level where the threat level was downgraded from ‘endangered’ to ‘threatened’ (Camak *et al.*, 2021). However, the Gila trout is still at risk from threats such as climate change and wildfires, which together may reduce the habitat available to the fish by 70% through the reduction in habitat within their thermal range (Kennedy *et al.*, 2009).

Effective management therefore is essential in maintaining or improving the health of populations of species under threat; this can require multiple approaches to issues. Improving habitat availability and quality is however essential, as species must have adequate habitat and resources to be able to live

successfully and for populations to grow. In fresh waters, habitat restoration and catchment management have shown a diversity of responses to their implementation: a majority of studies recorded in a meta-analysis had shown positive impacts, but one third of the studies showed no effect or a negative effect of restoration in metrics measured (Kail *et al.*, 2015). Management techniques such as removing non-native fish can be effective in restoring native fish communities (Hickerson *et al.*, 2021), whilst restoration of riverine habitats such as reducing channelisation, increasing meandering and restoring features such as large woody material can help to increase the density of aquatic invertebrates and fish (Perkins *et al.*, 2021). More major restoration work such as the removal of in-stream barriers can have large impacts on riverine fish assemblages, since they restore connectivity between artificially separated systems. These in-stream barriers are numerous: a recent analysis estimated that there were over 1.2 million barriers in European rivers, meaning that many species, particularly those that are migratory, have limited access to critical areas of habitat (Belletti *et al.*, 2020). Removal of such barriers can have rapid impacts, such as the removal of a tidal barrier resulting in a major increase in the upstream density of European eels (*Anguilla anguilla*) (Sun *et al.*, 2021).

Diadromous species such as eels are particularly vulnerable to pressures in aquatic systems, as their life histories mean that they encounter threats not solely in either marine or freshwater systems, but face adversity in both systems as well as while on migration. For example, the population size of the anadromous form of rainbow trout, the steelhead, has declined to just 4% of the total that was estimated from the commercial catch to be present in Puget Sound in 1895 (Gayeski *et al.*, 2011). These dramatic changes are estimated to be partly due not only to a reduction in the available freshwater habitat, but a large decline in its productivity (Gayeski *et al.*, 2011). At the same time, the marine survival of steelhead has also declined, and these factors have reduced adult abundance (Kendall *et al.*, 2017). Indeed, North American diadromous species have all shown evidence of population declines, and many species show large falls in population numbers when compared to their baseline (Limburg & Waldman, 2009). Due to their life histories, diadromous fish are thus subjected to numerous anthropogenic pressures, and may be of particular conservation importance when considering catchment management efforts to conserve populations.

## 1.3 Atlantic salmon as a case study

The Atlantic salmon (*Salmo salar*) is one such diadromous species facing threats in both the freshwater and marine realms. The species ranges from the East coast of North America to the west coast of the Atlantic, and also occurs in the Baltic Sea, from arctic populations in Greenland, Canada and Russia down to southern populations in Maine and Portugal (Jonsson & Jonsson, 2011). Atlantic salmon spawn in cold freshwater streams mostly between October and December, laying around 1600-1800 eggs per kg female in constructed nests called redds (Armstrong *et al.*, 2003; Bardonnet & Baglinière, 2000). Eggs remain in the redd over winter, but development time is temperature dependent, so this period can last between 4-7 months (Bardonnet & Baglinière, 2000). Hatchlings, known as alevins, feed on the yolk sac before emerging from the substrate as first-feeding fry, where their diet mostly consists of benthic and drifting stream invertebrates (Jones *et al.*, 2003; Jonsson & Jonsson, 2011). Fry begin feeding near their redd but soon disperse to establish and aggressively defend feeding territories (Gustafson-Greenwood & Moring, 1990). The size of feeding territories is partly dependent on the overall density of fry, with fry in high density streams defending smaller territories than those in low density streams (Lindeman *et al.*, 2015). Juveniles, which are known as parr after their first year, commonly spend 2-3 years in freshwater, but this period in fresh water is dependent on growth rates, so that at the warmer and colder extremes of their distributions it can last as little as one year or as much as eight years (Jonsson & Jonsson, 2011; Power, 1961; Robitaille *et al.*, 1989; Utrilla & Lobon-Cervia, 1999).

Juvenile males may also undergo precocious sexual maturation in fresh water before going to sea, but the frequency of this life-history tactic is variable within and between populations, being based on both local environmental factors and genetic background (Mobley *et al.*, 2021). These precocious males contribute to spawning by adopting a sneaky mating tactic (Aubin-Horth & Dodson, 2004). Anadromous males are usually estimated to sire more offspring than precocious male parr (Mobley *et al.*, 2021). However, in some areas precocious males can be of vital importance to populations, such as was found in the Nivelles River in France where up to 87% of offspring were sired by precocious parr (Grimardias *et al.*, 2010). Both the number of years that juveniles spend in fresh water, and the

numbers and ages of precociously mature males, represent important sources of life history variation within Atlantic salmon populations (Metcalf, 1998). This variation is mainly determined by environmental factors such as food supply and density, although genetics also play an important role (Åsheim *et al.*, 2023; Debes *et al.*, 2020; Niemelä *et al.*, 2022). Environmental conditions therefore govern much of the population structure and contribute greatly to life history variation in Atlantic salmon.

After a period of time Atlantic salmon reach a threshold size that triggers preparations for seaward migration. The time taken to reach this life-history stage is dependent on variation in their freshwater environment affecting their rate of growth, which in turn is conditional on temperature and light availability (Metcalf & Thorpe, 1990) dictating their feeding and growth opportunities (hence the geographical variation in the number of years they may spend in fresh water). After reaching this threshold size, Atlantic salmon undergo a physiological and behavioural change known as smoltification and are then known as smolts (Jonsson & Jonsson, 2011).

Smoltification allows for the adaptation to the marine environment, enabling a greater capacity for osmoregulation. Typically silvery in appearance, smolts begin their downstream seaward migration in the spring, usually reaching the sea in late May or June. The size at which fish turn into smolts plays an important role in determining their marine survival, with larger smolts being more likely to survive and successfully return to spawn (Armstrong *et al.*, 2018; Gregory *et al.*, 2019; Simmons *et al.*, 2021). At sea, Atlantic salmon postsmolts feed on fish larvae, euphausiids and amphipods (Utne *et al.*, 2021), and move out into the open ocean where they may spend between 1-4 years, growing substantially in size in comparison to their freshwater growth (Klemetsen *et al.*, 2003). Salmon from the northeast Atlantic have been recorded to migrate long distances, with smolts from Spain reaching Greenland and those from Denmark recorded in Svalbard (Rikardsen *et al.*, 2021).

After remaining at sea for this period, Atlantic salmon start to become sexually mature and make the migration back to fresh water to spawn. They usually return to their natal streams, although straying may occur in some cases (Stabell, 1984). The returning salmon cease feeding around the time of entering the river, so that they then rely on stored resources to fuel the riverine migration and breeding attempt; it has been estimated that adults use between 60-70% of

their energy reserves during migration and spawning (Jonsson *et al.*, 1997). Atlantic salmon are iteroparous, so are capable of returning to sea as a 'spent' fish or 'kelts', which may spawn again in a subsequent year, or may skip a year before returning in order to regain condition (Birnie-Gauvin *et al.*, 2019). Indeed, some salmon have been recorded as spawning as many as five times (Ducharme, 1969). However, even though iteroparity may be frequent among Atlantic salmon, repeat spawners only account for around 11% of the total number of anadromous spawners on average, meaning that a majority of adults die after spawning, either on the spawning grounds or nearby (Fleming, 1998).

## 1.4 Causes of decline in Atlantic salmon populations

One of the principal causes of the decline in Atlantic salmon populations in recent decades is a reduction in marine survival rates (Chaput, 2012). This is mainly thought to be driven by changes in marine ecosystems as a result of climatic change. Rises in sea surface temperatures are thought to cause a reduction in the population of the copepod *Calanus finmarchicus* in the North Atlantic along with other zooplankton such as euphausiids, and a decrease in these zooplankton has been followed by a decrease in the catch size and number of returning Atlantic salmon (Beaugrand & Reid, 2003, 2012). Population declines are also linked to the presence of in-stream barriers, which however are not a new phenomenon: historical data suggests that barriers such as water mills led to the Atlantic salmon population falling by 90% between ~450-900AD and ~1600AD (Lenders *et al.*, 2016). The use of hydropower systems can create migration barriers that may prevent adults from returning to spawn. For example, the construction of hydropower dams in two Swedish rivers, combined with poor fish-passage efficiency, has resulted in an average loss of 70% of potential spawning fish (Lundqvist *et al.*, 2008). However, the removal of barriers to increase stream connectivity has shown to benefit Atlantic salmon, for instance by creating passable road culverts widens the distribution of juvenile salmon by increasing the area of upstream habitat available (Erkinaro *et al.*, 2017).

Other threats faced by Atlantic salmon include climate change and how it may impact the freshwater environment. High temperatures that may curtail growth or reach physiologically stressful levels, alongside more extreme flow

levels, may have large impacts on juvenile fish (Thorstad *et al.*, 2021). In tree-less areas the effect of high temperatures may be mitigated by riparian tree planting, which can provide sufficient shade to reduce maximum stream temperatures and so maintain the viability of habitat which would otherwise warm to levels beyond the thermal window of Atlantic salmon (Jackson *et al.*, 2018a; O'Briain *et al.*, 2017).

Atlantic salmon are also threatened by commercial fish farming. Salmon farms have high levels of escapement of up to 2 million farmed fish per year (McGinnity *et al.*, 2003), such that areas with higher intensities of salmon farming have greater numbers of escaped farmed fish in wild salmon rivers (Fiske *et al.*, 2006). These escaped farmed fish pose a threat to wild fish populations, as genetic introgression into wild populations through hybridisation can introduce traits associated with farmed fish, reducing genetic diversity and thus the viability of offspring (Karlsson *et al.*, 2016). For example, average introgression from farmed fish into wild populations from Norway was 6.9%, but this ranged from between 0% to as high as 42% across 109 rivers sampled (Karlsson *et al.*, 2016). This introgression acts to lower the fitness of wild salmon and may potentially cause vulnerable populations to become extinct (McGinnity *et al.*, 2003). Escaped fish may also increase the competition faced by their wild conspecifics for feeding or spawning areas. Wild Atlantic salmon may also be threatened by parasites originating from farmed Atlantic salmon (Moriarty *et al.*, 2023), such as the salmon louse (*Lepeophtheirus salmonis*) alongside other parasites, which may cause mortality at high parasite loads (Grimnes & Jakobsen, 1996; Vollset *et al.*, 2023).

## 1.5 Conservation approaches for Atlantic salmon

Conservation methods to improve Atlantic salmon populations are typically targeted towards the freshwater life stages, as these stages are more accessible and intervention may be more practicable than at the marine stage in the life cycle (Thorstad *et al.*, 2021). The main intervention to reduce mortality in the marine phases of the Atlantic salmon life cycle is to close marine and coastal fisheries. These fisheries have been closed in areas such as Ireland and Scotland, but they have not been found to result in population recovery; instead they have at best altered populations from a declining to a stable position (Cotter *et al.*,

2022), suggesting that they provide some benefit but other factors such as environmental change are larger drivers of population declines.

One measure often undertaken to attempt to increase salmon population sizes is the use of stocking, where salmon are reared in hatcheries and then released into the wild, either as parr or smolts depending on the hatchery practice (Aprahamian *et al.*, 2003). As Atlantic salmon are a popular target species for anglers (Morton *et al.*, 2016), stocking of fish is designed to increase the number of returning fish for catch and release fishing (Aprahamian *et al.*, 2003). Stocking may be primarily used for conservation of current populations, as mitigation against lost production, or by restoration or enhancement of existing populations (Gilbey *et al.*, 2023). However, whether fish used for stocking are hatchery-bred fish, or offspring stocked from wild-caught adults, both face genetic consequences, with genetic changes in response to captivity occurring rapidly, as shown in steelhead (Christie *et al.*, 2012). Hatchery-bred fish show lower genetic variability than wild fish (Blanchet *et al.*, 2008), meaning that wild fish are at risk of introgression and development of traits which may not be positively associated with survival in the wild. Even the body shape of wild fish raised in hatcheries may differ from hatchery-bred fish, with wild fish having longer pectoral fins and deeper heads, associated with higher swim performance (Blanchet *et al.*, 2008). Though stocking is commonly used, evidence on its efficacy is limited. Young (2013) showed that there was no significant evidence that high stocking efforts resulted in greater catch numbers, and in rivers where stocking did appear to increase catches, areas where this did occur showed lower than average mean rod catches. Survival of hatchery-reared fish is usually poorer than that of wild fish, for example wild Atlantic salmon smolts were 13.9 times more likely to survive migration than hatchery-reared smolts (Larocque *et al.*, 2020). Stocking is therefore now seen as a less than ideal solution to declining salmon populations that may actually cause more harm than good, with 83% of publications detailing the practice of hatchery stocking showing adverse effects of stocking on wild fish (McMillan *et al.*, 2023).

The numerous current threats to wild Atlantic salmon populations highlight the essential need for effective conservation of this economically important species. The greatest success seen in restoring Atlantic salmon populations has arisen through increasing freshwater habitat quality (Lennox *et al.*, 2021), though this has generally resulted from specific actions such as the removal of

obstructions to upstream habitat rather than generalised habitat restoration. For example, work to remove barriers coupled with legislative changes, stocking programmes, and restoring spawning habitats in Denmark has resulted in increasing Atlantic salmon populations and an end to stocking programmes in rivers where populations may now be maintained through natural spawning (Koed *et al.*, 2020). Practices such as adding boulders and structures like woody material to streams and rivers to increase channel complexity, as well as restoring connectivity between river channels, have all been shown to increase the density, abundance and biomass of juvenile Atlantic salmon and brown trout (Floyd *et al.*, 2009; de Jong *et al.*, 1997; Marttila *et al.*, 2019; Scruton *et al.*, 1998). Though these studies did not detail increases in the growth or size of salmon, restoring high quality habitat is essential to increase the population size of salmon by increasing the number of juveniles able to make the seaward migration and thus improve population performance.

## 1.6 Atlantic salmon as nutrient transporters

Declines in adult Atlantic salmon may have indirect impacts on the freshwater habitat of juvenile fish. Migrating animals have been shown to transport nutrients and energy across ecosystem boundaries through processes such as decomposition and excretion, releasing nutrients and energy within their bodies to the environment (Doughty *et al.*, 2016). This occurs across many taxa. For example, the Bogong moth migration (*Agrotis infusa*) is estimated to transfer 7.2 tons of nitrogen (N) and 0.97 tons of phosphorus (P) from the plains to alpine systems in Australia each year (Green, 2011). During the mass migration of wildebeest (*Connochaetes taurinus*), many individuals drown, and this results in large amounts of carbon (C), N and P slowly leaching out from bones (e.g. over a period of 7 years in the case of P), so fertilising the Mara River (Subalusky *et al.*, 2017). Notably, Pacific salmon (*Oncorhynchus* spp.) transfer vast amounts of nutrients from marine systems to their freshwater spawning grounds due to their semelparous life cycle, with mortality occurring almost immediately after spawning (Schindler *et al.*, 2003). For example, a spawning run of 20 million sockeye salmon (*O. nerka*) can contribute  $2.4 \times 10^4$  kg P,  $1.8 \times 10^5$  kg N and  $2.7 \times 10^5$  kg calcium to freshwater systems (Gende *et al.*, 2002). These nutrients may

be available as a result of decomposition, excretion or from the deposition of gametes, as salmon eggs may themselves represent significant sources of nutrients and energy (Näslund *et al.*, 2015). Many organisms depend on the nutrients and energy these migrating fish provide, such as a variety of predators (Holtgrieve *et al.*, 2009) as well as riparian and in-stream plants which can show increased growth as a result of the nutrient input (Quinn *et al.*, 2018).

Predators and plants are not the sole beneficiaries of the Pacific salmon spawning migration. Others include the subsequent generation of fish that the spawning creates, as well as juvenile salmon which may already be present on the spawning grounds, both of which often show increased rates of growth in the proximity to adult carcasses (Bilby *et al.*, 1998; Kaylor *et al.*, 2019; Wilzbach *et al.*, 2005). Indeed, the effect of carcass deposition and spawner nutrients may be seen across the entire trophic web. Epilithic algae have been shown to increase in abundance in proximity to spawning salmon (Chaloner *et al.*, 2004), whilst aquatic invertebrates, the main diet of juvenile salmon, may commonly show increases in biomass or abundance (Minakawa *et al.*, 2002), and may benefit from the increased algal growth. In particular, the biomass of chironomids has been shown to increase in reaches where salmon spawn (Chaloner *et al.*, 2004), and these can form the bulk of the diet of juvenile salmon (Martinussen *et al.*, 2011).

However, as stated above, anadromous fish populations have declined markedly, and this results in a parallel decrease in the nutrient contribution from marine environments to freshwater ecosystems (Gresh *et al.*, 2000). Gresh *et al.* (2000) estimated that the levels of N and P currently delivered to Pacific salmon spawning streams are only at 6-7% of historical levels, and thus the benefits of these nutrients to freshwater systems is greatly reduced. As juvenile salmon show faster growth in the presence of carcasses (Bilby *et al.*, 1998), a reduction in the number of carcasses could potentially result in a reduction in juvenile growth.

This issue is not unique to Pacific salmon. Despite the iteroparity of Atlantic salmon and often smaller population sizes, their spawning migrations may still contribute important nutrients such as N and P to freshwater systems (Lyle & Elliott, 1998). Jonsson & Jonsson (2003) estimated that Atlantic salmon spawners import 3176 kg C, 735 kg N and 132 kg P to the Norwegian River Imsa annually. Atlantic salmon commonly spawn in upland streams, and these are commonly low in nutrients or oligotrophic (Jarvie *et al.*, 2018), meaning that even small levels of nutrient import can result in increased productivity. Juvenile Atlantic salmon

benefit from carcass deposition and nutrient excretion through the same processes which occur in the Pacific. Nutrients from spawning Atlantic salmon can increase algal growth, alongside increases in fungal and bacterial biomass (Samways *et al.*, 2015). Invertebrates show increases in number both physically on carcasses but also elevated numbers downstream of carcasses (Nislow *et al.*, 2010), and juvenile Atlantic salmon benefit from enhanced growth when spawning streams are fertilised with carcasses (Williams *et al.*, 2009).

## 1.7 Nutrient restoration as a potential conservation tool for Atlantic salmon

In a similar way to the reduction in nutrient transport as a result of falling salmon numbers in the Pacific, population declines in Atlantic salmon are resulting in a reduction in the import of marine-derived nutrients to upland streams, and may even change the flow of nutrients so that there is a net export of nutrients as salmon leave as smolts rather than a net import from the quantity of adult spawners (Nislow *et al.*, 2004). Alongside the decline in population size, other factors may also decrease the quantity of nutrients being imported to freshwater systems. For example, evidence shows that hydropower developments and the corresponding reductions in water flow have resulted in the body size of Atlantic salmon decreasing by one third through genetic changes (Jensen *et al.*, 2022). These reductions in body size may mean that not only are fewer salmon returning to freshwater to spawn, but that many of these salmon may be smaller and thus will contribute fewer nutrients to spawning habitats than previously.

As a result of these declines in nutrient concentrations, juvenile salmon may not receive the historic benefits to growth that the spawning migration of adults provided, meaning that juvenile body size may be reduced compared to their potential body size when raised in the presence of carcass nutrients. This is of consequence since (as stated earlier) the body size of salmon smolts is positively correlated with their marine survival (Armstrong *et al.*, 2018; Gregory *et al.*, 2018). Conservation measures are often targeted at the freshwater life stages, and aim to improve both the quantity and quality (in terms of body length, weight

and condition factor) of smolts in order to increase the number of returning adults (Simmons *et al.*, 2021; Thorstad *et al.*, 2021). One potential conservation measure is the restoration of carcass nutrients to upland streams, in order to attempt to provide the growth benefits to juveniles, theoretically increasing their size at smolting and thusly the marine survival rate of outgoing smolts. This could be used as a short-term intervention whilst further effort is expended on restoring high quality habitat, which would take time to implement. However, the use of actual carcasses to replace nutrients is not practicable, and this has led to the development of the use of carcass analogues (Pearsons *et al.*, 2007), which are typically pellets used in the aquaculture industry to feed farmed salmon; these contain similar marine-derived nutrients to salmon carcasses since they are made from marine fishmeal. However, it should be borne in mind that while these pellets are similar in terms of nutrient content, they cannot replicate the effect of a larger population size of spawners as they do not replace the bioturbation of sediment by spawners constructing redds (Holtgrieve & Schindler, 2011). Furthermore, the nutrients are not bound in the bodily structures of an organism such as the bones, which may leach nutrients at different rates compared to pellets which would be expected to have a much faster decay time. Carcass analogues are however much more nutrient-dense than carcasses, such that one kilogram of analogue may be equivalent to 5kg of carcass in terms of nutrients due to the high water content of salmon carcasses (Pearsons *et al.*, 2007).

Importantly, the use of carcass analogues has been shown to have positive effects on the growth of algae, invertebrates and both Pacific and Atlantic juvenile salmon. Kohler *et al.* (2012) showed that application of carcass analogues led to increases in the standing crop of periphyton, alongside increases in the density of macroinvertebrates and increased growth rates of salmonids. Increased biofilm was also evident in a number of studies (Collins *et al.*, 2016; Kohler *et al.*, 2008; Marcarelli *et al.*, 2014; Martin *et al.*, 2010), though Ebel *et al.* (2014) did not observe any significant change in the standing crop of biofilm over two intensities of treatment but did observe higher benthic primary productivity and respiration in the higher intensity carcass analogue treatment. Macroinvertebrate communities have commonly showed responses to the introduction of carcass analogues, with stable isotope analysis showing incorporation of marine-derived nutrients into invertebrate tissues (which may be by either direct consumption or through the consumption of enriched algae) (Guyette *et al.*, 2014; Nislow *et al.*,

2010), and many studies have also reported increases in the density, abundance or biomass of macroinvertebrates (Kohler & Taki, 2010; Kohler *et al.*, 2008; McLennan *et al.*, 2019). The impact of carcass analogues on juvenile Atlantic salmon has also been demonstrated, with increases in both body length and mass in response to carcass analogues (Guyette *et al.*, 2013; McLennan *et al.*, 2019). Interestingly, Auer *et al.* (2018) also showed an increase in the genetic diversity of juvenile salmon in streams treated with carcass analogues through an increase in the number of surviving families. This indicates that there is the potential for the use of the introduction of these pellets to act as a conservation tool with the aim of increasing the body size of juveniles and ultimately increasing the marine survival of smolts.

However, there are still unknowns around the efficacy of the use of these pellets and how they may be used in the best manner for beneficial conservation outcomes. For example, there has not been a standardised method of introducing nutrient pellets to streams, with some studies using pellets bound in mesh bags to simulate a carcass as a large concentrated resource (Auer *et al.*, 2018; Guyette *et al.*, 2014, 2013; McLennan *et al.*, 2019) while other studies have scattered pellets over the stream area to achieve a more even density of nutrients (Collins *et al.*, 2016; Kohler & Taki, 2010). Studies have also not addressed the effect that the number of applications of nutrient additions, or the timing of these additions, may have on stream systems, despite the impact of nutrient pellets being likely to be affected by seasonal environmental changes and the frequency of inputs.

Manipulating the freshwater growth rate of juvenile salmon is likely to influence life history traits such as age and size at smolting, and the probability of precocious maturation in males. While the potential change to life histories is speculated on by McLennan *et al.* (2019), there has been little direct investigation of these life history consequences. It may be that the use of carcass analogues results in fish that smolt at a younger but smaller size and thus are less likely to survive at sea, or an increased number of precocious male parr which have a reduced likelihood of smolting (Letcher & Gries, 2003a; Whalen & Parrish, 1999), and thus carcass analogues may produce adverse conservation effects. Understanding the fundamental effectiveness of analogues as a conservation measure is a critical knowledge gap, and improving the practical measures of implementation in order to achieve positive results is also vital.

## 1.8 Aims of the thesis

In this thesis I will cover the following topics in order to address these unanswered questions. In Chapter 2, I review the extent of nutrient limitation in Atlantic salmon streams, the processes contributing towards cultural oligotrophication, and the effectiveness of nutrient restoration on Atlantic salmon populations. In Chapter 3, I present an experiment comparing the effectiveness of two methods of applying carcass analogues to upland Scottish streams, and the impacts these have on macroinvertebrate communities and the performance of juvenile Atlantic salmon. In Chapter 4, I present an experiment which evaluates the impact of the number of nutrient applications on the growth and performance of juvenile Atlantic salmon. In Chapter 5, I address the question of how changes in early freshwater growth may impact the life histories of a salmon population using an individual-based model approach; this allows exploration of the long-term and population effects of growth manipulations, which are important issues that are not easily examined in field experiments. During the course of the fieldwork that generated the data for Chapters 3 and 4 I observed that there was very marked spatial and temporal (among-year) variation in stream temperatures, with some streams occasionally reaching temperatures that are known to be stressful to juvenile salmon. In Chapter 6, I therefore analyse these data so as to explore whether among-stream and -year variation in late summer densities of juvenile salmon was related to the incidence of stressful temperatures. The results suggest an adverse effect of high summer temperatures on survival rates. Finally, Chapter 7 is a general discussion of the implications of the findings presented in this thesis for both future research on the biology of salmon and the management and conservation of salmon populations.

# Chapter 2 | Nutrient limitation in Atlantic salmon rivers and streams: Causes, consequences, and management strategies

## Abstract

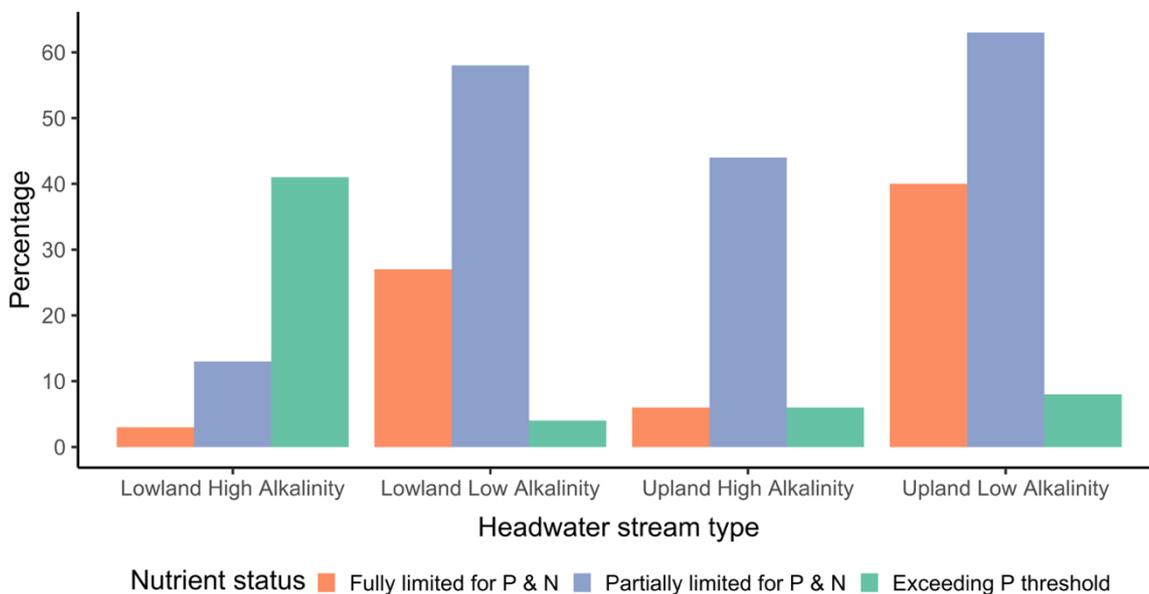
Freshwater catchments can experience nutrient deficits which result in reduced primary and secondary productivity. The most commonly limiting nutrients are nitrogen and phosphorus, either separately or together. This review considers the impact of increasing nutrient limitation in temperate basin stream and river systems, focusing on upland areas that currently or previously supported wild Atlantic salmon (*Salmo salar*) populations. Anthropogenic changes to land use and increases in river barriers have altered upland nutrient dynamics, with particular impacts on salmon and other migratory fish species which may be net importers of nutrients to upland streams. Declining salmon populations may further reduce nutrient sources, reducing ecosystem and fisheries productivity below desired levels. Experimental manipulations of nutrient levels have examined the impacts of this cultural oligotrophication. There is evidence that growth and biomass of juvenile salmon can be increased via appropriate additions of nutrients, offering potential as a conservation tool. However, further research is required to understand the long-term effects of these additions on salmon populations and stream ecosystems, and to assess the vulnerability of downstream habitats to eutrophication as a result. While purposeful nutrient addition with the aim of enhancing and conserving salmonid populations may be justified in some cases, it should be undertaken in an adaptive management framework. Further, nutrient addition should be linked to nutrient retention and processing, and integrated into large-scale habitat restoration and recovery efforts. Finally, both the scientific and the management community should recognise that the ecological costs and benefits associated with adding nutrients to salmon streams may change in a non-stationary world.

## 2.1 Introduction

Life depends on adequate supplies of key elements, such as carbon, nitrogen and phosphorus (Xia *et al.*, 2018). These can shape the productivity of entire ecosystems, and their relative supply is widely recognised to have profound consequences at an ecosystem level. Aquatic systems may be particularly vulnerable to variation in nutrient supply, triggering a variety of ecological consequences with implications for conservation. High nutrient levels, often as a result of human influences, may result in eutrophication, which is characterised by changes to community structure through excessive growth of planktonic algae and periphyton (Page *et al.*, 2012). Macrophyte growth can also increase, leading to the competitive exclusion of less nutrient-tolerant species in affected water bodies (Bergheim & Hesthagen, 1990). Increased epiphytic algal growth on macrophytes may lead to a reduction in light availability, exacerbating the change in community composition from macrophyte-dominated to algal dominance (Hilton *et al.*, 2006; O'Hare *et al.*, 2018). Further impacts of eutrophication include declines in dissolved oxygen, which can lead to sudden fish mortality especially if coinciding with warmer temperatures (Schinegger *et al.*, 2016).

However, whereas eutrophication is more likely to be a feature of lowland systems, upland streams may be more likely to experience the other extreme of oligotrophication, where the biological demand for nutrients outstrips supply (Elser *et al.*, 2007; Hecky & Kilham, 1988; Jarvie *et al.*, 2018). Since these upland streams can be tributaries of lowland rivers, eutrophication and oligotrophication can exist simultaneously at different locations within the same catchment (see Figure 2.1, also Stockner *et al.*, 2000). Upland streams are widely recognised as conduits that connect terrestrial and aquatic systems and influence downstream waters (Alexander *et al.*, 2007). They are strongly influenced by runoff from surrounding hill slopes, and so receive sediments, biological matter and nutrients (Gomi *et al.*, 2002). Despite these inputs, upland streams may experience nutrient limitation; usually a single element is lacking (typically P or more rarely N), or there can be co-limitation due to both P and N being scarce ((Jarvie *et al.*, 2018; Myrstener *et al.*, 2018). Nutrient limitation reduces primary production by taking the availability of the key elements C, N and P away from the optimal ratio of 106C:16N:1P, termed the Redfield ratio (Redfield, 1958) with dramatic impacts on

the productivity and diversity of the aquatic ecosystem (Smith *et al.*, 2017). Naturally low nutrient concentrations in upland streams can be reduced still further as a result of human activity (e.g. through habitat and land-use change), a process called cultural oligotrophication (Stockner *et al.*, 2000).



**Figure 2.1** | Levels of phosphorus and nitrogen in headwater streams in Great Britain in relation to elevation and alkalinity. Streams ‘exceeding P threshold’ show phosphorus concentrations which exceed  $0.05 \text{ mg P L}^{-1}$ , and so are at risk of eutrophication; ‘partially limited’ streams are those in which P and N are moderately low, and ‘fully limited’ streams are those where P and N are so low as to cause significant limitation of primary productivity. A median elevation of 200m separates ‘lowland’ and ‘upland’, and the boundary between ‘low’ and ‘high’ alkalinity is a mean alkalinity of  $50 \text{ mg CaCO}_3 \text{ L}^{-1}$ . Adapted from data in Jarvie *et al.* (2018).

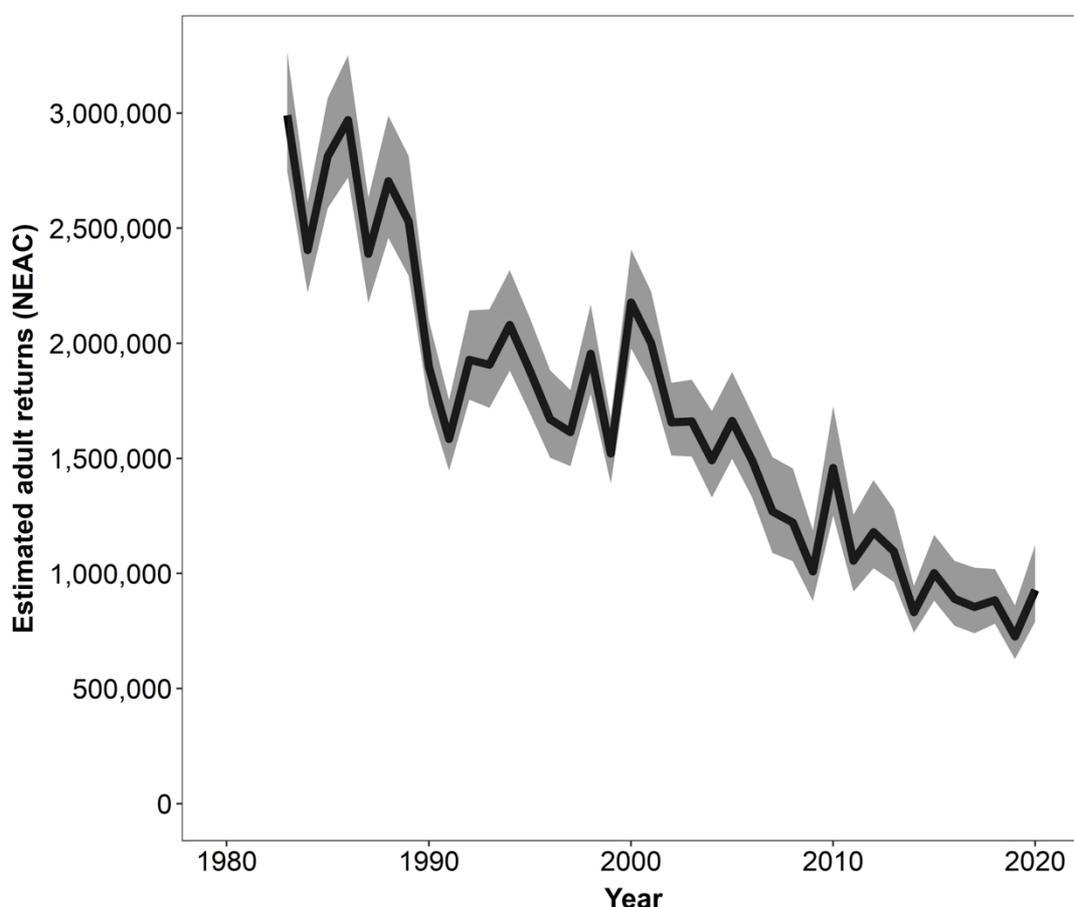
The oligotrophic nature of upland streams may be partially offset by resource subsidies that cross ecosystem boundaries, often through the process of animal migrations (Doughty *et al.*, 2016). Perhaps the most famous of these migrations acting as resource subsidies are the spawning migrations of salmon, both Pacific (*Oncorhynchus* spp.) and Atlantic (*Salmo salar*). Salmon spawn in fresh water, mostly in fast-flowing tributary streams (Jonsson & Jonsson, 2011; Quinn, 2018). Juveniles (parr) spend a variable period of time (depending on species) growing in fresh water before transforming into the seawater-tolerant smolt stage and migrating to sea (Mobley *et al.*, 2021). They gain weight rapidly at sea before returning to their natal stream to spawn (Mobley *et al.*, 2021; Quinn,

2018). Their migrations from the oceans to the spawning grounds involve the transfer of large quantities of nutrients in the form of eggs, excreta and carcasses of spent adults, a process that is well documented in species of Pacific salmon (Gende *et al.*, 2002; Schindler *et al.*, 2003). While the populations of spawning migrants (and hence the nutrients transferred) tend nowadays to be on a larger scale in species of Pacific compared to Atlantic salmon, there is evidence that Atlantic salmon populations were once far larger, even before the declines documented over the last century (Lenders *et al.*, 2016) so that their baseline 'natural' population size (and hence level of nutrient transfer) is unclear. Nonetheless, even current populations of Atlantic salmon are capable of delivering significant levels of marine-derived nutrients to tributary streams, with positive impacts on algal growth, invertebrate populations and juvenile fish growth (McLennan *et al.*, 2019; Nislow *et al.*, 2004).

The documented decline in populations of Atlantic salmon over recent decades (Figure 2.2) has occurred across much of their natural range (Chaput, 2012). Pressures on salmon are various, and operate in both the freshwater and marine environments (Beaugrand & Reid, 2012; Forseth *et al.*, 2017; Olmos *et al.*, 2020; Todd *et al.*, 2012). These population declines are of serious concern, given the economic, cultural, and conservation value of Atlantic salmon: in 2017, total expenditure from recreational angling alone was estimated to be €300-500 million across the North Atlantic (Myrvold *et al.*, 2019). This has led to wide-ranging conservation initiatives. For example, in the European Union, Atlantic salmon are designated for protection in freshwater habitats under Annexes II and V of the European Habitats Directive (Council of the European Communities, 1992). Under Annex II, core areas of habitat are required to be protected under the Natura 2000 Network, whilst for Annex V, member states are obliged to ensure that any exploitation in the wild is consistent with maintenance of a favourable conservation status.

With the closure of many commercial fisheries and control of recreational angling, conservation efforts have moved towards improving juvenile salmon survival and growth (and hence the production of smolts) through freshwater habitat restoration (Thorstad *et al.*, 2021). This includes consideration of the impact of declines in resource subsidy in upland streams resulting from decreased spawner abundance. Lower nutrient inputs from spawners results in reduced growth rates of juvenile salmon (Auer *et al.*, 2018; McLennan *et al.*, 2019) and

potential alterations to marine survival arising from changes in size attained by the time of smolt migration, since this correlates with return rates (Armstrong *et al.*, 2018; Gregory *et al.*, 2018). This has led to the suggestion that nutrient restoration to spawning streams that have experienced cultural oligotrophication could be used as a conservation tool to manage and enhance important fish populations. However, cultural oligotrophication often escapes recognition as a key stressor limiting effective restoration efforts in the literature (Lennox *et al.*, 2021). Such action could be part of a strategy to mitigate losses of salmon at sea to counter current declines in Atlantic salmon. However, this requires assessment of associated risks to receiving bodies of water and scale of potential benefits. This is therefore a complex and potentially contentious issue that presents challenges for managers, practitioners, regulators and policy makers.



**Figure 2.2** | Variation over years in estimated numbers of Atlantic salmon returning to coasts within the North-east Atlantic Commission after one sea winter (ICES Scientific Reports, 2021), 90% confidence bands shown in grey.

This review describes the impact of nutrient limitation in upland temperate streams (which are the typical spawning habitat of salmon)- a topic that has received far less attention than the issue of eutrophication further downstream. Evidence is presented that experimental nutrient additions to upland streams can increase stream invertebrate populations and the growth rates and biomass of the fish that feed on them. Given this complexity, my objective is to synthesise the state of science on nutrient limitation of aquatic ecosystem production, from the perspective of management of Atlantic salmon and the ecosystems within their current and historical watersheds, but within a wider context of other anadromous freshwater fishes. The review is particularly oriented towards Holarctic river basins and watersheds where migratory fishes are an important resource and play key roles in ecosystems. The aim is to inform conservation and restoration practice by providing an integrated perspective allowing policy-makers and practitioners to identify relevant principles and case studies, as well as signposting areas of study warranting further attention.

## 2.2 Sources of nutrients in headwater streams

Nitrogen is supplied to headwaters mainly through atmospheric distribution, often originating from agricultural use and the combustion of fossil fuels, returning to land or water through wet and dry deposition (Boyer *et al.*, 2006). It is abundant in the atmosphere but in an inert form ( $N_2$  gas) which must be transformed into reactive nitrogen to be biologically available (Stein & Klotz, 2016). As a consequence, in both Europe and North America a greater percentage of the total continental N inputs are of anthropogenic origin (61% and 59% respectively) than results from natural sources such as nitrogen fixation (Boyer *et al.*, 2006). In aquatic systems, organic nitrogen is degraded through ammonification producing ammonium and ammonia ( $NH_4^+$ ,  $NH_3$ ) which then undergo nitrification leading to oxidation into nitrate ( $NO_3^-$ ) (Xia *et al.*, 2018).

Phosphorus may be present in a number of different forms within a system. In natural waters it is usually present as inorganic phosphate ( $PO_4^{3-}$ ), also known as orthophosphate, which may be present in either dissolved or particulate form, with particulate forms making up the majority of the P load (Spivakov *et al.*, 1999). Since there are multiple P species, P can be measured in a variety of ways,

usually involving the separation of particulate and dissolved P by filtration, after which separate measurements are made of the different fractions (Spivakov *et al.*, 1999). Soluble reactive phosphorus (SRP) is a measure of the dissolved inorganic P, usually orthophosphate, that is biologically available to plants and algae within a sample. The combined amount of all forms of P in a sample is defined as the total phosphorus (TP). Phosphorus may also be present in an organic form (i.e. bound to plant or animal tissue). Measurements of stream water P may not reflect the true amount of P within a system, since organic P can also be taken up and used by algae (Schoffelen *et al.*, 2018; Whitton & Neal, 2011). Additionally, low concentrations of P in stream water may not always indicate limitation for primary production, since luxury uptake by algae during periods of high P availability can allow for growth during periods of P scarcity, and thus may not appear in soluble P sampling (Jarvie *et al.*, 2013). The sources of P are more complex than are those for N, and so will be considered in more detail in the following sections.

### 2.2.1 Geological and atmospheric sources of phosphorus

Bedrock, soils and streambed sediments are primary sources of P in upland streams (Bol *et al.*, 2016), and parent lithology is a principal determinant of overall stream structure and function. Porder & Ramachandran (2013) highlighted that the concentration of P can vary 30-fold among rock types, with the highest P concentrations found in iron-rich, silica-poor igneous rocks such as basalt. Sedimentary rocks may also be rich in P, with the highest concentrations in mudstone, claystone and siltstone, with P concentration reducing as grain size increases. Metamorphic rocks show broadly similar P concentrations to the rocks from which they derive. Soil P availability is positively correlated with the P concentration of the underlying bedrock (Porder & Ramachandran, 2013), and this effect of bedrock can translate into SRP levels in the streams that run over them through the erosion of bankside soils and sediments (van der Perk *et al.*, 2006). The presence of alkali elements in these rocks increases P availability, so that more acidic streams are more likely to be P limited than where the alkalinity is high (Jarvie *et al.*, 2018).

The P content of stream banks is determined in part by localised land use, but also from the deposition of upstream sediments (Fox *et al.*, 2016). Phosphorus,

which has no gaseous phase, may also be supplied to catchments by atmospheric deposition as dust (Gibson *et al.*, 1995; Mladenov *et al.*, 2012). Atmospheric P can be supplied in sufficient amounts to cause ecological effects in areas where the bedrock is nutrient poor (Vicars *et al.*, 2010). However, atmospheric deposition associated with early industrialisation in lowland and coastal urban centres tended to acidify upland surface waters and reduce P availability, except in the most remote regions (Jüttner *et al.*, 2021).

### 2.2.2 Biological sources of phosphorus

The input of material in the form of logs, sticks and leaves may exceed  $1\text{ kg m}^{-2}\text{ yr}^{-1}$  in streams with heavily forested riparian zones; leaves form the dominant nutrient input due to both their quantity and rate of breakdown (Webster *et al.*, 1999). A perhaps surprising P input to streams comes from pollen, which is high in phosphorus (Lee *et al.*, 1996). Though the quantity of P supplied via pollen may be low, deposition in summer when biological demand is high has important implications for the overall P budget: indeed, in the Precambrian Shield catchment, Ontario, Canada, pollen accounted for up to 30% of TP deposition (Eimers *et al.*, 2018). Most of the North Atlantic basin was originally forested and these forests have been subjected to major changes including large-scale deforestation. The replacement of native forests with plantation monocultures (primarily conifers) that are intensively managed for timber, alongside reductions in age-class and species diversity, has likely resulted in reductions in the quantity of leaf and pollen inputs of P.

The movement and migration of animals results in the transfer of nutrients across ecosystem boundaries. As mentioned earlier, the spawning migrations of salmon and other anadromous fish species results in the release of gametes, excreta and (in some cases) carcasses of spent adults on or close to the spawning grounds. This often results in a net import of marine-derived nutrients to upland systems (Gende *et al.*, 2002; Gresh *et al.*, 2000; Schindler *et al.*, 2003). The examples that have received the most attention to date are those associated with Pacific salmon. These are large scale migrations occurring across much of the Pacific Northwest, with up to 280 million salmon from five species of the genus *Oncorhynchus* migrating upstream every year, importing large quantities of

marine-derived nutrients such as C, N and P, but also smaller quantities of essential micronutrients such as calcium, iron, magnesium, sodium and cobalt (Currier *et al.*, 2020; Gresh *et al.*, 2000; Schindler *et al.*, 2003). These nutrient inputs support a wide variety of predators and scavengers, including bears, wolves, eagles, corvids and many other large vertebrates (Shardlow & Hyatt, 2013). However, the spawning behaviour of Pacific salmon can also lead to the export of nutrients from streams, often as a result of bioturbation from the excavation of nests in the stream bed. Pacific salmon spawning behaviours have been shown to shift ecosystems from primary production to heterotrophic production, and also export large quantities of nutrients downstream through increased transport of suspended sediment (Holtgrieve & Schindler, 2011; Moore *et al.*, 2007).

Nutrient deposition is not limited to semelparous Pacific salmonids. The Atlantic salmon is an iteroparous species capable of repeat spawning, but many individuals may still die on or adjacent to the spawning grounds (Williams *et al.*, 2010). The species was estimated to import 1.7-5.3t of P each year to the river Tweed in Northern England (Lyle & Elliott, 1998), and even in a short river in south west Norway the annual import from Atlantic salmon was 132 kg P (Jonsson & Jonsson, 2003). The phenomenon also occurs in other anadromous species of the North Atlantic basin, such as the semelparous sea lamprey (*Petromyzon marinus*) (Nislow & Kynard, 2009; Weaver *et al.*, 2015), the European river lamprey (*Lampetra fluviatilis*) (Masters *et al.*, 2006) and multiple species of river herring (alosids) such as the alewife (*Alosa pseudoharengus*) (Barber *et al.*, 2018). While many adults of iteroparous species such as alewives and Atlantic salmon will return to the ocean after spawning, they nonetheless still excrete waste products (including P) while in fresh water. Additionally, P can be deposited by reproductive material, such as gametes or the mortality of embryos and fry. For instance, although alewives spawn in lakes, the streams through which they migrate are the recipients of their waste products, estimated to be 2.17 µg P per gram of wet fish mass per hour (Walters *et al.*, 2009; West *et al.*, 2010).

Fish spending the entirety of their lives in fresh water are also capable of playing a role in the transport of P. In North America, longnose suckers (*Catostomus catostomus*) migrate from the Great Lakes into tributary streams, with spawning populations reaching 10<sup>2</sup>-10<sup>4</sup> individuals in small streams (Klingler *et al.*, 2003). The proportion of suckers that die in the spawning streams is low,

but the contribution from excretory products and eggs can be significant (Childress & McIntyre, 2015). One difference between these nutrient sources is their availability; P in excretory products is more immediately available to primary producers than P contained in eggs, which requires mineralisation in order to be taken up (Childress & McIntyre, 2015; Childress & McIntyre, 2016). However, eggs are immediately available for consumption by stream resident fish (Childress & McIntyre, 2016). Other species of fish such as European and American eels (*Anguilla anguilla*, *A. rostrata* respectively) may export nutrients from freshwater to marine systems, though this nutrient export has not been quantified.

### 2.2.3 Anthropogenic sources of nutrients

Anthropogenic inputs are increasingly important sources of nutrients in freshwater ecosystems but tend to be less significant in headwater streams than further downstream. In upland catchments these may be grouped into atmospheric sources, point sources (e.g. wastewater discharge, such as from sewage treatment plants or sewer outflows), which tend to have a continuous flow, or diffuse sources (such as agricultural and urban runoff, septic tank leakage, logging and construction) which are often interrupted and irregular (see Carpenter *et al.*, 1998). These sources of nutrients can be sufficient to cause changes to community structure. For example, P-rich discharge from a wastewater treatment plant into an Austrian stream was shown to result in an 80% increase in mean daily macroinvertebrate secondary production further downstream, due to an increase in the proportion of gatherers and grazer/gatherers (Singer & Battin, 2007). Withers *et al* (2009) concluded that a large proportion of the anthropogenic inputs of nutrients into fresh waters may not be from agricultural fertilisers (as is commonly assumed), but from multiple diffuse sources in rural areas (see Withers & Jarvie, 2008 for review). For example, up to 25% of P in waste water originates from household detergents (Richards *et al.*, 2015).

## 2.3 Factors causing nutrient limitation

Though the streams in which salmon spawn receive nutrient inputs from multiple sources, these may be insufficient to prevent the habitats being oligotrophic. Before human influence, this limitation was primarily restricted to acidic catchments with naturally low nutrient levels; this form of oligotrophication does not require any remediation. Over more recent times, however, anthropogenic causes have become of overriding importance in some systems, leading to the phenomenon of cultural oligotrophication (Stockner *et al.*, 2000). The concept of nutrient limitation originates from Liebig's 'Law of the Minimum', with the 'minimum' being the nutrient present in the smallest proportion relative to the growth demands of an organism (Harpole *et al.*, 2011; Liebig, 1842). Nutrient limitation is complex, with systems able to experience limitation by a primary nutrient, secondary limitation from another nutrient, or co-limitation from two or more nutrients (Tank & Dodds, 2003). In aquatic systems, phosphorus and nitrogen are usually assumed to be the major limiting nutrients (Dodds & Welch, 2000). Phosphorus can become limiting when the N:P ratio exceeds 16:1, whilst N becomes the main limiting nutrient at lower N:P ratios (Allan & Castillo, 2007; Redfield, 1958).

The most extensive limitation in catchment streams is often found for P in upland low-alkalinity areas, with more than 60% of such streams in Great Britain being partially limited for P and 40% fully limited; co-limitation of P and N is also extensive (Jarvie *et al.* (2018); Figure 1). However, nitrogen is increasingly being recognised as a limiting nutrient in its own right (Jarvie *et al.* 2018). There is particular evidence for N limitation across boreal Fennoscandia, resulting in constraints on biofilm primary production; activities such as clear-cutting result in the export of N downstream, contributing to further N losses (Burrows *et al.*, 2015; Schelker *et al.*, 2016). Another contributor to nitrogen limitation in upland streams is denitrification. During this process denitrifying microbes produce N<sub>2</sub> gas from nitrates, which is lost to the atmosphere through the anaerobic respiration of nitrite (NO<sub>2</sub><sup>-</sup>), nitric oxide (NO), and N<sub>2</sub>O, ultimately reducing the in-stream availability of nitrogen (Stein & Klotz, 2016). The percentage of nitrogen entering streams and rivers that is removed through this process varies among catchments,

but has been estimated to be between 5-50% (Alexander *et al.*, 2007; Galloway *et al.*, 2004; Holmes *et al.*, 1996).

### 2.3.1 Nutrient storage, retention, and fate

Phosphorus and nitrogen may be stored in a variety of ways in upland catchments. On a small scale, microbes, algae, diatoms and cyanobacteria make up periphyton, forming biofilms on the substrate or on larger macrophytes. Periphyton can store significant concentrations of nutrients structurally within the polysaccharide matrix, and can also retain suspended particles (Battin *et al.*, 2003; Godwin *et al.*, 2009). Macrophytes, though less dominant than periphyton in upland streams, still play a role in storing P and N by buffering the water current and catching suspended material, varying seasonally with macrophyte growth (Riis *et al.*, 2019). These processes may be further enhanced by epiphytic algae on the leaves of macrophytes, which take up P and N from the water column and may act to reduce water velocity, allowing for further nutrient storage (O'Hare *et al.*, 2018).

Downstream transport of P and N is closely linked to nutrient cycling. As nutrients are moved downstream, they may be cycled through different forms in a process known as 'spiralling' (Webster & Patten, 1979). During a single cycle of a spiral, a nutrient atom would pass through three compartments whilst being transported downstream: water, particulates, and consumer phases, and the average distance over which this cycle is completed forms the 'nutrient spiral length' (Newbold *et al.*, 1981). A short spiral or uptake length indicates a high biological demand, so in nutrient-limited waters, the uptake length would be expected to be low (Schade *et al.*, 2011). Headwater streams are characterised by a low water volume to benthic area ratio, providing a greater capacity for exchange of P and N between inorganic and organic materials (Withers & Jarvie, 2008).

Land use changes can result in a reduced capacity for systems to both store and retain limiting nutrients. Over the past 150 years, the spread of low-intensity agriculture in the North Atlantic basin (usually in the form of rough grazing) has led to some temperate upland stream catchments becoming P- and N-export systems (Stockner *et al.*, 2000). Channelisation (the widening, deepening and

straightening of streams) is carried out as a means to improve land drainage and is widespread: in northwest Europe, over one third of land is now drained for agriculture (Abbot & Leeds-Harrison, 1998). This stream channel simplification leads to increases in water velocity, therefore reducing the potential for nutrient uptake (and incidentally increasing the risk of eutrophication further downstream since nutrients are less likely to be retained in the tributaries). Evidence for reduced nutrient retention in simplified channels comes from Austrian agricultural headwater streams, where average SRP uptake length was shortest in open meanders (0.5km), followed by forested streams (1.9km), and longer still in channelised reaches (3.8km) (Weigelhofer, 2017).

Streams are hydrologically linked to wetlands and floodplains, which also provide nutrient storage and retention capacity. Wetlands are particularly effective at retaining N, being approximately twice as effective as lakes (Saunders & Kalff, 2001). Indeed, construction of artificial wetlands is used in the removal of nutrients from wastewater treatment plants, with uptake from plants playing a major role in N removal (Vymazal, 2007). In wetlands, nutrient storage by emergent macrophytes is particularly important since complex below-ground structures assist in P and N storage and in trapping sediments. However, in the North Atlantic basin, these wetlands are under threat of being transformed to agricultural land or land for housing (Čížková *et al.*, 2013).

The recent reintroductions of the North American and Eurasian beavers (*Castor canadensis*, *Castor fiber* respectively) in areas where these species have been extirpated may help to increase nutrient storage by altering hydrological regimes through dam construction, so creating ponds and wetlands. For example, Eurasian beavers reintroduced to headwater streams in Eastern Scotland have been shown to reduce P and N concentrations by 46% and 43% respectively in water directly downstream of their dams compared to unmodified sites (Law *et al.*, 2016). However, the dams may prevent or impede fish migration, particularly under low-flow conditions, whilst also increasing siltation, thereby reducing the availability of fish spawning habitat (Kemp *et al.*, 2012).

The majority of nutrient transport (especially that of particulates) occurs during periods of peak flow (Martin & Harrison, 2011). Meyer & Likens (1979) demonstrated that within a stream in New Hampshire, USA, 46% of the annual P transport occurred in the short periods of time (less than 10%) when discharges were highest, although the concentration of dissolved P did not change with

stream discharge. Sediment particle size also plays a role in nutrient cycling in upland streams (Gottselig *et al.*, 2017). Phosphorus is transported 2-5 times further in particulate form than in the dissolved form, and fine particulates are readily colonised by bacteria (Froelich, 1988; Walters *et al.*, 2014). Reductions in tree cover may increase soil erosion and sediment mobility, which, when combined with increased overland flow during rain events, may temporarily increase nutrient supply to streams, with deforested areas receiving greater pulses of particulates (Prairie & Kalff, 1988, but see Sweeney *et al.*, 2004). Riparian buffer zones have previously been shown to reduce TP and N concentrations in streams, with wider buffers being more effective (Mayer *et al.*, 2007).

Sediment and biological material transported during periods of high flows can enter lakes and reservoirs, and may accumulate in bed sediment, storing nutrients over long periods (Busteed *et al.*, 2009). Human population growth, especially in the North Atlantic basin, has led to the construction of reservoirs and impoundments, which may lead to increased numbers of nutrient sinks in uplands. These may increase as hydropower gains in importance with the transition away from fossil fuels (Zarfl *et al.*, 2015).

### 2.3.2 Reductions in nutrient inputs

Inputs of nutrients to upland streams can also be affected by human interventions, for instance through changes to forest composition or management. The removal of riparian vegetation, by reducing leaf litter inputs, may reduce a key source of nutrients (Webster *et al.*, 1990). In general, rural uplands have steadily become depopulated as settlement, industry and agriculture have moved to the lowlands and coasts. Improvements in the efficacy of P removal from wastewater over time is also likely to have resulted in reduced P inputs. These reductions in anthropogenic sources of nutrients in upland streams may have contributed to P and N (co-) limitation - a process that might continue even in the face of increasing global human populations.

The capacity for migratory fish to deliver P and N to upland streams is affected by the erection of impassable instream barriers - a process which in Europe has occurred over many centuries (Lenders *et al.* 2016). On European rivers

there are currently at least 1.2 million instream barriers, with a mean density of one every 0.7km (Belletti *et al.*, 2020). Indeed, Duarte *et al.* (2021) show that over half of European river networks have impaired connectivity for diadromous fish. In the United States, there are over 80,000 dams and barriers reducing upstream connectivity, and this number does not include smaller, historic barriers (Magilligan *et al.*, 2016). Although many weirs and dams now have incorporated structures that purportedly allow the passage of fish, some have limited effectiveness, letting through less than half the migratory fish biomass when compared to free-flowing rivers (Noonan *et al.*, 2012). In recent years, however, conservation initiatives across Europe and the United States have led to the removal of river barriers, increasing upstream connectivity for migratory species including Atlantic salmon (Bellmore *et al.*, 2019; Birnie-Gauvin *et al.*, 2020), and hence the potential for increased upstream nutrient transport.

The widespread decline in migratory fish populations (van Puijenbroek *et al.*, 2019) has led to a reduction in P inputs to the headwaters. Gresh *et al.* (2000) report that in the Pacific Northwest USA, large declines in Pacific salmon populations mean that only 6-7% of marine-derived P and N now reach inland waters when compared to historic levels. Indeed, Moore *et al.* (2011) demonstrated that a shift from P import to P export occurred when spawning populations in Californian coastal streams decreased in size. Hence, recommendations have been made to set escapement targets for Pacific salmon at levels sufficient not just for egg deposition, but also to account for the return of adequate amounts of marine-derived nutrients (Bilby *et al.*, 2001) although it is unclear whether these recommendations have had any effect. The pattern of nutrient export is not limited to Pacific salmonids, since a net export of P was also demonstrated for Atlantic salmon when spawning populations declined (Nislow *et al.*, 2004a). Moreover, salmon stocked into upland streams as part of a mitigation response can cause sustained nutrient export contrary to the net nutrient importation by wild salmon when a system is unimpeded (Nislow *et al.*, 2004a).

## 2.4 Consequences of nutrient limitation for upland river systems

Upland catchments are often remote, with little agricultural or urban nutrient inputs. Evidence that nutrients are often limiting in upland tributary streams

comes from nutrient supplementation experiments which typically result in enhanced primary and/or secondary biomass (Peckarsky *et al.*, 2015; Samways *et al.*, 2015). Increases in the productivity of food webs can arise through alteration of biogeochemical cycling once systems are released from P and N limitation (Brailsford *et al.*, 2019). There may also be changes to community composition through alterations in the proportion of different functional feeding guilds. For example, Demi *et al.* (2020) demonstrated a 52% increase in total organic-matter flows to primary consumers in streams treated with aqueous P and N. Macroinvertebrates in this detritus-based system were observed to reduce consumption of animal prey, but this was counteracted by an increase in the biomass of larger shredders. This system was also shown to be highly limited in P, with an increase of just  $7\mu\text{g L}^{-1}$  SRP being sufficient to significantly alter resource nutrient content (Demi *et al.*, 2020).

Though an increase in nutrient availability is often shown to have the greatest impact at the base of food webs, the stimulation to autotrophic production can have cascading effects to the highest trophic levels (Bumpers *et al.*, 2017) making it relevant in the context of fisheries management. These effects can arise through natural causes, as when the P inputs arising from alpine woodland wildfires led to increased algal and macroinvertebrate biomass, resulting in an increase in the size and weight of cutthroat trout (*Onchorhynchus clarki*) (Silins *et al.*, 2014). However, of greater current interest is the concept of deliberate manipulation of nutrient levels.

## 2.5 Nutrient addition as remediation for cultural oligotrophication

Adding nutrients to oligotrophic streams has been shown to have effects which propagate up the food web to higher trophic levels, for example increasing the mean weight of underyearling salmonids of a range of species (Johnston *et al.*, 1990; Slavik *et al.*, 2004). Such observations have led to the concept of adding salmonid carcasses as a method of nutrient remediation for streams experiencing declining fish populations. These carcasses increase the immediate supply of nutrients such as SRP, often with a short-term spike peaking after 2 weeks and then declining (Wipfli *et al.*, 2010). The effect can propagate up trophic levels

through invertebrate consumption of enriched biofilm, which is in turn taken up by fish. Another pathway is through direct consumption of carcass material by invertebrates and fish, as shown by Bilby *et al.* (1996). Carcasses may also result in increases in fish density (Bilby *et al.*, 1998). Though carcass addition experiments were initially focused on Pacific salmon, a growing body of literature has investigated the impacts that nutrient additions may have on juvenile Atlantic salmon (Table 2.1). It is clear that the addition of salmon carcasses or alternative nutrient sources has demonstrable effects at multiple levels within a food web, ultimately appearing to stimulate growth and biomass of juvenile Atlantic salmon, suggesting that increasing nutrient availability can have beneficial impacts on salmonid populations (Auer *et al.*, 2018; Guyette *et al.*, 2014; McLennan *et al.*, 2019; Williams *et al.*, 2009).

The impact of nutrient additions is not limited to Atlantic salmon, having been demonstrated across a range of systems and taxa (Table 2.2). Periphyton and fish assemblages have been noted to change in response to slight increases in nutrients (Taylor *et al.*, 2014). For example, P levels in upland streams have been linked to increased fish diversity: Gavioli *et al.* (2019) observed that higher P levels in Italian mountain streams were associated with an increased local contribution to overall diversity from native fish. In a Spanish headwater stream, N and P enrichment over one year resulted in changes to diatom community composition, with some species declining in abundance whilst others became more abundant, whilst some species were unaffected (Veraart *et al.*, 2008). Changes in the trophic state of a waterbody, from oligotrophic to mesotrophic, may result in changes to invertebrate functional groups, which may have implications for larger ecosystem processes. For example, the biomass of 'shredders' in stream leaf litter declined as the trophic level of streams from oligotrophic to hypertrophic in a French stream system (Baldy *et al.*, 2007). Though studies have shown increases in macroinvertebrate abundance and biomass as a result of nutrient additions in the context of a conservation tool for Atlantic salmon (McLennan *et al.*, 2019), the effect on macroinvertebrate diversity and functional groups is not yet known, and there are potentially changes in ecosystem function that may only emerge after prolonged nutrient addition. The use of actual carcasses may often not be practicable, which has led to the development of salmon carcass analogues, usually derived from salmon carcasses or other fishmeal and produced as dry pellets, with an N:P ratio of 6:1 (Pearsons

*et al.*, 2007). These analogues contain a similar mixture of elements as carcasses, including P, N and C, though the rate of release is likely to differ due to their homogenous makeup. An alternative is to use bags of feed pellets produced by the aquaculture industry, which have traditionally been based on marine fishmeal.

**Table 2.1** | Summary of impacts resulting from restoration of nutrients (in the form of adult salmon carcasses, carcass analogues or other marine-derived nutrients (MDN)) to Atlantic salmon spawning areas in upland streams. Continued overleaf.

Nutrient addition	Location	Study duration	Response variables	Result	Citation
Salmon carcasses	Scotland	4 months	Juvenile salmon biomass	Increase in juvenile salmon density, size and biomass	Williams <i>et al.</i> , 2009
Salmon carcasses	Scotland	7 months	Carcass decomposition and invertebrate colonisation	No detectable increase in stream water total P and N, rapid colonisation by range of invertebrate taxa	Nislow <i>et al.</i> , 2010
			Isotopic enrichment	$\delta^{15}\text{N}$ enriched in periphyton, macroinvertebrate and juvenile salmon after carcass addition	
Carcass analogue pellets mimicking June lamprey spawning and October salmon spawning	Maine, USA	2 years	Invertebrate abundance Water chemistry	Increased downstream of carcass sites Increases in total dissolved P for 1 month	Guyette <i>et al.</i> , 2013, Guyette <i>et al.</i> , 2014
			Juvenile Atlantic salmon	Increases in mass and length in juvenile salmon	
			Atlantic salmon lipids	Treatment and temporal effects on total lipid	
			Isotopic enrichment	Higher in macroinvertebrates and juvenile Atlantic salmon	
MDNs from range of anadromous spawning fish	New Brunswick and Nova Scotia, Canada	10 months	Biofilm communities	Algal, fungal and bacterial abundance increased post-MDN enrichment, positive effect on community standing stock, greatest in bacteria	Samways <i>et al.</i> , 2015
			Biofilm $\delta^{15}\text{N}$ enrichment	Significant during spawning, later returning to baseline levels	

Nutrient addition	Location	Study duration	Response variables	Result	Citation
MDNs from range of spawning anadromous fish	New Brunswick and Nova Scotia	7 months	Isotopic enrichment	$\Delta^{15}\text{N}$ and $\delta^{13}\text{C}$ enrichment in biofilm, macroinvertebrates and resident salmonids	Samways <i>et al.</i> , 2018
Carcass analogue pellets	Scotland	2 years	Reliance on MDNs	Parr derived 23% of nutrients from MDN spawning subsidies	Auer <i>et al.</i> , 2018; McLennan <i>et al.</i> , 2019, 2021
			Macroinvertebrate biomass and abundance	Increases in nutrient-treated streams	
			Juvenile Atlantic salmon	Increases in length, body mass, biomass, but not density	
			Salmon natural selection	No longer selection for larger eggs or higher metabolic rate, and increased genetic diversity	
			Salmon standard metabolic rate (SMR)	Higher SMR individuals found in better microhabitats in control but not in nutrient-treated streams	
Salmon carcasses	Scotland	5 months	Salmon telomere length Atlantic salmon	Reduced rate of cellular ageing in poor microhabitats Increase in juvenile survival but no impact on growth rates	Burton <i>et al.</i> , 2020

**Table 2.2** | Examples of experiments exploring the impact of adding phosphorus or other nutrients to upland temperate streams. For an extended summary, see Gerwing & Plate (2019). Continued overleaf.

Nutrient addition	Location	Study duration	Response variables	Result	Citation
Phosphorus (as liquid H <sub>3</sub> PO <sub>4</sub> )	Alaska, USA	16 years	Primary producers	Increase in standing stock and bryophyte coverage	Slavik <i>et al.</i> 2004
			Macroinvertebrates	Increased densities of some invertebrate taxa	
			Arctic grayling ( <i>Thymallus arcticus</i> )	Increased weight and growth rate	
Phosphorus (as liquid H <sub>3</sub> PO <sub>4</sub> ), nitrogen (as liquid NH <sub>4</sub> NO <sub>3</sub> )	North Carolina, USA	2 years	Prey quantity, prey size and prey biomass of salamanders	Increase in prey size and number but not biomass, change in dietary composition compared to pre-treatment	Bumpers <i>et al.</i> 2017
Sockeye salmon ( <i>Oncorhynchus nerka</i> ) carcasses	Alaska, USA	20 years	Streambank tree growth	Increase in growth rate	Quinn <i>et al.</i> 2018
			Isotopic enrichment	Higher δ <sup>15</sup> N in needles	
Chum salmon ( <i>Oncorhynchus keta</i> ) carcasses	British Columbia, Canada	2 years	Juvenile coho salmon growth	Increased growth rate when fish were initially small and at high densities	Giannico & Hinch, 2007
			Pre-smolt size	Increased size in some situations	
Coho salmon ( <i>Oncorhynchus kisutch</i> ) carcasses	Washington, USA	8 months	Population density	Increased juvenile salmonid densities	Bilby <i>et al.</i> 1998
			Body condition	Increase body condition of juvenile salmonids	
			Stomach contents	Evidence of feeding on eggs and carcasses	

Nutrient addition	Location	Study duration	Response variables	Result	Citation
Sea lamprey carcasses + key nutrients	Maine, USA	7 weeks	Chlorophyll <i>a</i> Macroinvertebrate isotopes	Change in nutrient levels over time Enrichment in $\delta^{13}\text{C}$ in some taxa	Weaver <i>et al.</i> 2016
Salmon carcasses and carcass analogues	Idaho, USA	4 years	Biofilm standing crop Phosphorus	Chlorophyll <i>a</i> and ash-free dry mass (AFDM) increased for up to 6 weeks Short term increase in SRP, TP, and total dissolved P	Marcarelli <i>et al.</i> 2014
Salmon carcass analogue pellets	Idaho, USA	2 years	Periphyton chlorophyll <i>a</i> and AFDM Macroinvertebrate biomass Water chemistry	Increase in chlorophyll <i>a</i> and AFDM Increase in biomass but not density except in some taxa No detectable effect	Kohler <i>et al.</i> 2008

These analogues are widely viewed to have almost the same nutritional value as salmon carcasses themselves, and have been found to have broadly similar effects within streams, but limited removal to the riparian zone, in contrast to the transport of real carcasses by scavengers (Collins *et al.*, 2015). Ease of storage and application has led to such carcass analogues becoming a common form of nutrient supplementation. Like real carcasses, they produce large increases in nutrient concentrations soon after being applied to a stream. Guyette *et al.* (2014) demonstrated a 4-fold increase in P concentrations in treated versus untreated streams, with dissolved P levels elevated for up to five weeks. This elevation tends to lead to an increased abundance of the benthic macroinvertebrates that form the majority of the diet of juvenile stream-living fish: McLennan *et al.* (2019) demonstrated in Scottish streams that carcass analogues enhanced the growth of juvenile Atlantic salmon, concurrent with an increased abundance of macroinvertebrates. Similar results were obtained by Guyette *et al.* (2013) in streams in Maine, USA. Increases in fish biomass in response to the addition of nutrient subsidies may thus be due to faster growth rates of individual fish rather than changes in fish density (Auer *et al.*, 2018; Collins *et al.*, 2016; McLennan *et al.*, 2019). Interestingly, Auer *et al.* (2018) showed higher Atlantic salmon genetic diversity in streams treated with carcass analogues, as a result of more salmon families having surviving representatives. However, effects of nutrient additions are not always clear: some studies have shown only limited effects of carcass analogues on stream communities, although they did increase SRP concentrations (Wipfli *et al.*, 2010). Additionally, the provision of carcasses and carcass analogues cannot fully replicate the effect of salmon spawning, as it omits the excretion of waste products and deposition of gametes as well as the bioturbation occurring during nest construction, so that the input and transport of nutrients is reduced.

## 2.6 Applying science to conservation and management

Management and conservation strategies for declining populations of Atlantic salmon often focus on the freshwater phase of the lifecycle, where interventions are more easily facilitated than during the marine phase, and where the species is subject to domestic legal protection. Increasing both the number and quality of

migrating smolts is recognised to be a priority conservation strategy for the fish, both to combat low levels of marine survival but also to mitigate the impacts of environmental change (Thorstad *et al.*, 2021). One way in which this might prove possible is to restore nutrient levels in culturally oligotrophic tributary streams in which they spend the first year or more of life, since the evidence presented above shows that nutrient limitation may be widespread in these streams and that nutrient restoration may result in faster growth of the fish and larger size-at-age (Auer *et al.*, 2018; Guyette *et al.*, 2013; McLennan *et al.*, 2019). Size and condition (weight per unit length) of salmon smolts correlate directly with subsequent marine survival (Armstrong *et al.*, 2018; Gregory *et al.*, 2018). Therefore, if the increased size of salmon parr that has been observed after nutrient additions results in larger smolts, then there would be clear expected benefits in terms of numbers of returning adult salmon. Modelling by Benjamin *et al.* (2020) has demonstrated the potential for this method with chinook salmon (*Oncorhynchus tshawytscha*), with increases in potential smolt output and size. However, in some cases faster growth may result in salmon reaching the size that triggers smolting a year earlier, at a smaller smolt size (McLennan *et al.*, 2019). In such cases, nutrient additions may result in lower *per capita* chances of survival at sea, but increased numbers within a cohort surviving to become smolts, because of less time in the river and reduced inter-cohort competition. An additional factor is that faster growth may result in a greater proportion of male salmon maturing precociously as parr (Aubin-Horth *et al.*, 2006) which may have an effect on their chances of surviving to become smolts. Therefore an increase in the size-at-age of juvenile Atlantic salmon will not necessarily translate into more or larger adult fish; the overall effect of nutrient restoration on numbers and sizes of anadromous salmon thus depends on how these demographic factors balance out, and so warrants future investigation (Table 2.3).

The majority of experimental studies of nutrient addition for Atlantic salmon have been of short-term duration (usually lasting a year at most), hence the impact on salmon smolt and returning adult size and survival has not been assessed (Table 2.1). No study, including in other salmonids, has yet attempted repeated annual nutrient additions following a cohort of fish from hatching to returning spawners (Table 2.2). Clearly there is a need for longer term repeated dose experiments, especially since both empirical and modelling studies provide evidence that effects of nutrient addition tend to fade quickly once additions

cease (Benjamin *et al.*, 2020; Ericksen *et al.*, 2009). However, these experiments are extremely challenging to design and deliver at an appropriate scale and level of replication (Table 2.4). Therefore, predictive modelling using best available information on salmon demographics in response to growth variation based on short-term experiments (e.g. Auer *et al.*, 2018) is also recommended. Short term experiments also, by definition, are not examining streams in the state that may develop after years of nutrient supplementation, which is likely to be most relevant to applied management scenarios. For example, it may take some years for invertebrate communities to stabilise when nutrient levels are increased. Furthermore, the nutrient intervention may change the shape of the consumer pyramid (Leroux & Loreau, 2015) such that a greater biomass of salmon parr may ultimately support a larger predator population rather than increase the output of smolts. To overcome these issues, it may be possible to use extensive monitoring of invertebrate and juvenile salmon population responses to nutrients, coupled with water chemistry information, to build predictive models of the changes in production that could be achieved through nutrient restoration. Advantages and limitations of these experimental and observational approaches are summarised in Table 2.4.

It is important to consider that Atlantic salmon are also vulnerable to environmental changes as a result of a changing climate (Thorstad *et al.*, 2021). This intersects with nutrient dynamics along several dimensions. Warmer and wetter conditions are predicted as a result of climate change, with increased heavy rainfall (Alexander & Smith, 2006). The predicted greater frequency and intensity of extreme precipitation and associated flood flows has important implications for both upland rivers and lowland receiving waters. Phosphorus and nitrogen inputs to streams and rivers may therefore increase over the short term due to an increased frequency and magnitude of floods. However, these nutrients may be rapidly lost in the uplands due to increased rates of transport from flood flows, while further downstream the receiving waters will experience higher nutrient loading rates and greater risk of eutrophication. The balance between these processes is complex, but there is a clear need to manage riparian and floodplain habitats to hold back water and so retain nutrients in the upper reaches of catchments as much as possible.

Given that fish are ectothermic, a rise in water temperature will result in greater metabolic costs. In the high-latitude cold water aquatic ecosystems which

support salmonids, studies suggest that increasing water temperatures during the spring may result in the potential for increased salmonid growth and larger body size, but only if the food supply is not limiting (Bacon *et al.*, 2005; O’Gorman *et al.*, 2016; Xu *et al.*, 2010). Deliberate nutrient addition could therefore mitigate some adverse effects of climate change by maintaining sufficient prey availability and supporting growth and production as streams warm. However, a further complication is that warmer downstream receiving waters may be more vulnerable to oligotrophication (Arora *et al.*, 2016; Bolotov *et al.*, 2018).

It should always be borne in mind that the addition of nutrients to streams which may be of important conservation value is not without contention. Manipulating nutrient levels in oligotrophic streams which may be considered to have high ‘naturalness’ (Boon *et al.*, 2002) requires assessment of various trade-offs and uncertainties in a rapidly changing world. Impacts on receiving waters and the surrounding habitats are important considerations, together with evaluation of whether such nutrient inputs could result in alterations to river or stream conservation status under legislation including the European Habitats and European Water Framework Directives (Council of the European Communities 1992, 2000). In general, nutrient restoration may be suitable within watersheds designated for their current conservation value only if there would be no deleterious consequences for designated species, habitats, or characteristics.

Aiming to return to a historical baseline is widely agreed to be contentious and often not attainable in a non-static world, but if there is evidence of a reduction in salmon abundance over previous decades then the restoration of nutrients could be considered a return to a more ‘natural’ state (*sensu* Boon *et al.*, 2002), such as existed before human impacts. However, the addition of nutrients may have the potential to downgrade the ecological status of rivers; by way of example, under the EU Water Framework Directive (WFD) (Council of the European Communities, 2000) nutrient supplementation might cause a stream to lose a designation of ‘high’ ecological status (“species composition and abundance correspond totally or nearly totally to undisturbed conditions”) and instead be classified as having ‘good’ ecological status (“slight changes in species composition and abundance from the type-specific communities attributable to anthropogenic impacts on physicochemical and hydromorphological quality elements”). Indeed, nutrient supplementation is likely to not solely affect focal species such as salmon but may also affect the wider ecological community. In

particular, brown trout share a similar life history to Atlantic salmon and are frequently co-occurring and competing (Klemetsen *et al.*, 2003), so may be likely to be similarly impacted by nutrient supplementation. Changes in the densities and productivity of salmonid populations as a result of nutrient supplementation could have unforeseen effects, which may alter interspecific competition and could result in changes in the numbers of fish adopting different life histories in these species. In turn, this could impact the conservation goals of the nutrient supplementation strategy, as juvenile salmon could be outcompeted by brown trout and populations may decline rather than increase. Nutrient supplementation may also negatively impact other species of conservation importance, such as the freshwater pearl mussel (*Margaritifera margaritifera*), which requires nutrient-poor habitats (Gosselin, 2014). The aims of nutrient supplementation to aid Atlantic salmon conservation may thus conflict with the conservation aims of other species with differing habitat requirements, and thus requires consideration of potential trade-offs between the management and conservation of different species within the same habitat. Currently the potential impacts of an adaptive nutrient remediation strategy on the conservation status of rivers are unknown, as the current research in this area cannot adequately answer these large-scale uncertainties without further long-term study.

## 2.7 Conclusions and recommendations

Consideration of stream water chemistry and land/water/fisheries management history suggest that P and N are likely to be limiting to juvenile fish production in temperate upland river systems, and that nutrient addition may increase production of juvenile salmon through a combination of increases in survival and individual growth rates. However, further understanding is required to determine how such responses vary among different river systems and community structures, how they may affect a stream's conservation value, and how these effects map on to changes in numbers and sizes of adult (including precocious male) salmon (Table 2.3).

Given these considerations, the stage is set for incorporating nutrient restoration into the management of salmonid fisheries in the region, but with some caveats. As an overarching concern, I propose that wherever possible,

additions of P and N should be coupled with actions (such as restoration of habitat and channel complexity, increasing flowpath length in channelised reaches, fostering floodplain/channel connectivity) that enhance the ability of upland systems to retain and process limiting nutrients while also increasing their ‘naturalness’. This will serve the dual purpose of allowing these nutrient additions to be more effective *in situ* and limiting negative downstream impacts; they will also have additional ecosystem and fish habitat benefits. Nutrient restoration can therefore be coupled with habitat management such as planting of riparian trees to provide additional protection from climate change by shading and also enhancing local nutrient retention and cycling (O’Brian *et al.*, 2017).

Multiple replicates are required in appropriately balanced designs (Underwood, 1994) to measure effects of nutrient additions. Potentially such experiments may incorporate paired comparisons between bifurcating tributaries to increase power to detect experimental manipulation of nutrients controlling for other environmental variables (e.g. rainfall, geology and temperature) (Table 2.4).

**Table 2.3 | Suggestions for future research regarding the potential use of nutrient restoration to support migratory fish populations (in particular Atlantic salmon).**

<b>Knowledge gap</b>	<b>Issue</b>	<b>Relevant studies</b>
<i>Geographic range</i>	Literature currently biased towards North America; no studies relevant to migratory salmonids at the southern edge of European range, where populations are most fragile	Almodóvar <i>et al.</i> 2019
<i>Taxonomic skew</i>	Existing literature too focused on <i>Oncorhynchus</i> salmon, which tend to transport nutrients on a scale very atypical for migratory fish. Information needed on iteroparous species and those spawning at lower densities	Guyette <i>et al.</i> , 2013, Auer <i>et al.</i> , 2018
<i>Method of adding nutrients</i>	More information is needed on how the method, dose and frequency of application of nutrients can be made most cost-effective and environmentally sustainable	Pearsons <i>et al.</i> , 2007; Wipfli <i>et al.</i> , 2010
<i>Lack of long-term studies</i>	There is a need for multi-year dosing experiments in order to understand long-term effects on target species	Slavik <i>et al.</i> 2004
<i>Impact on rest of the catchment</i>	Little is known of the ‘safe’ level of nutrients that can be added to upland streams without causing eutrophication further downstream	

<i>Co-limiting factors</i>	P is commonly viewed as the main limiting nutrient, but N and P may often be co-limiting, other factors such as light levels may also constrain primary production	Jarvie <i>et al.</i> 2018
<i>Life-history considerations</i>	Complex interactions between the growth rate, migration and mortality of fish influence both the direction and strength of nutrient transport, with potential feedbacks to fish vital rates and population sizes	McLennan <i>et al.</i> , 2019
<i>Environmental change</i>	Expected increases in the frequency and magnitude of extreme flows will affect nutrient retention in streams, while increased temperatures will affect ectotherm energy budgets and nutritional requirements	Jonsson <i>et al.</i> , 2016; Kovach <i>et al.</i> , 2016

**Table 2.4 | Comparison of advantages and limitations of observational, small-scale experimental and large-scale adaptive management approaches to assessing effects of nutrient status on salmon populations.**

<b>Approach</b>	<b>Advantages</b>	<b>Limitations</b>
<i>Observational</i>	Large quantities of empirical data can be collected using natural variations across landscapes in real-world situations and interrogated with multi-variate modelling. The scenario may be immediately highly relevant to potential outcomes of changing nutrient state under prevailing environmental conditions.	Power to detect effects of any one variable likely to be limited especially a) at extremes of variable distributions, which is often the case for low nutrients, and b) where there are interactions among habitat variables. The distributions of variable distributions are not controlled and therefore are likely to be unbalanced.
<i>Small-scale experimental</i>	Tight control enables high power to detect effects of small changes in nutrient levels on a number of response variables (e.g. salmon number, size, condition, probability of early smolting or maturity).	Challenging logistics, usually relatively short-term and limited to a specific set of general habitat conditions. Consequently, results may not be generalisable to multiple real-world situations.
<i>Adaptive management and monitoring</i>	Facilitates rapid application of nutrient additions in real-world management scenarios based on best available information, while checking for potential damage and assessing potential benefits. The approach potentially provides large temporal and spatial scale and possibility of monitoring at various life stages.	Challenging to organise replication needed to provide power to detect effects of nutrient interventions with confidence. Substantial resource is required to sustain high-quality monitoring efforts across potentially multi-generational timespans.

In view of the difficulty of conducting such large scale experiments, I recommend that an adaptive management approach is adopted. This approach would fast-track likely benefits while providing the capacity to identify and minimise any damage due to inadvertent eutrophication. Such an approach will require the application of well co-ordinated and designed management and monitoring regimes. Additionally, the use of linked ecosystem modelling approaches, such as the Aquatic Trophic Productivity model, coupled with salmonid life cycle models, may help to provide insights into the relationship between nutrient additions and habitat restoration efforts, since these have previously shown the potential benefits for salmonids through carcass restoration (Bellmore *et al.*, 2017; Benjamin *et al.*, 2020). These approaches may provide a framework for the results of these small-scale but focused studies to contribute to more integrated answers.

In conclusion, nutrient restoration may well have the potential to help conserve and enhance protected Atlantic salmon populations in river systems that have experienced cultural oligotrophication. However, a combination of continued experiments and modelling, incorporating large-scale adaptive management monitoring is required to evaluate and refine the approach and minimise the risk of potentially adverse effects.

# Chapter 3 | How does the application method affect the impact of adding Atlantic salmon carcass analogues to upland streams?

## Abstract

Refining practical conservation measures to increase their efficacy may help threatened populations, by increasing our understanding of the impacts of conservation measures whilst allowing simplification of methods and implementation. A range of measures have been suggested to mitigate declines in Atlantic salmon (*Salmo salar*) populations. These include restoring nutrient levels in the streams in which the young fish live prior to migrating to sea. These streams have often become more oligotrophic as a result of both habitat deterioration and a decline in the number of spawning adults that release marine-derived nutrients from their carcasses if they die shortly after spawning. The lower nutrient levels in these streams potentially reduces the early growth rate of the juvenile salmon. Therefore the addition of nutrient pellets may help to mitigate nutrient loss and provide juveniles with an important boost to growth, which is correlated with increased marine survival. However, the most effective method for the application of nutrient pellets has not been assessed. Here I test the efficacy over two years of pellets applied either by placing in mesh bags or by hand-scattering, in streams with identical initial egg densities of Atlantic salmon. There was an increase in the individual body mass of invertebrates in the scattered pellet treatment compared to the control sites receiving no nutrients. However, there was no effect of either bagged or scattered pellets on the total biomass or abundance of invertebrates. Juvenile Atlantic salmon in the bagged pellet treatment showed increased growth in one of the two years. The scattered pellet treatment led to higher densities of juvenile salmon but poorer growth of fish compared to controls, presumably because of increased density-dependent competition. These results highlight the variability in outcomes of adding nutrients, and show the need for further study to reduce the possibility of adverse conservation effects.

### 3.1 Introduction

Upland streams are important freshwater habitats that can be critical for a range of species, as in total they cover large expanses of landscape. However, as the catchment areas they cover are small, streams may thus be more sensitive to environmental parameters than lowland systems, with particular respect to temperature, water chemistry, substrate and food availability (Meyer *et al.*, 2007). As a result of their upland locations, these streams are often low or limited in nutrients, and may often be oligotrophic (see Chapter 2). This makes upland streams particularly sensitive to changes in nutrient supply, such as nutrients imported to upland streams by the movement of animals, particularly by migratory species (Doughty *et al.*, 2016).

One group of species of particular importance to upland streams are salmon, both the Atlantic *Salmo salar* and Pacific *Onchorynchus* spp., which both use headwater streams as spawning and juvenile habitats prior to their migration to sea (Gende *et al.*, 2002; Jonsson & Jonsson, 2011). *Onchorynchus* spp. are semelparous and mortality occurs after spawning, whilst Atlantic salmon often die near the spawning grounds but are iteroparous and capable of returning to sea (Fleming, 1998; Jonsson & Jonsson, 2003). The carcasses of salmon dying on or near the spawning grounds, plus nutrients released through excretion, all contribute to a pulse of nutrients that is marine in origin, as salmon gain most of their biomass at sea (Jonsson & Jonsson, 2003; Naiman *et al.*, 2002). This represents an import of nutrients to upland streams, and it has been shown that this has beneficial effects on the growth of juvenile salmon, but also of algae and aquatic invertebrates within the stream (Bilby *et al.*, 1998; Nislow *et al.*, 2010; Williams *et al.*, 2009; see also Chapter 2). Stream biofilms have been shown to become enriched with marine-derived nutrients from spawning Atlantic salmon, with increased abundance and density (Samways *et al.*, 2015). Invertebrates have been shown to increase in abundance with exposure to marine-derived nutrients, but also to increase in nutritional quality through fatty acid incorporation in lipids (Samways *et al.*, 2017).

However, both Atlantic and Pacific salmon have experienced large population declines in recent decades, as a result of climatic changes to marine food webs and losses in freshwater habitat (Dadswell *et al.*, 2021; Mills *et al.*,

2013). In-stream barriers pose a particular issue, either preventing or reducing upstream passage success for populations already in decline, with some systems containing multiple barriers that exert a cumulative effect on success of reaching the spawning ground (Belletti *et al.*, 2020). In Scotland, Gowans *et al.* (2003) showed that only around 7% of tagged adult Atlantic salmon successfully passed multiple barriers to reach the spawning ground.

This population decline has resulted in fewer marine-derived nutrients being imported to spawning areas, as fewer adults return, with salmon in some river systems becoming net exporters of nutrients as smolts (Nislow *et al.*, 2004a). Consequently, stream habitats are benefitting less from these pulses of nutrients, and juvenile salmon may not receive the parental nutrients that increase growth to the same level as previous generations. As smolt size is positively correlated with survival at sea (Armstrong *et al.*, 2018; Gregory *et al.*, 2018), the impact of this nutrient reduction may be to reduce the overall survival of salmon at sea, as those from streams not enriched with parental nutrients may go to sea at a smaller body size (McLennan *et al.*, 2019). Therefore, the overall number of returning salmon to spawn may be further reduced, as fewer fish might survive to reach this stage, leading to a downward spiral in population size.

A potential mitigation tool to increase the production of juvenile salmon and counteract the loss of parental nutrients is the use of salmon carcass analogues; these are usually in the form of pellets, either made from processed salmon carcasses or industrial fish feed, and often containing marine fishmeal (Kohler *et al.*, 2012; Pearsons *et al.*, 2007). These pellets have broadly similar effects to those of actual salmon carcass nutrients, with multiple studies showing increases in periphyton, invertebrate biomass and abundance, and increased growth in juvenile salmon (Guyette *et al.*, 2014, 2013; McLennan *et al.*, 2019; see also Chapter 2). While these pellets have been used successfully to boost production in Pacific salmon streams (Kohler & Taki (2010) and Kohler *et al.* (2008)), they may be of limited applicability in those ecosystems since Pacific salmon carcass availability is usually high due to the semelparous nature of their lifecycle. However, they may have a bigger role in management of Atlantic salmon due to the marked decline in population sizes (Lenders *et al.*, 2016). There has thus been significant interest in the impact of carcass analogues on freshwater production of Atlantic salmon (Auer *et al.*, 2018; Guyette *et al.*, 2014, 2013; McLennan *et al.*, 2019, 2021).

Previous work using carcass analogues has involved adding pellets to mesh bags in the style of a ‘carcass’; this has been shown to be effective in increasing both the growth of fish but also of invertebrates in both Maine, USA, and Scotland, UK (Auer *et al.*, 2018; Guyette *et al.*, 2014, 2013; McLennan *et al.*, 2019). However, the use of bagged pellets as carcass analogue requires anchoring or burying of the bags in the substrate to prevent downstream dislodgement during periods of high flow, and if implemented as a conservation measure, would require considerable time and resources depending on the area covered. An alternative to the bagged pellet method is simply to hand-scatter pellets over the stream area, which can be done from the bank side (depending on stream width) and would not require anchoring of pellets in the substrate and thus be less resource intensive as a practical conservation measure. However, the effects of this direct application of pellets to streams, such as the impacts on invertebrate size and abundance and the impacts on salmon growth and condition, have not been investigated.

Here I compare the effect of two contrasting methods of nutrient application using carcass analogues on the biomass, abundance and diversity of stream invertebrate communities, and on the growth and condition of juvenile Atlantic salmon, in streams in northern Scotland. The two methods were carcass analogues applied using bags of pellets, and carcass analogues applied via scattering the same number of pellets; both were compared to untreated control areas. I predicted that the biomass, abundance and diversity of invertebrates and the growth (fork length, body mass) and condition (body condition, relative mass, density and biomass) of Atlantic salmon in both nutrient treatments would increase relative to the control, but that greater increases in these metrics would be observed in the bagged treatments relative to the scattered treatment due to the nutrients in loose pellets being dispersed downstream more quickly.

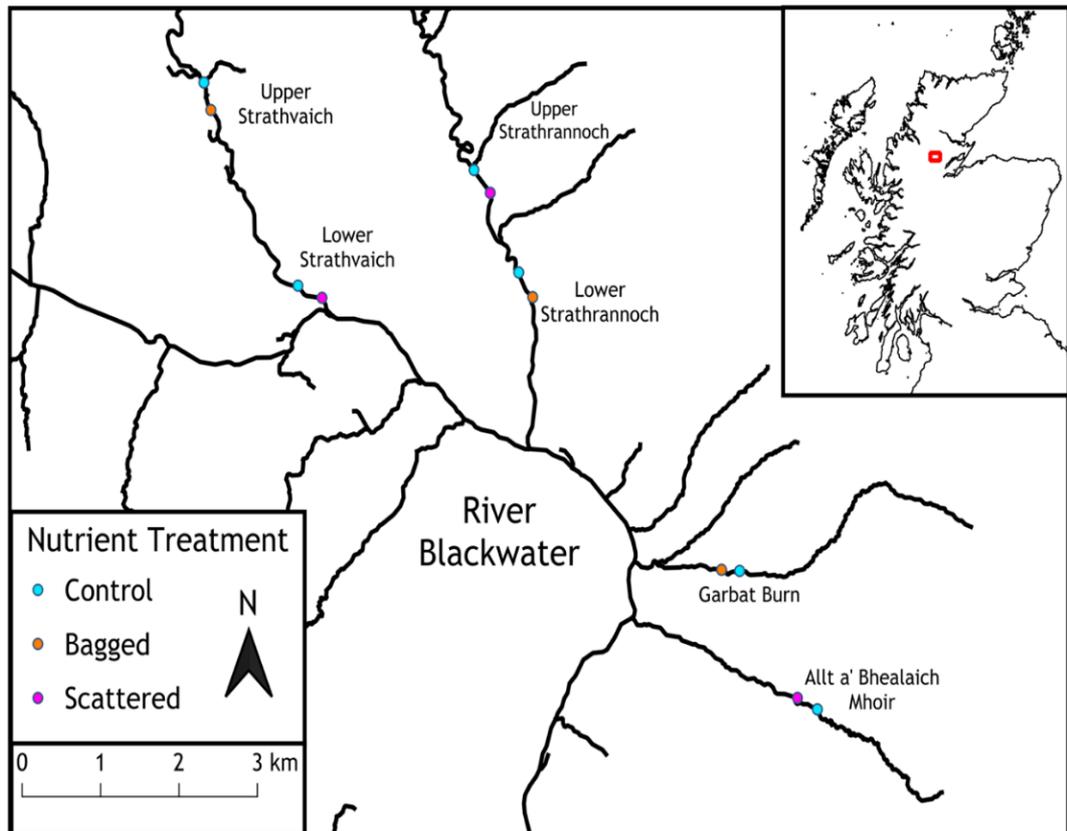
## 3.2 Methods

### 3.2.1 Site selection

In December 2019, six sites were selected across four headwater tributaries of the River Blackwater, which forms part of the River Conon catchment in northern Scotland (Fig. 3.1, Table A.1). These streams were in close proximity (a

maximum of 10.5km apart) and so had a similar climate and shared broadly similar characteristics, being in open moorland with occasional tree cover, with two streams (Allt' a Bhealaich Mhoir and the Garbat Burn) being slightly higher in elevation and thus narrower than the other streams (Rannoch and Vaich). Resident fish include brown trout (*Salmo trutta*) and minnow (*Phoxinus phoxinus*), however the upstream passage of returning Atlantic salmon is prevented by hydropower dams. Atlantic salmon have therefore been stocked as eggs (derived from wild returning spawners caught in the catchment - see below) since the hydropower system was installed in the 1960s, so that fry and parr are present in stocked areas. Upon reaching the smolt stage of the lifecycle, the fish are able to pass the dams on their downstream seaward migration.

Each site consisted of two 500m<sup>2</sup> experimental 'zones' of stream, separated by a 300m long section of stream defined as a buffer zone. The upstream zone within each site was designated as the control, while the downstream zone was one of two carcass analogue application treatments: 'bagged' or 'scattered'. Over the six sites, three sites were assigned to each nutrient treatment. The bagged treatment consisted of 15kg of fish food pellets (LR Ignite 51 2000 53pn, BioMar Ltd, Grangemouth, UK) divided into five 3kg hessian bags, that were anchored in the stream substrate using rocks. The 5 bags were evenly distributed across each of the 500m<sup>2</sup> treatment zones. The scattered treatments received the same 15kg quantity of pellets per 500m<sup>2</sup> treatment zone, but these were applied via hand scattering at an even density across the substrate. The pellets immediately sank and rested amongst the gravel and pebbles that formed the substrate. The Rannoch and Vaich tributaries had two sites each, designated 'upper' and 'lower', and these were a minimum of 1km apart. The experiment was run in two years (2020 and 2021), although in the second year the Allt' a Bhealaich Mhoir and Garbat Burn sites were not used. The Rannoch and Vaich tributaries were also subject to stocking of non-experimental eggs outside of the study sites by fisheries managers, although efforts were made not to stock close to the experimental study sites.



**Figure 3.1** | Locations of the six sample sites located across four tributaries of the River Blackwater, Northern Scotland. Each site consisted of a control and a nutrient treatment zone.

### 3.2.2 Atlantic salmon egg rearing and planting

The Atlantic salmon used within this study were sourced from 25 full sibling Atlantic salmon families which were conceived by IVF using gametes of wild, previously stocked returning fish caught at a fish trap further downstream on the River Blackwater in late autumn 2019 and 2020 respectively. All parents were one sea winter fish (i.e. had spent one winter at sea before returning to spawn), and the eggs from each female were fertilised with the sperm of a single male (with no re-use of males between females). Fin clips were taken from each parent for later family assignment via genotyping. Eggs were reared at the SSE hatchery at Contin until the eyed stage, at which point they were then divided into 12 mixed-family batches, consisting of 2500 eggs in total, with 100 eggs selected randomly from each family.

Each batch of eggs was assigned to an experimental zone, producing a density of 5 eggs m<sup>-2</sup>. The eggs were planted out concurrently with the application

of carcass analogue pellets between 26-27<sup>th</sup> February 2020, and between 25<sup>th</sup> February - 1<sup>st</sup> March 2021. Two Vibert boxes, each containing 100 eggs from each mixed-family batch, were placed at the upstream and downstream limit of each treatment and control zone, in order to assess egg survival. The upstream Vibert box from each area contained a HOBO temperature logger (-20 to 70 ± 0.53°C; Onset Computer Corporation, Bourne MA, USA), which recorded hourly in 2020 and every 2 hours in 2021 over the duration of the field experiment. The remaining 2300 eggs per experimental zone were planted into a series of artificial redds between the two Vibert boxes.

### 3.2.3 Sampling and habitat surveys

Between 21-26<sup>th</sup> September 2020, and between 15-20<sup>th</sup> August 2021, triple-pass electrofishing (E-fish ltd, Grange-over-Sands, UK; 350V, 60Hz and a 10% duty cycle adjusted to local water conditions) was used to capture surviving age 0+ Atlantic salmon stocked as eggs; in 2021 an assessment was also made of age 1+ parr that had been stocked as part of the same experiment the previous year. Bank-to-bank electrofishing was performed using the same electrofishing team throughout. The entire 500m<sup>2</sup> area of each experimental zone was not fished, but fishing began from the lower limit of each experimental zone working upstream, divided into sections using bankside marker pegs, the number of which was dependent on the total area of the experimental zone. All fish captured were lightly anaesthetised using benzocaine, weighed and fork length was recorded, along with the stream section in which they were captured. In 2020, fin clips were taken from 0+ Atlantic salmon for family assignment. Fish were allowed to recover from anaesthesia and were then placed into keep nets downstream of continuing electrofishing; they were then released back into the zone they were captured when electrofishing was complete.

Subsequent to the electrofishing within each site, macroinvertebrate samples were taken between 21-26<sup>th</sup> September 2020. Invertebrates were captured via 60 sec kick samples in six randomly-selected locations per 500m<sup>2</sup> zone; these were then combined into a pooled sample which was immediately preserved in 70% ethanol. Invertebrates were also sampled 500m downstream of each bagged and scattered zone.

Instream habitat surveys were conducted at the time of sampling. At each sampling zone within a site, 10 water depth measurements were taken at random points across the fished area, and three bank-to-bank widths were recorded. Flow and substrate surveys were visually conducted by estimating the percentage of the fished zone covered by differing flow rates and substrate sizes (SFCC, 2007). For flow rate, this covered four classes, 'pool', 'glide', 'run', 'riffle' and 'torrent', with each class given a value based on the percentage of the area it covered. Substrate contained eight classes, 'gravel', 'pebble', 'cobble', 'boulder' and 'bedrock', which were based on given substrate sizes. These classes were then assigned numbers, with 1 being the slowest flow or smallest substrate, while 5 represented the fastest flow and 6 the largest substrate particle size. An average score was then calculated for each of flow and substrate for each zone by taking the class number (each class was numbered numerically with the lowest value given to the slowest flow/smallest substrate) and multiplying it by the proportion of the zone covered by the flow or substrate class.

### 3.2.4 Processing of macroinvertebrates

Macroinvertebrates were sorted and identified to family level using a dichotomous key (Dobson *et al.*, 2012). An image was taken of each individual and lengths and widths measured to the nearest 0.01 mm using ImageJ software. Length-weight relationships from the literature (Table A.2) were then used to calculate the dry mass of each individual. Macroinvertebrates were then sorted on size criteria based on the gape limitation of juvenile salmon. Criteria for exclusion were: width greater than 2.5mm, mass equal or less than 0.01mg, and mass greater than 5mg (Wańkowski, 1979). This size range excluded items only consumable by fish over ~100mm in fork length, based on previous behavioural observations and growth trials for juvenile Atlantic salmon fed items of differing size (Wańkowski, 1979). All data were analysed post-exclusion of invertebrates outside of the gape criteria.

### 3.2.5 Data analysis

Linear mixed effects models in R (v4.2.0) were used to analyse invertebrate data. Invertebrate mass data were non-normally distributed so were log-transformed. Abundance was calculated as a total, and also separately for the orders Diptera, Ephemeroptera, Plecoptera and Trichoptera (DEPT). These orders were selected as they include common Atlantic salmon prey items (Martinussen *et al.*, 2011), particularly Diptera, and the abundance of Ephemeroptera, Plecoptera and Trichoptera are commonly used as an assessment tool for river health (Barbour *et al.*, 1996). Total log mass was also calculated as an overall total and for DEPT by summing the masses of all individuals and then logging the value. Invertebrate diversity (Shannon's index and Simpson's index, based on family ID, family number and family evenness) metrics were calculated using the R package 'vegan' (Pielou, 1966; Simpson, 1949; Spellerberg & Fedor, 2003). Linear mixed effects models were also used to analyse invertebrate data. All models had treatment as a fixed effect with site as a random effect. PC1 was not included in invertebrate models as no habitat data were taken at the sample sites downstream of the treatment areas.

To differentiate between juvenile salmon age cohorts, frequency histograms of fork lengths were generated for each site in order to determine the upper size limit for 0+ fish. Fish body condition was calculated using Le Cren's Index (equation 1), where  $W$  is weight,  $L$  is length,  $a$  is a constant, and  $b$  is the exponent of the arithmetic form of the weight-length relationship (Le Cren, 1951; Froese, 2006):

$$\frac{W}{aL^b} \quad (1)$$

Fish density (individuals/m<sup>2</sup>) and biomass (g/m<sup>2</sup>) were calculated by dividing the number or weight of fish caught within each section of a zone divided by the area of that section.

A principal component analysis using the R package 'stats' was conducted using four habitat variables: mean water depth, mean width, flow and substrate scores. This was used to reduce the habitat data for a zone to a single PC1 variable, comprised of the four aforementioned variables collected during the

habitat surveys. Positive values for this PC1 variable were associated with larger substrate particles, whilst negative values were associated with higher flow rates and greater width. PC1 was calculated separately for each year.

The data on water temperatures allowed calculation of expected growth rates for juvenile salmon if food was unlimited, based on a previous model of salmon growth (Elliott & Hurley, 1997). This allowed an assessment of the extent to which growth was food-limited at each site. The expected time of first feeding was determined in an iterative process by first calculating the mean temperature from fertilisation until mid May (the typical time of first feeding). This was calculated as the sum of (mean daily hatchery temperature × days that eggs spent in the hatchery) + (estimated number of days in the stream prior to first feeding × mean stream temperature over that time), divided by the total number of days. This gave a mean temperature which was then visually assessed against values for the relationship between incubation temperature and days to first feeding given by Kane (1988), in order to give a first estimate for the number of days from fertilisation to first feeding. The number of days in the stream prior to first feeding was then refined to produce a closely matching temperature with number of days from fertilisation. An initial body mass of 160mg at first feeding (Peterson & Martin-Robichaud, 1995) was assumed for all fish. Using the estimated date of first feeding as the start date, a growth equation (equation 2, taken from Elliott & Hurley, 1997) was applied on a site-specific basis, following site-specific temperature data obtained from the loggers.

$$W_t = [W_o^b + bc \frac{(T - T_{LIM})t}{\{100(T_M - T_{LIM})\}}]^{1/b} \quad (2)$$

$W_o$  is defined as initial fish mass (160mg), with  $W_t$  defined as the final fish mass (i.e. at the time of electrofishing) after  $t$  days at  $T$  °C.  $T_{LIM}$  was defined as =  $T_L$  if  $T \leq T_M$ , or  $T_{LIM} = T_U$  if  $T > T_M$ ;  $T_M$  is the temperature for optimum growth (15.94°C), while  $T_L$  and  $T_U$  are 5.99 °C and 22.51 °C respectively.  $b$  is the power transformation of body mass which captures linear growth with time ( $b = 0.31$ ), whilst  $c$  is the growth rate of a 1g fish at optimum temperature ( $c = 3.53$ ; all parameter values are from Elliott & Hurley (1997)).

This equation was used to calculate a weekly increase in body mass, using the mean weekly water temperature at each site and  $t = 7$ . This was continued until

the date of electrofishing to produce an expected body mass at that time. This expected body mass is indicative of fish grown under *ad libitum* laboratory conditions and so reflects the maximum expected body mass under the temperatures experienced. Deviations from this expected body mass were then calculated by subtracting actual body mass from expected body mass to produce a relative body mass value. Relative mass was only calculated for 0+ fry.

Linear mixed effects models were used to examine the effects of the contrasting nutrient application methods on juvenile fork length, body mass, body condition, relative mass, density, and biomass. Site was used as a random effect to reflect the paired control-treatment experimental design. Fork length, body mass, body condition and relative mass models also contained section as a random effect nested within site, but this was not used for the density and biomass models as there was only a single measure of density or biomass per section. Control sections were organised as A1, B1 *et cetera*, whilst both bagged and scattered sections were organised as A2, B2 *et cetera* in order to differentiate between the control and treatment zones within each site. Fixed effects always included treatment and the habitat variable PC1.

### 3.3 Results

#### 3.3.1 Impact of contrasting nutrient application methods on upland stream invertebrate communities

Invertebrate samples collected in 2020 showed differences between the bagged and scattered treatment when compared to the control, and samples taken downstream of both the bagged and scattered treatment also differed in comparison to both the control and the two treatments. The individual log mass of invertebrates was significantly greater in both the scattered treatment zone and 500m downstream of the scattered treatment zone in comparison to the control, but there was no effect of the bagged treatment or 500m downstream of the bagged treatment (Fig. 3.2A, Table 3.1). Although individual log mass was greater in the scattered treatment zone and the samples taken downstream of the scattered treatment zone, there was no significant difference in invertebrate

total abundance or invertebrate total log mass across either treatment, nor downstream of either treatment (Fig. 3.2B and C, Table 3.2).

The orders Diptera, Ephemeroptera, Plecoptera and Trichoptera (DEPT) were examined independently. The log mass of individual animals was significantly higher in the scattered zone, downstream of the bagged and downstream of the scattered treatment zones for Dipterans, but showed no difference for Ephemeropterans (Fig. 3.3A and B, Table 3.3). There was a significant negative effect in the bagged treatment for Plecopterans, and downstream of the scattered treatment for Trichopterans (Fig. 3.3C and D, Table 3.4). DEPT total abundance and total log mass were also examined, but there was no effect of treatment (Fig. A.1-A.2, Tables A.3-A.6).

The taxonomic diversity of invertebrates across the treatments was also assessed. Shannon’s family diversity was significantly lower downstream of the scattered treatment, whilst Simpson’s family diversity did not differ between treatments (Fig. 3.4A and B, Table 3.5). The number of families was significantly lower downstream of the scattered treatment, however family evenness did not differ between the treatments (Fig. 3.4C and D, Table 3.6).

**Table 3.1 | Results of linear mixed effects models analysing effects of nutrient treatment on the log mass of individual invertebrates sampled in 2020. Bagged and scattered treatments (and their downstream counterparts) are compared to the control (no nutrients added).**

<i>Predictors</i>	<b>Log mass</b>				
	<i>Estimates</i>	<i>std. Error</i>	<i>t value</i>	<i>p</i>	<i>df</i>
(Intercept)	-2.11	0.13	-16.40	<0.001	2479.00
Treatment [Bagged]	-0.12	0.08	-1.62	0.106	2479.00
Treatment [Scattered]	0.18	0.09	2.10	<b>0.035</b>	2479.00
Treatment [Downstream of Bagged]	0.05	0.07	0.63	0.531	2479.00
Treatment [Downstream of Scattered]	0.47	0.08	5.71	<0.001	2479.00
<b>Random Effects</b>					
$\sigma^2$	1.26				
$\tau_{00}$ site	0.09				
Observations	2486				

**Table 3.2 | Results of linear mixed effects models analysing effects of nutrient treatment on the total abundance and total log mass of invertebrates sampled in 2020. Bagged and scattered treatments (and their downstream counterparts) are compared to the control (no nutrients added).**

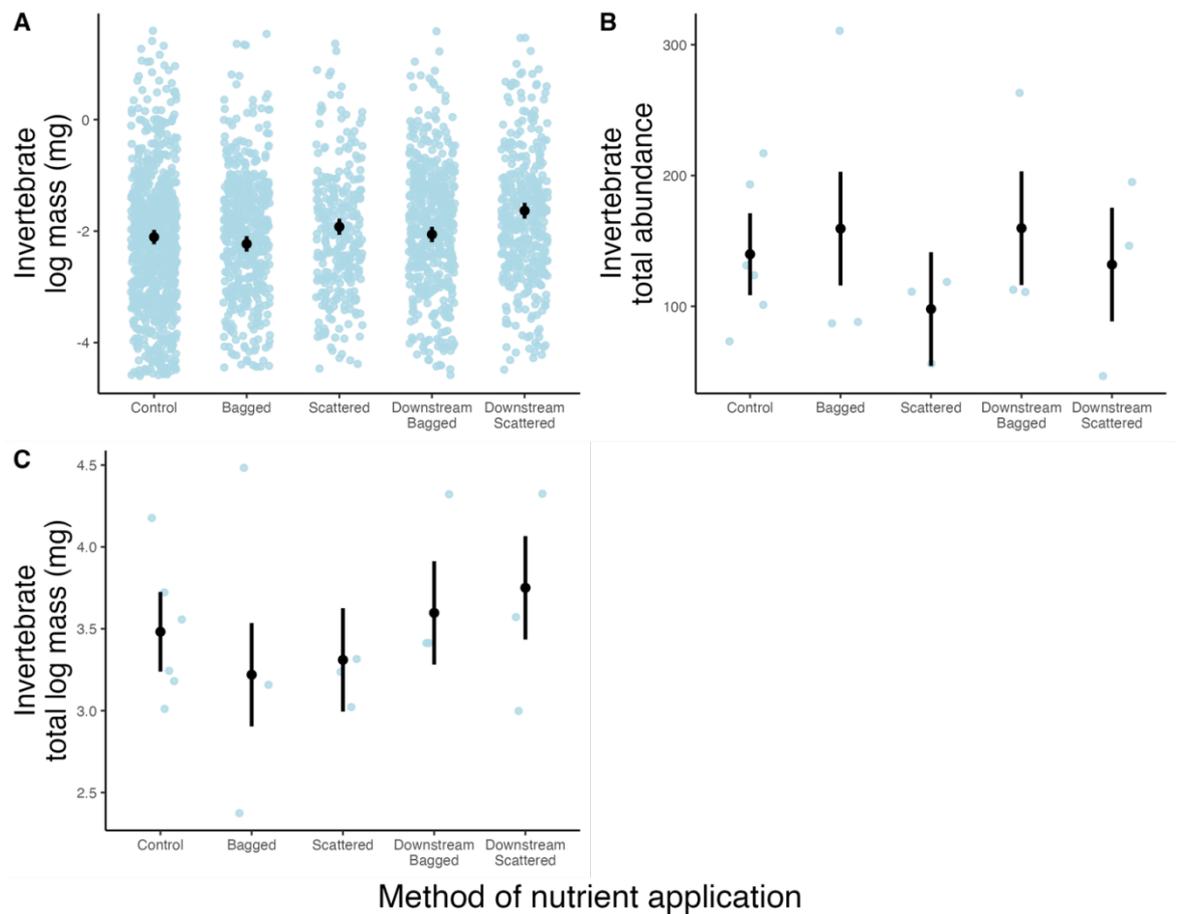
<i>Predictors</i>	<b>Total abundance</b>					<b>Total log mass</b>				
	<i>Estimates</i>	<i>std. Error</i>	<i>t value</i>	<i>p</i>	<i>df</i>	<i>Estimates</i>	<i>std. Error</i>	<i>t value</i>	<i>p</i>	<i>df</i>
(Intercept)	139.83	31.32	4.46	0.001	11.0	3.48	0.24	14.31	<0.001	11.0
Treatment [Bagged]	19.57	48.29	0.41	0.693	11.0	-0.26	0.30	-0.86	0.407	11.0
Treatment [Scattered]	-41.90	48.29	-0.87	0.404	11.0	-0.17	0.30	-0.56	0.583	11.0
Treatment [Downstream of Bagged]	19.90	48.29	0.41	0.688	11.0	0.12	0.30	0.38	0.712	11.0
Treatment [Downstream of Scattered]	-7.90	48.29	-0.16	0.873	11.0	0.27	0.30	0.88	0.396	11.0
<b>Random Effects</b>										
$\sigma^2$	4274.18					0.16				
$\tau_{00}$	1611.19 <sub>site</sub>					0.20 <sub>site</sub>				
Observations	18					18				

**Table 3.3 | Results of linear mixed effects models analysing effects of nutrient treatment on the log mass of individual Diptera and Ephemeroptera sampled in 2020. Bagged and scattered treatments (and their downstream counterparts) are compared to the control (no nutrients added).**

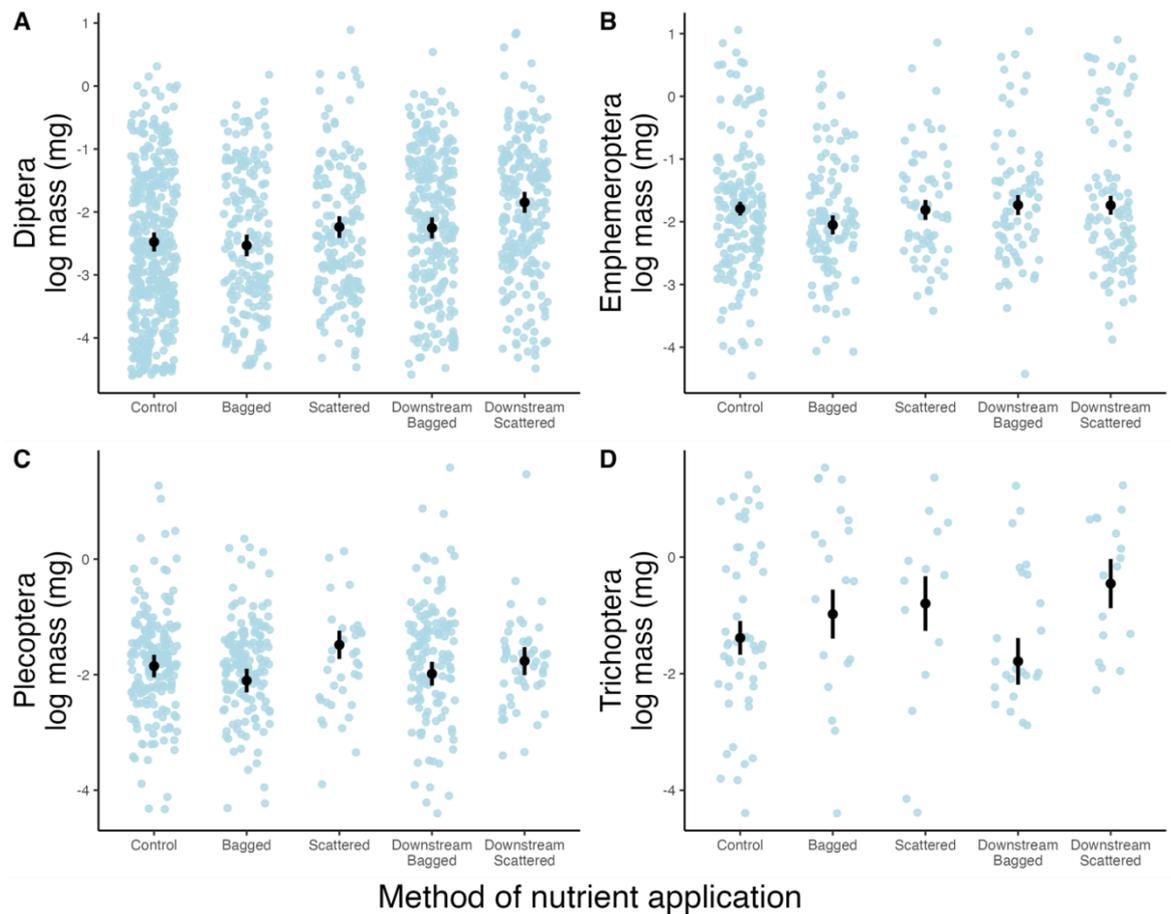
<i>Predictors</i>	Diptera individual log mass					Ephemeroptera individual log mass				
	<i>Estimates</i>	<i>std. Error</i>	<i>t value</i>	<i>p</i>	<i>df</i>	<i>Estimates</i>	<i>std. Error</i>	<i>t value</i>	<i>p</i>	<i>df</i>
(Intercept)	-2.48	0.15	-16.37	<0.001	1220.0	-1.79	0.11	-16.26	<0.001	514.0
Treatment [Bagged]	-0.06	0.11	-0.49	0.625	1220.0	-0.26	0.15	-1.74	0.083	514.0
Treatment [Scattered]	0.24	0.11	2.12	<b>0.034</b>	1220.0	-0.02	0.16	-0.13	0.898	514.0
Treatment [Downstream of Bagged]	0.22	0.11	2.06	<b>0.040</b>	1220.0	0.06	0.16	0.36	0.720	514.0
Treatment [Downstream of Scattered]	0.63	0.10	6.07	<0.001	1220.0	0.05	0.15	0.35	0.727	514.0
<b>Random Effects</b>										
$\sigma^2$	1.17					1.01				
$\tau_{00}$	0.12 <sub>site</sub>					0.03 <sub>site</sub>				
Observations	1227					521				

**Table 3.4** | Results of linear mixed effects models analysing effects of nutrient treatment on the log mass of individual Plecoptera and Trichoptera sampled in 2020. Bagged and scattered treatments (and their downstream counterparts) are compared to the control (no nutrients added).

<i>Predictors</i>	<b>Plecoptera individual log mass</b>					<b>Trichoptera individual log mass</b>				
	<i>Estimate</i>	<i>std. Error</i>	<i>t value</i>	<i>p</i>	<i>df</i>	<i>Estimate</i>	<i>std. Error</i>	<i>t value</i>	<i>p</i>	<i>df</i>
(Intercept)	-1.85	0.19	-9.55	<0.001	533.0	-1.39	0.29	-4.77	<0.001	118.0
Treatment [Bagged]	-0.25	0.11	-2.33	0.020	533.0	0.41	0.41	1.00	0.320	118.0
Treatment [Scattered]	0.37	0.20	1.86	0.063	533.0	0.59	0.49	1.21	0.230	118.0
Treatment [Downstream of Bagged]	-0.13	0.11	-1.21	0.227	533.0	-0.40	0.39	-1.04	0.300	118.0
Treatment [Downstream of Scattered]	0.09	0.20	0.43	0.664	533.0	0.93	0.42	2.20	0.030	118.0
<b>Random Effects</b>										
$\sigma^2$	0.77					1.98				
$\tau_{00}$	0.19 <sub>site</sub>					0.23 <sub>site</sub>				
Observations	540					125				



**Figure 3.2** | Log mass of individual animals (A), total abundance (B) and total log mass (C) of invertebrates sampled across the control, nutrient treatments, and 500m downstream of the nutrient treatments over six sites across four tributaries of the River Blackwater in 2020 (data plotted as model predictions  $\pm$  standard error (SE),  $n = 2486$  animals (A),  $n = 18$  samples (B, C)).



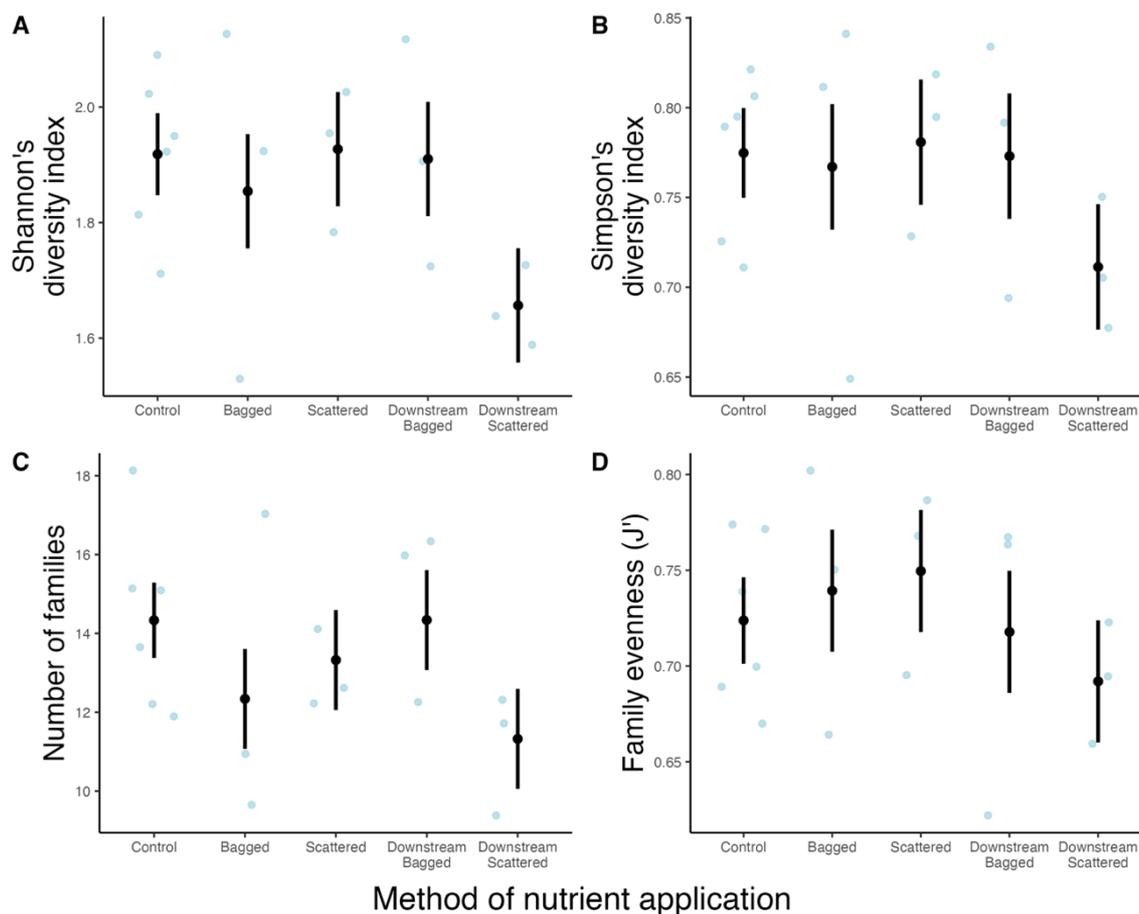
**Figure 3.3** | Individual log masses of Diptera (A, n=1227), Ephemeroptera (B, n=521), Plecoptera (C, n=540) and Trichoptera (D, n=125) sampled across the control sections, nutrient treatment sections, and 500m downstream of the nutrient treatment sections over six sites across four tributaries of the River Blackwater in 2020 (data plotted as model predictions  $\pm$  SE).

**Table 3.5** | Results of linear mixed effects models analysing effects of nutrient treatment on the Shannon-Weiner family and Simpson family diversity for invertebrates sampled in 2020. Bagged and scattered treatments (and their downstream counterparts) are compared to the control (no nutrients added).

<i>Predictors</i>	Shannon-Weiner diversity					Simpson diversity				
	<i>Estimates</i>	<i>std. Error</i>	<i>t value</i>	<i>p</i>	<i>df</i>	<i>Estimates</i>	<i>std. Error</i>	<i>t value</i>	<i>p</i>	<i>df</i>
(Intercept)	1.92	0.07	27.01	<0.001	11.00	0.77	0.02	31.01	<0.001	11.00
Treatment [Bagged]	-0.06	0.11	-0.58	0.575	11.00	-0.01	0.04	-0.20	0.849	11.00
Treatment [Scattered]	0.01	0.11	0.08	0.939	11.00	0.01	0.04	0.15	0.882	11.00
Treatment [Downstream of Bagged]	-0.01	0.11	-0.07	0.942	11.00	-0.00	0.04	-0.05	0.965	11.00
Treatment [Downstream of Scattered]	-0.26	0.11	-2.36	<b>0.038</b>	11.00	-0.06	0.04	-1.60	0.137	11.00
<b>Random Effects</b>										
$\sigma^2$	0.02					0.00				
$\tau_{00}$	0.01 <sub>site</sub>					0.00 <sub>site</sub>				
Observations	18					18				

**Table 3.6 | Results of linear mixed effects models analysing effects of nutrient treatment on the family diversity and evenness diversity for invertebrates sampled in 2020. Bagged and scattered treatments (and their downstream counterparts) are compared to the control (no nutrients added).**

<i>Predictors</i>	<b>Number of families</b>					<b>Family evenness</b>				
	<i>Estimates</i>	<i>std. Error</i>	<i>t value</i>	<i>p</i>	<i>df</i>	<i>Estimates</i>	<i>std. Error</i>	<i>t value</i>	<i>p</i>	<i>df</i>
(Intercept)	14.33	0.96	14.99	<0.001	11.00	0.72	0.02	32.05	<0.001	11.00
Treatment [Bagged]	-1.99	1.28	-1.56	0.147	11.00	0.02	0.04	0.41	0.689	11.00
Treatment [Scattered]	-1.01	1.28	-0.79	0.447	11.00	0.03	0.04	0.68	0.510	11.00
Treatment [Downstream of Bagged]	0.01	1.28	0.01	0.996	11.00	-0.01	0.04	-0.16	0.878	11.00
Treatment [Downstream of Scattered]	-3.01	1.28	-2.36	<b>0.038</b>	11.00	-0.03	0.04	-0.84	0.419	11.00
<b>Random Effects</b>										
$\sigma^2$	2.80					0.00				
$\tau_{00}$	2.69 <sub>site</sub>					0.00 <sub>site</sub>				
Observations	18					18				



**Figure 3.4 |** Diversity metrics for invertebrates sampled across the control, nutrient treatments, and 500m downstream of the nutrient treatments over six sites across four tributaries of the River Blackwater in 2020. A) Shannon's family diversity, B) Simpson's family diversity, C) number of families, D) family evenness (data plotted as model predictions  $\pm$  SE, n= 18 samples).

### 3.3.2 Impact of contrasting nutrient application methods on Atlantic salmon

In 2020, 957 age 0+ Atlantic salmon fry were caught, alongside 287 Atlantic salmon parr (survivors of those stocked in previous years) and 713 resident brown trout. In 2021, 226 age 0+ Atlantic salmon fry and 495 parr were captured, along with 13 resident brown trout.

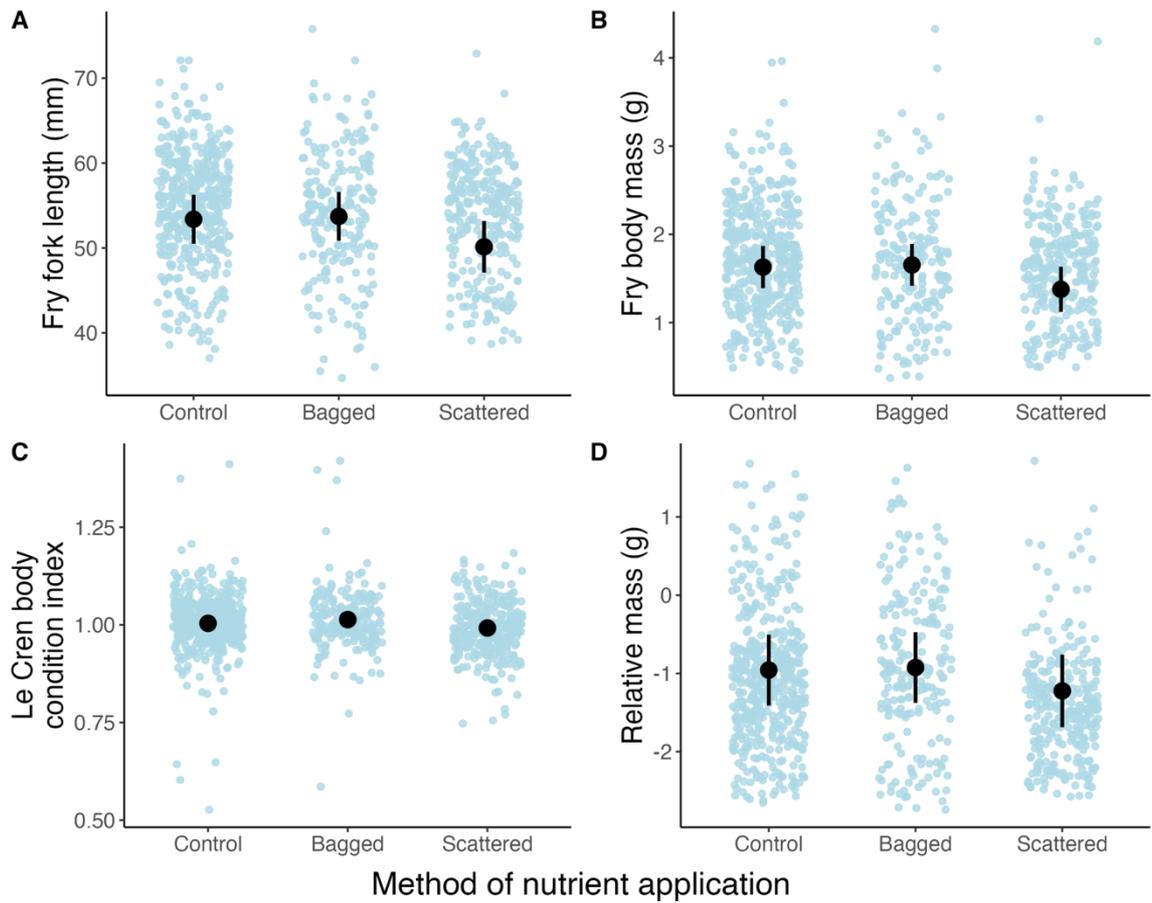
*Impact of contrasting nutrient application methods on Atlantic salmon fry sampled in 2020*

The contrasting methods of nutrient application impacted juvenile salmon in a number of ways. The fork length of 0+ Atlantic salmon was slightly but significantly lower (a mean difference of 2.2%) in sites which received the scattered pellet treatment when compared to salmon in the control or bagged pellet treatment. There was no significant difference in fork length between fish in the control and bagged treatment (Fig. 3.5A, Table 3.7). The body mass of fry was also significantly lower in the scattered treatment (a mean difference of 8.8%) but did not differ significantly from the control in the bagged treatment (Fig. 3.5B, Table 3.7). There was no significant effect of the combined habitat variable PC1 on either the fork length or body mass.

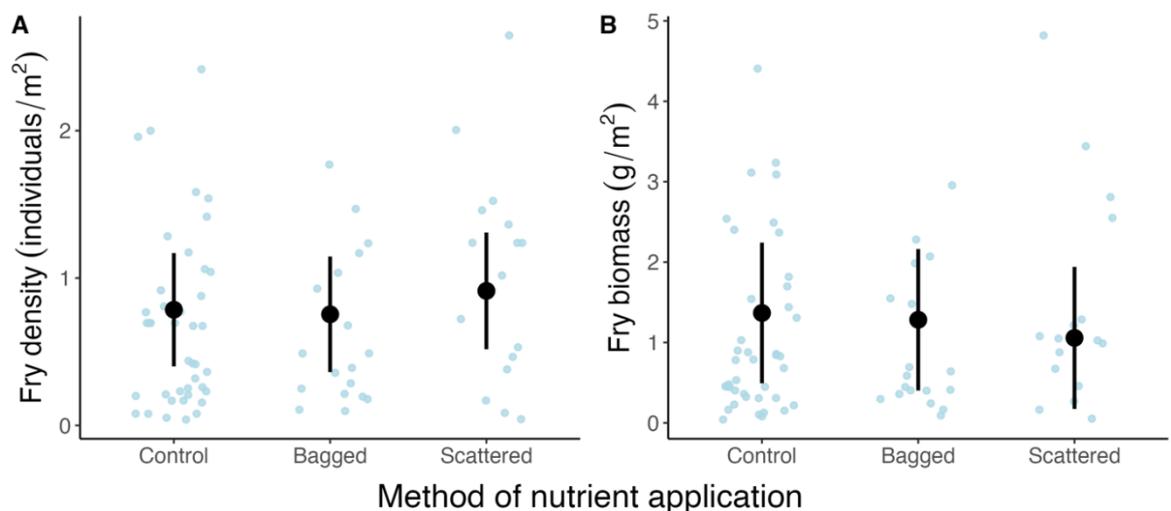
Le Cren's body condition index did not differ significantly from the control in either the bagged or the scattered treatments, but there was a strongly significant negative effect of PC1 on body condition, due to 0+ fish being in better condition in sites with narrower width and larger substrate (Fig. 3.5C, Table 3.8).

In all sites the mean mass of 0+ salmon was less than that predicted by the growth model for fish on *ad libitum* rations, indicating that food was limiting. However, the relative mass of these fish was significantly lower in the scattered treatment than in the control, whereas the bagged treatment did not differ from the control (Fig. 3.5D, Table 3.8).

There was no significant difference in the density of 0+ Atlantic salmon between either the bagged or scattered treatment when compared to the control, nor was there an effect of PC1 (Fig. 3.6A, Table 3.9). There was also no significant difference in 0+ salmon biomass between the bagged and the scattered treatment compared to the control, although in this case there was a significant negative relationship between biomass and PC1, with greater fry biomass in narrower streams with larger substrate (Fig. 3.6B, Table 3.9).



**Figure 3.5 |** Size and condition metrics of 0+ Atlantic salmon fry across the control and nutrient treatments applied to six sites across four tributaries of the River Blackwater in September 2020 (data plotted as model predictions  $\pm$  SE,  $n = 957$  fry). A) Mean fork length of Atlantic salmon fry. B) Mean body mass of Atlantic salmon fry. C) Mean Le Cren body condition index of Atlantic salmon fry. D) Mean relative mass of Atlantic salmon fry (where a value of zero indicates a body mass equal to the mean expected for fish on *ad libitum* food and experiencing the observed temperature regime).



**Figure 3.6 |** Atlantic salmon fry density (A) and biomass (B) across the sections of control experimental zones ( $n = 28$ ) and sections of nutrient treatment zones ( $n = 18$  bagged,  $n = 16$  scattered) applied to sites across six tributaries of the River Blackwater in 2020 (data plotted as model predictions  $\pm$  SE).

**Table 3.7 | Results of linear mixed effects models analysing effects of nutrient treatment and habitat (PC1 score) on fork length and body mass of 0+ Atlantic salmon fry in 2020. Bagged and scattered treatments are compared to the control (no nutrients added).**

<i>Predictors</i>	<b>Fork length</b>					<b>Body mass</b>				
	<i>Estimates</i>	<i>std. Error</i>	<i>t value</i>	<i>p</i>	<i>df</i>	<i>Estimates</i>	<i>std. Error</i>	<i>t value</i>	<i>p</i>	<i>df</i>
(Intercept)	54.30	2.86	19.01	<0.001	950.00	1.66	0.23	7.06	<0.001	950
Treatment [Bagged]	0.33	0.51	0.64	0.521	950.00	0.03	0.05	0.51	0.613	950
Treatment [Scattered]	-3.25	0.72	-4.54	<0.001	950.00	-0.25	0.07	-3.65	<0.001	950
PC1	1.33	0.70	1.89	0.059	950.00	0.04	0.07	0.66	0.506	950
<b>Random Effects</b>										
$\sigma^2$	18.69					0.19				
$\tau_{00}$	0.08 <sub>section:site</sub>					0.00 <sub>section:site</sub>				
	48.60 <sub>site</sub>					0.33 <sub>site</sub>				
Observations	957					957				

**Table 3.8** | Results of linear mixed effects models analysing effects of nutrient treatment and habitat (PC1 score) on Le Cren body condition and relative mass of 0+ Atlantic salmon fry in 2020. Bagged and scattered treatments are compared to the control (no nutrients added).

<i>Predictors</i>	<b>Le Cren body condition index</b>					<b>Relative mass</b>				
	<i>Estimates</i>	<i>std. Error</i>	<i>t value</i>	<i>p</i>	<i>df</i>	<i>Estimates</i>	<i>std. Error</i>	<i>t value</i>	<i>p</i>	<i>df</i>
(Intercept)	0.99	0.00	233.92	<0.001	950.00	-0.91	0.45	-2.03	<b>0.043</b>	950.00
Treatment [Bagged]	0.01	0.01	1.37	0.172	950.00	0.03	0.05	0.63	0.526	950.00
Treatment [Scattered]	-0.01	0.01	-1.76	0.079	950.00	-0.27	0.07	-3.71	<0.001	950.00
PC1	-0.02	0.00	-7.88	<0.001	950.00	0.06	0.07	0.87	0.387	950.00
<b>Random Effects</b>										
$\sigma^2$	0.00					0.19				
$\tau_{00}$	0.00 <sub>section:site</sub>					0.00 <sub>section:site</sub>				
	0.00 <sub>site</sub>					1.21 <sub>site</sub>				
Observations	957					957				

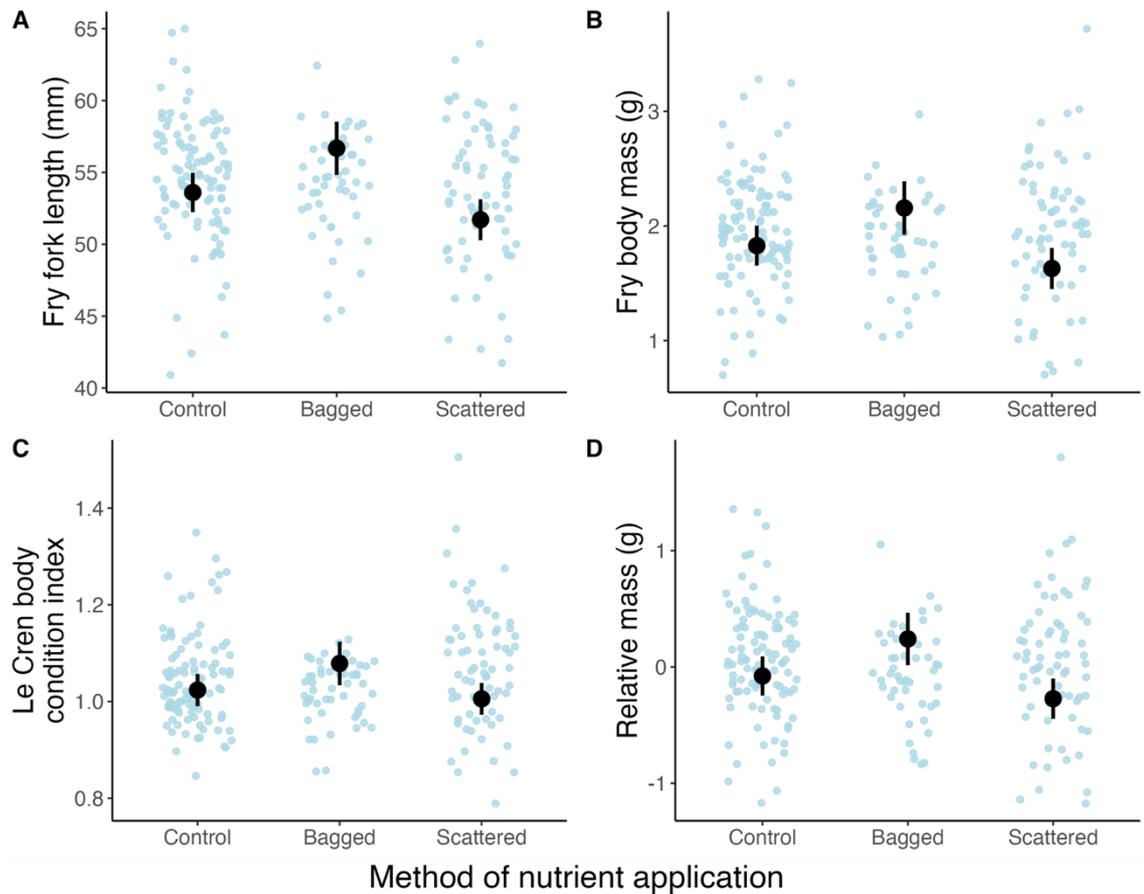
**Table 3.9 | Results of linear mixed effects models analysing effects of nutrient treatment and habitat (PC1 score) on the density and biomass of 0+ Atlantic salmon fry in 2020. Bagged and scattered treatments are compared to the control (no nutrients added).**

<i>Predictors</i>	<b>Fry density</b>					<b>Fry biomass</b>				
	<i>Estimates</i>	<i>std. Error</i>	<i>t value</i>	<i>p</i>	<i>df</i>	<i>Estimates</i>	<i>std. Error</i>	<i>t value</i>	<i>p</i>	<i>df</i>
(Intercept)	0.76	0.38	1.99	0.050	69.00	1.27	0.79	1.60	0.113	69.00
Treatment [Bagged]	-0.03	0.10	-0.31	0.759	69.00	-0.07	0.17	-0.44	0.660	69.00
Treatment [Scattered]	0.13	0.15	0.87	0.388	69.00	-0.17	0.25	-0.68	0.502	69.00
PC1	0.25	0.16	1.60	0.114	69.00	0.65	0.27	2.36	<b>0.021</b>	69.00
<b>Random Effects</b>										
$\sigma^2$	0.10					0.27				
$\tau_{00}$	0.86 <sub>site</sub>					3.72 <sub>site</sub>				
Observations	75					75				

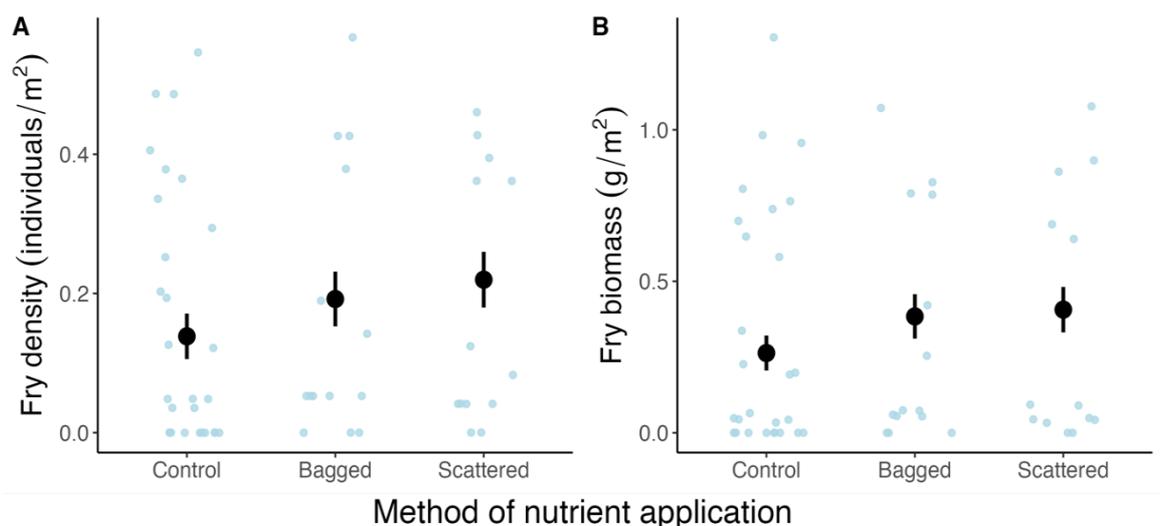
*Impact of contrasting nutrient application methods on Atlantic salmon fry and parr sampled in 2021*

The results for Atlantic salmon differed between the experiments run in 2020 and 2021. In 2021, there were significant differences in fry fork length between the two nutrient treatments. There was a significant increase in the fork length of fry in the bagged treatment relative to the control, whilst fish in the scattered treatment had a significantly smaller fork length compared to the control; there was also a significant positive effect of the habitat variable PC1 (Fig. 3.4A, Table 3.4). Fry body mass showed the same significance patterns and direction as those for fork length (Fig. 3.4B, Table 3.4). There was a significant increase in fry body condition in the bagged treatment but no effect in the scattered treatment, or any effect of PC1 (Fig. 3.5C, Table 3.5). Fry relative mass was significantly greater in the bagged treatment than the control and significantly lower in the scattered treatment when compared to the control, but there was no effect of PC1 (Fig. 3.4D, Table 3.5). Fry density was significantly greater in the scattered treatment in 2021 in comparison to the control, but there was no significant effect of the bagged treatment on fry density. PC1 also had a significant positive effect on fry density (Fig. 3.5A, Table 3.6). However, fry biomass did not follow the same pattern, with neither treatment having a significant effect on fry biomass, although there was a significant positive effect of PC1 on fry biomass (Fig. 3.5B, Table 3.6).

Salmon that would have been subject to the nutrient treatments as 0+ fry in 2020 were measured as 1+ parr in 2021 (when they would have experienced a second year of the same treatment). In terms of fork length, there was no effect of either nutrient treatment, but there was a significant negative effect of PC1 (Fig. 3.6A, Table 3.7). Despite the lack of an effect of nutrient treatment on fork length, parr body mass was significantly lower in the scattered treatment, but did not differ in the bagged treatment. There was also a significant negative effect of PC1 on parr body mass (Fig. 3.6B, Table 3.7). Parr had a significantly greater Le Cren body condition in the bagged treatment, but there was no effect of the scattered treatment, or of PC1 (Fig. 3.6C, Table 3.8). Neither parr density nor biomass was affected by either nutrient treatment, though both displayed a significant positive effect of PC1 (Fig. 3.7, Table 3.9).



**Figure 3.7** | Size and condition metrics of Atlantic salmon fry across the control and nutrient treatments applied to four sites across two tributaries of the River Blackwater in 2021 (data plotted as model predictions  $\pm$  SE,  $n = 226$ ). A) Fork length of Atlantic salmon fry. B) Body mass of Atlantic salmon fry. C) Le Cren body condition index of Atlantic salmon fry. D) Relative mass of Atlantic salmon fry, where a value of zero indicates a body mass equal to that expected for fish on *ad libitum* food and experiencing the observed temperature regime).



**Figure 3.8** | Atlantic salmon fry density (A) and biomass (B) across the sections of control experimental zones ( $n = 28$ ) and sections of nutrient treatment zones ( $n = 14$  bagged,  $n = 13$  scattered) applied to sites across two tributaries of the River Blackwater in 2021 (data plotted as model predictions  $\pm$  SE).

**Table 3.10** | Results of linear mixed effects models analysing effects of nutrient treatment and habitat (PC1 score) on fork length and body mass of 0+ Atlantic salmon fry in 2021. Bagged and scattered treatments are compared to the control (no nutrients added).

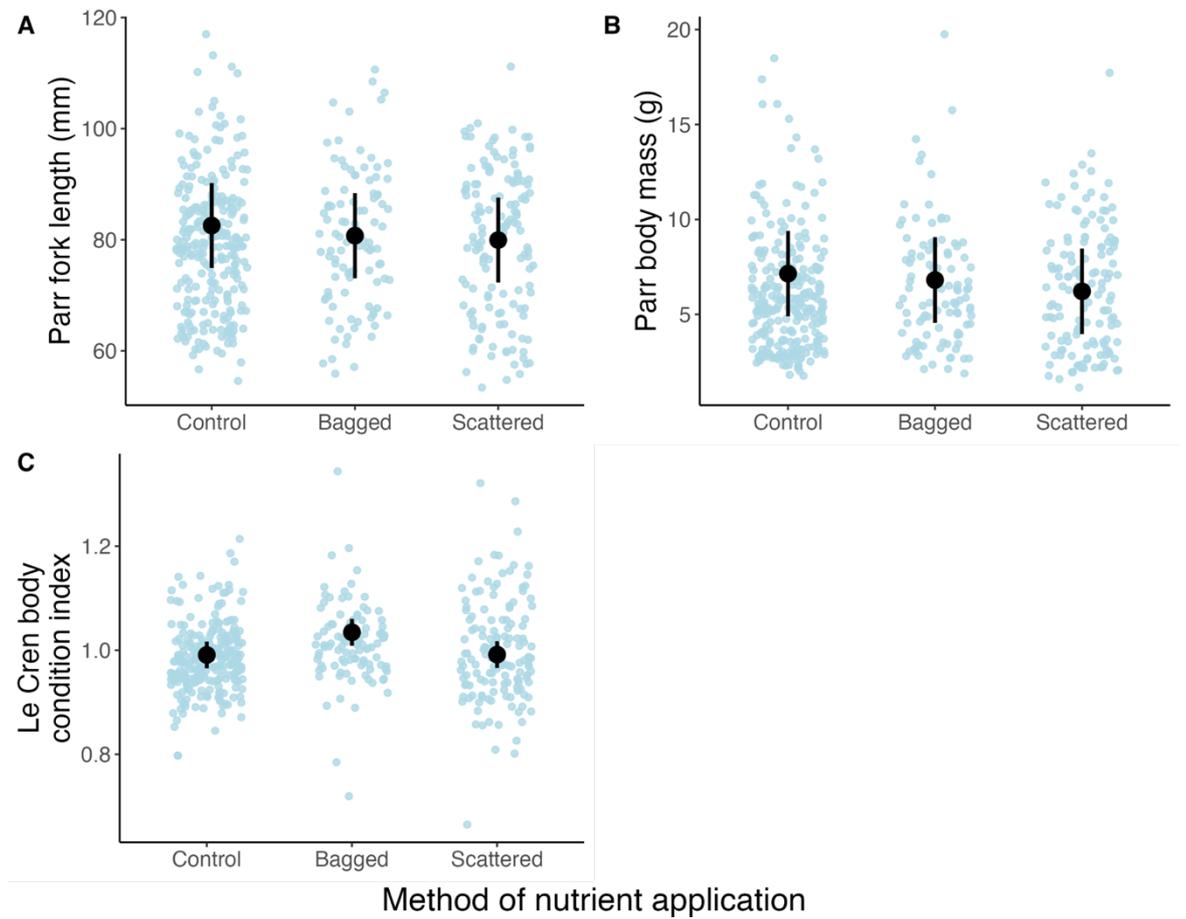
<i>Predictors</i>	<b>Fork length</b>					<b>Body mass</b>				
	<i>Estimates</i>	<i>std. Error</i>	<i>t value</i>	<i>p</i>	<i>df</i>	<i>Estimates</i>	<i>std. Error</i>	<i>t value</i>	<i>p</i>	<i>df</i>
(Intercept)	50.76	1.24	40.92	<0.001	219.0	1.55	0.16	9.84	<0.001	219.0
Treatment [Bagged]	3.08	1.04	2.95	0.003	219.0	0.33	0.13	2.62	0.009	219.0
Treatment [Scattered]	-1.89	0.83	-2.28	0.024	219.0	-0.20	0.10	-2.03	0.044	219.0
PC1	2.89	0.79	3.67	<0.001	219.0	0.29	0.10	2.90	0.004	219.0
<b>Random Effects</b>										
$\sigma^2$	9.70					0.13				
$\tau_{00}$	1.15 <small>section:site</small>					0.02 <small>section:site</small>				
	5.01 <small>site</small>					0.08 <small>site</small>				
Observations	226					226				

**Table 3.11** | Results of linear mixed effects models analysing effects of nutrient treatment and habitat (PC1 score) on Le Cren body condition and relative mass of 0+ Atlantic salmon fry in 2021. Bagged and scattered treatments are compared to the control (no nutrients added).

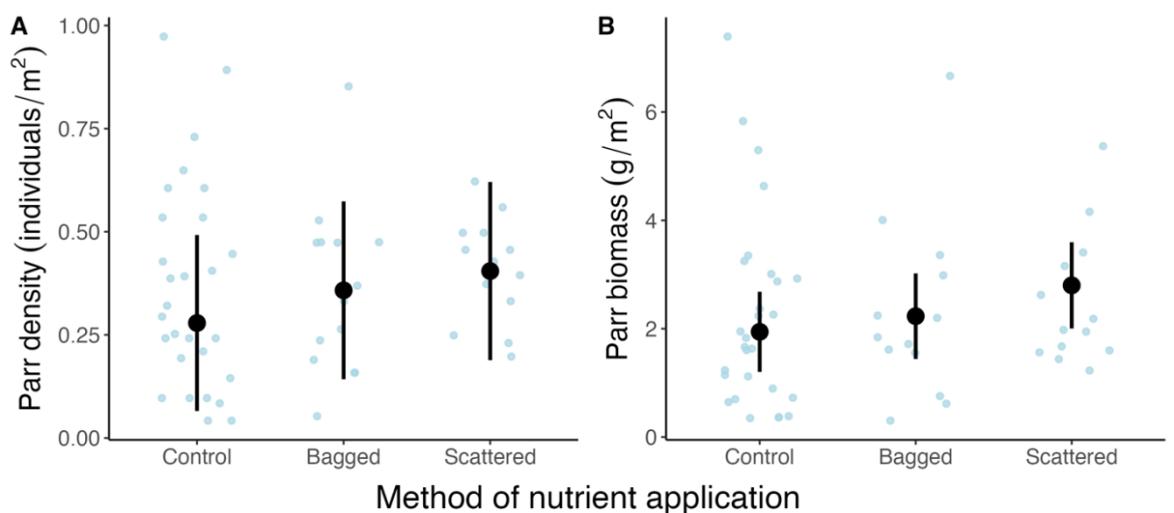
<i>Predictors</i>	<b>Le Cren body condition index</b>					<b>Relative mass</b>				
	<i>Estimate</i> <i>s</i>	<i>std.</i> <i>Error</i>	<i>t value</i>	<i>p</i>	<i>df</i>	<i>Estimates</i>	<i>std.</i> <i>Error</i>	<i>t value</i>	<i>p</i>	<i>df</i>
(Intercept)	0.99	0.03	32.98	<0.001	219.0	-0.35	0.15	-2.29	0.023	219.0
Treatment [Bagged]	0.06	0.02	2.40	0.017	219.0	0.32	0.12	2.57	0.011	219.0
Treatment [Scattered]	-0.02	0.02	-1.16	0.245	219.0	-0.19	0.10	-1.99	0.047	219.0
PC1	0.04	0.02	2.02	0.045	219.0	0.27	0.10	2.86	0.005	219.0
<b>Random Effects</b>										
$\sigma^2$	0.01					0.13				
$\tau_{00}$	0.00 <sub>section:site</sub>					0.02 <sub>section:site</sub>				
	0.00 <sub>site</sub>					0.08 <sub>site</sub>				
Observations	226					226				

**Table 3.12 | Results of linear mixed effects models analysing effects of nutrient treatment and habitat (PC1 score) on the density and biomass of 0+ Atlantic salmon fry in 2021. Bagged and scattered treatments are compared to the control (no nutrients added).**

<i>Predictors</i>	<b>Fry density</b>					<b>Fry biomass</b>				
	<i>Estimates</i>	<i>std. Error</i>	<i>t value</i>	<i>p</i>	<i>df</i>	<i>Estimates</i>	<i>std. Error</i>	<i>t value</i>	<i>p</i>	<i>df</i>
(Intercept)	0.16	0.03	5.01	<0.001	49	0.31	0.06	5.52	<0.001	49
Treatment [Bagged]	0.05	0.03	1.54	0.131	49	0.12	0.07	1.68	0.099	49
Treatment [Scattered]	0.08	0.04	2.26	<b>0.028</b>	49	0.14	0.07	1.92	0.061	49
PC1	0.11	0.02	5.03	<0.001	49	0.25	0.04	6.48	<0.001	49
<b>Random Effects</b>										
$\sigma^2$	0.01					0.04				
$\tau_{00}$	0.00 <sub>site</sub>					0.01 <sub>site</sub>				
Observations	55					55				



**Figure 3.9 |** Size and condition metrics of age 1+ Atlantic salmon parr across the control and nutrient treatments applied to four sites across two tributaries of the River Blackwater in 2021 (data plotted as model predictions  $\pm$  SE,  $n = 495$ ). A) Fork length of Atlantic salmon parr. B) Body mass of Atlantic salmon parr. C) Le Cren body condition index of Atlantic salmon parr.



**Figure 3.10 |** Age 1+ Atlantic salmon parr density (A) and biomass (B) across the sections of control experimental zones ( $n = 28$ ) and sections of nutrient treatment zones ( $n = 14$  bagged,  $n = 13$  scattered) applied to sites across two tributaries of the River Blackwater in 2021 (data plotted as model predictions  $\pm$  SE).

**Table 3.13** | Results of linear mixed effects models analysing effects of nutrient treatment and habitat (PC1 score) on fork length and body mass of 1+ Atlantic salmon parr in 2021. Bagged and scattered treatments are compared to the control (no nutrients added).

<i>Predictors</i>	<b>Fork length</b>					<b>Body mass</b>				
	<i>Estimates</i>	<i>std. Error</i>	<i>t value</i>	<i>p</i>	<i>df</i>	<i>Estimates</i>	<i>std. Error</i>	<i>t value</i>	<i>p</i>	<i>df</i>
(Intercept)	82.12	7.61	10.79	<0.001	488.00	7.00	2.25	3.12	0.002	488.00
Treatment [Bagged]	-1.83	1.89	-0.97	0.334	488.00	-0.34	0.46	-0.74	0.463	488.00
Treatment [Scattered]	-2.62	1.56	-1.67	0.095	488.00	-0.93	0.38	-2.47	0.014	488.00
PC1	-3.94	1.99	-1.98	0.049	488.00	-1.32	0.49	-2.71	0.007	488.00
<b>Random Effects</b>										
$\sigma^2$	97.45					5.81				
$\tau_{00}$	0.79 <sub>section:site</sub>					0.02 <sub>section:site</sub>				
	228.11 <sub>site</sub>					19.95 <sub>site</sub>				
Observations	495					495				

**Table 3.14** | Results of linear mixed effects models analysing effects of nutrient treatment and habitat (PC1 score) on Le Cren body condition of 1+ Atlantic salmon parr in 2021. Bagged and scattered treatments are compared to the control (no nutrients added).

<b>Le Cren body condition index</b>					
<i>Predictors</i>	<i>Estimates</i>	<i>std. Error</i>	<i>t value</i>	<i>p</i>	<i>df</i>
(Intercept)	0.99	0.03	39.13	<0.001	488.00
Treatment [Bagged]	0.04	0.01	3.98	<0.001	488.00
Treatment [Scattered]	0.00	0.01	0.08	0.937	488.00
PC1	0.01	0.01	1.16	0.246	488.00
<b>Random Effects</b>					
$\sigma^2$	0.00				
$\tau_{00}$ section:site	0.00				
$\tau_{00}$ site	0.00				
Observations	495				

**Table 3.15** | Results of linear mixed effects models analysing effects of nutrient treatment and habitat (PC1 score) on the density and biomass of 1+ Atlantic salmon parr in 2021. Bagged and scattered treatments are compared to the control (no nutrients added).

<i>Predictors</i>	<b>Parr density</b>					<b>Parr biomass</b>				
	<i>Estimates</i>	<i>std. Error</i>	<i>t value</i>	<i>p</i>	<i>df</i>	<i>Estimates</i>	<i>std. Error</i>	<i>t value</i>	<i>p</i>	<i>df</i>
(Intercept)	0.33	0.21	1.56	0.125	49.00	2.16	0.73	2.98	0.005	49.00
Treatment [Bagged]	0.08	0.07	1.16	0.251	49.00	0.29	0.49	0.59	0.556	49.00
Treatment [Scattered]	0.13	0.07	1.93	0.059	49.00	0.86	0.49	1.76	0.085	49.00
PC1	0.26	0.08	3.28	<b>0.002</b>	49.00	1.10	0.44	2.51	<b>0.015</b>	49.00
<b>Random Effects</b>										
$\sigma^2$	0.02					1.48				
$\tau_{00}$	0.18 <sub>site</sub>					1.88 <sub>site</sub>				
Observations	55					55				

### 3.4 Discussion

The method of application of carcass analogue had differing effects on the growth and condition of Atlantic salmon, and this varied between the two years of the experiment. Moreover, the results did not conform to the predictions. The scattered pellet treatment consistently resulted in reduced growth and condition for juvenile Atlantic salmon fry, with a reduction in fork length, body mass and relative mass when compared to the control in 2020, and reduced fork length, body mass, and relative mass in 2021. This was contrary to the prediction that increases in growth and condition would be observed in the scattered treatment. However, there was a non-significant tendency for fry density to be greater in the scattered than the control and bagged treatments in 2020, and a significant increase in fry density in the scattered treatment compared to the control in 2021.

The results from the bagged treatment conformed partially to the hypothesis, though this varied between the years. In 2020, there was no difference in fry fork length, body mass, or in body condition and relative mass between the

control and the bagged treatment, whilst in 2021 fry showed significant increases in fork length, body mass, body condition and relative mass relative to controls, but no difference in density or biomass.

Older juvenile Atlantic salmon (parr) were also measured in 2021, as these would have been subject to the nutrient additions beginning in 2020. Parr showed no treatment differences in fork length, density or biomass, but had significantly lower body mass in the scattered treatment compared to the control, and body condition in the bagged treatment was significantly greater when compared to the control.

The predictions for the invertebrates were only partially met. Impacts of nutrient additions on the invertebrate communities was mainly driven by changes in the log mass of individual animals, with significant increases in log mass relative to controls in the scattered treatment, both in the experimental section and 500m downstream of it. There was no overall treatment effect on either total log mass or total abundance of invertebrates. Effects on invertebrates varied among taxa, with Diptera showing significant increases in individual log mass in the scattered treatment, and downstream of both the bagged and scattered treatments, whilst Plecoptera showed a significant decrease in individual log mass in the bagged treatment. Diversity was mainly unaffected by nutrient additions, apart from a significant decrease in Shannon's diversity index downstream of the scattered treatment.

The increases in the log mass of individual invertebrates may have been increased by algal growth within the experimental zones. Algal biofilms, stream invertebrates and fish have all been shown to become enriched with marine-derived nutrients from natural spawning of anadromous fish (Samways *et al.*, 2018), and the same process can occur through the use of carcass analogues. More generally, the long term addition of phosphorus has been shown to significantly increase the level of gross primary production, and to significantly elevate epilithic chlorophyll (Slavik *et al.*, 2004). Other studies have illustrated that the addition of carcass analogues generally increases the amount of biofilm in streams (Collins *et al.*, 2016; Kohler *et al.*, 2008; Marcarelli *et al.*, 2014; Martin *et al.*, 2010), indicating an increase in the primary production of the stream as the pellets degraded and fertilised the stream. However, Ebel *et al.* (2014) found no increase in biofilm chlorophyll a nor in biofilm ash-free dry mass in streams treated with carcass analogues, though the authors found an increase in stream metabolism.

Carcass analogue additions have previously been shown to slightly alter invertebrate community composition, shifting towards an increase in Chironomidae and members of the 'collector' functional feeding group, which consume both autochthonous and allochthonous food, and may consume degrading pellets (Kohler & Taki, 2010). Greater amounts of biofilm may increase the amount of food available for 'scrapers' such as Heptageniidae, which showed increased densities in streams treated with carcasses in a study by Wipfli *et al.* (1998). This did not occur in the present study, where there was no increase in the log mass, total mass or abundance of Ephemeroptera (which includes Heptageniidae). However, the body mass of individual Diptera was significantly increased within the scattered treatment zone, and in samples taken 500m downstream of this zone, which may indicate that the impact of nutrient additions may be stronger via direct consumption by collector groups than through indirect consumption via algal grazing. Though previous studies have not demonstrated an increased body size of Diptera such as Chironomidae, the abundance of Chironomids in Scottish streams treated with salmon carcasses was shown to increase (Nislow *et al.*, 2010), and this may have increased concurrently with body size.

The choice of kick sampling may have also led to the overrepresentation of sessile species and the underrepresentation of motile species in comparison to other techniques such as electrobugging (Lento & Morin, 2014). However, as electrobugging is less effective at capturing attached or less motile species, kick sampling was able to capture these taxonomic groups known to be important components of the diet of juvenile salmon such as chironomids (Martinussen *et al.*, 2011). Other more motile taxa such as Perlidae and Baetidae (Lento & Morin, 2014) were captured during kick sampling, so this sampling method appears appropriate within this system. However, further sampling techniques such as drift-netting may have led to a more balanced view of the invertebrate communities predated on by juvenile Atlantic salmon. Additionally, it is likely that due to the time of sampling in September, there may have been an underrepresentation of taxa with an emergence period over the summer, however, this was unavoidable due to sampling restrictions imposed by the pandemic.

The reduction in Atlantic salmon growth and body condition found in the scattered treatment may be due to the higher density of fry. Although this was not significant in 2020, in both years fry density was higher in the scattered

treatment. Pearsons *et al.* (2007) demonstrated that 50% of carcass analogue pellets were either consumed or dissolved after two weeks, although the application of pellets in that study occurred in the late summer. In the present study, pellets could be expected to remain in the stream for longer periods since they were added in late winter, at a time of low temperatures and biological activity. As the pellets and salmon eggs were planted out concurrently, but as the first feeding date of fry was calculated to be around three months after planting out the eggs, this would have provided time for the pellets to break down or be consumed by invertebrates. Since the mass of individual invertebrates was significantly greater in the scattered treatment, including 500m downstream from the treatment section, invertebrates in these sites may have represented higher quality food resources, being larger and thus containing more energy (Gill, 2003), but also as they may have incorporated fatty acids from the nutrient additions (Samways *et al.*, 2017). This could have sustained a larger population of fry within the scattered area, but due to the larger population, the individual growth of fish may have been reduced as a consequence of density-dependent competition. Lindeman *et al.* (2015) illustrated both a decrease in territory size and a decrease in the specific growth rate of young of the year (YOY) Atlantic salmon as density increased, whilst Imre *et al.* (2005) demonstrated a consistent decrease in the fork length of YOY Atlantic salmon with increasing density. However, Einum *et al.* (2006) showed contrasting results to the aforementioned studies, with no detectable effect of density on body size for Atlantic salmon fry.

The lack of an effect of bagged nutrient additions on the body size and condition of fry in the bagged treatment in 2020 was surprising, given that several studies within the same River Conon catchment showed increases in body size and biomass when adding the same quantity of bagged pellets (Auer *et al.*, 2018; McLennan *et al.*, 2019). However, the present study differed from Auer *et al.* (2018) and McLennan *et al.* (2019) with regards to the size of the study area and the stocking density of eggs, with these previous studies using 300m<sup>2</sup> stream areas stocked at a density of 10 eggs m<sup>2</sup>, whilst this study used 500m<sup>2</sup> areas stocked at a lower density of 5 eggs m<sup>2</sup>. Since the bagged pellets were anchored to the substrate using rocks, it is possible that the impact of the nutrient additions may have benefitted fewer fish than in the scattered treatment, as these remained static and may not have overlapped with many fry territories. Gustafson-Greenwood & Moring (1990) observed Atlantic salmon fry defending territories of

near 100 cm<sup>2</sup> at first feeding, expanding these territories one month later to 1100 cm<sup>2</sup>, before dispersing downstream. The bagged pellets were still present in the streams at the time of sampling, with algal plumes reaching around 1m downstream from each bag, and this could indicate that bagged pellets may have primarily enriched the individual territories immediately downstream of the bag. Nonetheless, there were still significant increases in growth and condition of fry in the bagged treatment in 2021. In contrast, the scattered pellets were spread over the stream area and were more mobile, and these may have enriched multiple territories in comparison to the bagged pellets. However, as sampling was undertaken in late September in 2020, and late August in 2021, there may have been a diminishment of effects over the additional month of the study in 2020, so that the impact of nutrient additions may have been harder to detect in that year.

The lack of increases in invertebrate abundance and total log mass also contrasted with previous work, as Auer *et al.* (2018) and McLennan *et al.* (2019) showed increased invertebrate abundance and biomass as a consequence of the application of bagged pellets in the same river catchment. Though changes in abundance and total log biomass were not observed in the present study, the log mass of invertebrate individuals increased in the scattered treatment zone and 500m downstream of that zone. This may have been due to scattered pellets enriching a larger stream area, and it may have been possible for the scattered pellets to move downstream and enrich the downstream sampling points.

Although the individual mass of invertebrates increased in the scattered treatment zone and downstream of it, there was variation within the DEPT orders assessed. This increase in individual mass may have been due to faster growth within a species or a shift in community composition towards larger species, though it was not possible to establish the reason behind this in the present study. Diptera, which includes important dietary prey from the families Chironomidae and Simuliidae (Martinussen *et al.*, 2011), saw significant increases in body mass in both the scattered treatment zones and downstream of them. There was no difference in any treatment for Ephemeroptera, which is also an important dietary prey item, while in Plecoptera there was a significant decrease in log mass within the bagged treatment zones. Within Trichoptera, there was a significant increase in log mass downstream of the scattered treatment zones. When conspecific density is high, Atlantic salmon fry have been shown to consume larger prey and

are likely to broaden the diet to include suboptimal prey (Martinussen *et al.*, 2011). Within the scattered treatment, as a result of higher densities, fry may have needed to consume larger prey with a greater handling time or to shift to suboptimal prey (Gill, 2003; Martinussen *et al.*, 2011), and this may have contributed to the smaller body size and condition factors in the scattered treatment.

A consequence of this smaller body size found in fry from the scattered treatment may be that marine survival could be reduced as a result of smaller smolt sizes (Armstrong *et al.*, 2018; Gregory *et al.*, 2018). However, in parr which were subject to nutrient additions for two years of life, there was no significant difference in fork length between the scattered and bagged treatment, although body mass was significantly lower in the scattered treatment, and parr body condition was significantly higher in the bagged treatment. Additionally, the effects of nutrient additions, even within the same river system, seem to vary both between years and through differing densities of fish (present study compared with Auer *et al.*, 2018; McLennan *et al.*, 2019). These results suggest that further research is required in order to optimise and refine nutrient additions as a possible conservation measure, so as to avoid producing smaller smolts which may be more likely to suffer marine mortality.

The abundance of brown trout varied dramatically between sites and years of the study, partially driven by the reduced number of study sites in 2021. It is possible that in 2020 the abundance of brown trout in some sites impacted the effects of the nutrient additions on juvenile Atlantic salmon. As juvenile brown trout directly compete with juvenile Atlantic salmon and share a similar diet and habitat (Klemetsen *et al.*, 2003), the impacts of the nutrient additions may have had similar impacts on brown trout as Atlantic salmon. However, broadly similar results were found for the scattered treatment on fork length in 2021 as in 2020, despite a much lower abundance of juvenile brown trout, indicating that competitive effects from trout may not have broadly influenced the processes leading to reduced growth. The lower density of trout may have allowed for the significant increase in the density of salmon in the scattered treatment in 2021 compared to 2020 through competitive release. Despite this, in 2021 in the bagged treatment there was a significant increase in the growth of salmon, which may indicate that at low trout densities the bagged treatment may be more effective, and that this effect may have been masked at high trout densities in 2020. Whilst

it was not possible to control the densities of trout during this study, understanding the impacts of nutrient additions on both Atlantic salmon and brown trout is likely to be important as these species often co-occur, and the relationship between the species may have practical effects on the conservation outcomes.

This study was limited in some aspects, partially as a result of fieldwork restrictions imposed by the COVID-19 pandemic. Assessment of potential egg mortality from the visual inspection of Vibert boxes earlier in the season was not possible, and nor was the ability to separate potential effects of mortality from emigration, which may occur for over 1km upstream or 2km downstream (Eisenhauer *et al.*, 2021). Some areas of the same streams were stocked with other eggs by fisheries managers as part of their normal activities; while attempts were made not to stock close to the study sites, the immigration of non-focal fish into the experimental reaches may have occurred to an unknown extent, adding a degree of noise (but no obvious bias) to the data. A further limitation was the pooled sampling of invertebrates, leading to only a single sample per site. As such, the reliability of the statistical models assessing abundance, total log biomass and diversity metrics should be treated with caution.

In conclusion, I found that two methods of applying the same quantity of nutrients resulted in contrasting effects on both invertebrate and salmon body size, growth and condition metrics. Scattering pellets resulted in smaller individual body sizes for fish, but a greater density, and a greater mass of individual invertebrates, in particular Diptera. There were limited effects of the bagged treatment on growth, but this varied between years, and was not consistent with previous research. The continued effect of nutrient additions over two years did not impact the length of parr, though body mass of 1+ fish was significantly lower in the scattered treatment. This study has implications for the use of nutrient remediation as a conservation measure, as it reveals the variability of impacts between differing methods of application, and provides direction for further research, namely whether nutrient remediation can have positive outcomes for salmon conservation by increasing body size and sea survival, or whether adverse effects may arise as a result of intervention.

# Chapter 4 | Impacts of frequency of nutrient supplementation on the growth and local survival of juvenile Atlantic salmon

## Abstract

The availability of resources at critical points in the year can play a strong role in the growth and survival of organisms. Synchronising resource availability to times of peak growth, or when organisms may have greater metabolic demands due to higher temperatures, may create population-structuring effects. This is especially so in animals such as fish where body size is a key determinant of life history events. Atlantic salmon (*Salmo salar*) populations have declined in recent decades, leading to the suggestion of adding nutrients to spawning streams as a tool to mitigate the impact of declining imports of marine-derived nutrients from adults returning to fresh water. These marine-derived nutrients can provide an important growth benefit for juveniles, which may lead to increased survival rates. The aim of adding nutrients to oligotrophic streams is to replicate these increases in growth rates of juvenile salmon. However, the consequences of varying the number of nutrient applications is not yet known. Here I compare the impacts of applying a single or double dose of nutrient pellets on the growth and population performance of juvenile Atlantic salmon, using streams stocked with identical egg densities. A single dose of nutrients in late winter led to poorer growth, but increased density, compared to control sites. However, adding a second summer dose led to increased density and biomass of juvenile salmon alongside increases in individual growth rates. These results suggest that targeting nutrient additions to key periods of growth by manipulating the number of doses of application may be more likely to lead to positive conservation outcomes. Nutrient additions may thus be a practical and effective conservation measure that can mitigate the impact of declining imports of marine-derived nutrients.

## 4.1 Introduction

Seasonal variation in environmental factors such as temperature and light availability can impact stream ecosystem metabolism, with gross primary production and ecosystem respiration both peaking during as temperatures increase after winter (Nakano *et al.*, 2022; Savoy *et al.*, 2019). In northerly latitudes, the uptake of nutrients in streams usually reaches its peak in the late summer months, when water temperatures are highest and hence there is the strongest demand for both energy and nutrients (Skovsholt *et al.*, 2020). Changes in the growth rates of fish living within these streams tend to reflect these seasonal changes in nutrient uptake, but not perfectly. In an experimental stream system, the mean mass-specific growth rate of juvenile Atlantic salmon was higher in summer compared to winter, and on average fish studied doubled their body mass during the summer period (Teichert *et al.*, 2010). However, while the growth rate of age 0+ juvenile steelhead (*Oncorhynchus mykiss*) was greatest during the summer months, that of older juveniles showed little seasonal variation due to food intake not keeping pace with energy demands in warmer periods of the year (Myrvold & Kennedy, 2020). In brook trout (*Salvelinus fontinalis*), growth rate was highest in the spring months, when temperatures were rising but had yet to reach their peak, again suggesting that energetic constraints (and possibly food availability) can limit growth of stream-living fish at the higher temperatures reached in summer (Letcher *et al.*, 2022). Indeed, a modelling study by Bacon *et al.* (2005) demonstrated that the highest growth in juvenile Atlantic salmon may occur in the spring, with the biomass of drifting prey being lower in the summer, suggesting that food availability is the limitation on growth during the summer period.

As stream temperatures and metabolic rates rise, juvenile salmon may initiate behavioural avoidance strategies to avoid temperatures outside of their thermal optimum (Breau *et al.*, 2007). Maintenance costs for physiological processes may be greater at higher temperatures (Jonsson, 2023), and older (age 2+) parr ceased feeding at 24°C in an experimental setup, whilst younger (age 0+) fish were shown not to cease feeding at high temperatures up to 28°C (Breau *et al.*, 2011). Modelling of seasonal growth and energy expenditure in Atlantic salmon by (Jones *et al.*, 2002) showed that during early spring net growth was high, and

then decreases in summer as basal maintenance costs increase as a result of high temperatures.

The growth of juvenile Atlantic salmon has important consequences for their life history, for example juvenile body size being a determinant of males becoming precociously mature whilst in freshwater (Mobley *et al.*, 2021). It also affects the age at which they undergo the physiological process of smolting to migrate out to sea (Klemetsen *et al.*, 2003), and has consequences for their at-sea survival, as the body size of smolts is positively correlated with marine survival (Armstrong *et al.*, 2018; Gregory *et al.*, 2018). Hence, the body size of juvenile fish is important when management decisions are made to try to increase fish populations, by which the best practice is understood to be to improve both the number and quality (where body size may be a proxy for marine survival) of juveniles and smolts (Simmons *et al.*, 2021; Thorstad *et al.*, 2021). However, Atlantic salmon populations have declined in recent decades (Beaugrand & Reid, 2012), meaning fewer adults are returning to freshwater to spawn. As Atlantic salmon are likely to die on or around their spawning grounds, their carcasses deliver marine-derived nutrients to streams, providing a benefit to their offspring which may see increases in growth, often as a result of increased abundance or biomass of invertebrate prey (Nislow *et al.*, 2004, 2010; Williams *et al.*, 2009). Consequently, this may impact the potential marine survival and population dynamics of Atlantic salmon, as population declines may be resulting in a reduction in body size, further hastening population declines as salmon may smolt at smaller sizes associated with poor sea survival.

In order to address the potential impact of the decline in marine-derived nutrients imported to Atlantic salmon spawning grounds by adult fish, the use of pellets as an analogue to carcasses has been investigated (Pearsons *et al.*, 2007). Studies have shown that the use of these pellets can have beneficial impacts on the growth of juvenile Atlantic salmon, often through the pathway of increasing the size and abundance of macroinvertebrate prey (Guyette *et al.*, 2014, 2013; Kohler & Taki, 2010; McLennan *et al.*, 2019; see also Chapter 3). However, studies have taken different approaches with regard to the details of how carcass analogue pellets are used, in terms of the timing and number of pellet applications. In Maine, USA, Guyette *et al.* (2014, 2013) added carcass analogue pellets in two doses, one in July to mimic the spawning event of sea lamprey (*Petromyzon marinus*) and then again in October to mimic the spawning of Atlantic

salmon. However, in Scotland, studies by Auer *et al.* (2018, 2020) and McLennan *et al.* (2019, 2021) added a single dose of carcass analogue pellets in late February-March, as did the study described in Chapter 3. The rationale for this was that little nutrient take-up would occur over the winter, and adding pellets in late winter would minimise the risk that they would be washed downstream by spates before having any effect. Of the studies which examined the effect of carcass analogue nutrient additions on salmon, both Guyette *et al.* (2014, 2013) and McLennan *et al.* (2019) showed increases in the body size of fish in streams treated with additional nutrients. Adding nutrient pellets in the summer and autumn, as in studies by Guyette *et al.* (2014, 2013), resulted in an average increase of 10-11% in the body size of age 0+ salmon, whilst in the McLennan *et al.* (2019) study where nutrient application occurred in late winter/early spring, the body size of age 0+ salmon increased on average by ~17%. In contrast, my own study (Chapter 3) found no such increases in growth. Environmental and population variation may account for differences between these nutrient addition studies, though it is possible that the number of nutrient additions and seasonal differences may be contributing factors.

As nutrient remediation may have value as a conservation tool by increasing the body size of juvenile salmon, it is of interest to determine whether the frequency and timing of application of nutrients has impacts on juvenile salmon growth. As McLennan *et al.* (2019) demonstrate, the addition of a single dose of nutrients in late winter/early spring can increase both the size and abundance of invertebrates, and by adding this dose at the time of egg planting may allow the nutrient pellets to break down and marine derived nutrients to be consumed by invertebrates, which in turn may be consumed by salmon when they reach the first-feeding stage. However, since streams have a high biological demand for energy and nutrients during the summer period (Birkel *et al.*, 2013), and the metabolic rate and thus energy demands of salmonids increase as stream temperatures rise (Jonsson, 2023), the addition of a second dose of nutrients in the summer may help to maximise the growth potential of juvenile Atlantic salmon. Increasing the availability of food during the summer months through the addition of nutrient pellets, may increase the abundance and biomass of macroinvertebrate prey (McLennan *et al.*, 2019). Pellets could also be fed upon directly, and a second addition of nutrient pellets may help to reduce the energy required to deal with high temperatures. This could further lead to resources

allocated towards growth, resulting in larger fish than might result from a single application of nutrient pellets in the early spring.

In this experimental study, I test the effect of the number of nutrient applications on the growth and performance of juvenile Atlantic salmon in northern Scotland. One treatment received an application of nutrient pellets at the time of egg-planting, whilst the second treatment received this same application of pellets at the time of egg-planting but also a second application in the summer. A control treatment received no pellets. I predicted that, based on the findings in Chapter 3, the growth of juvenile Atlantic salmon in the single application treatment would be lower than that of the control, but in the double dose treatment growth would be greater than that of the control. I expected that the density of juvenile Atlantic salmon in both the single and double doses would be greater than that of the control, whilst the fry biomass of the double dose would be greater than the control and single dose.

## 4.2 Methods

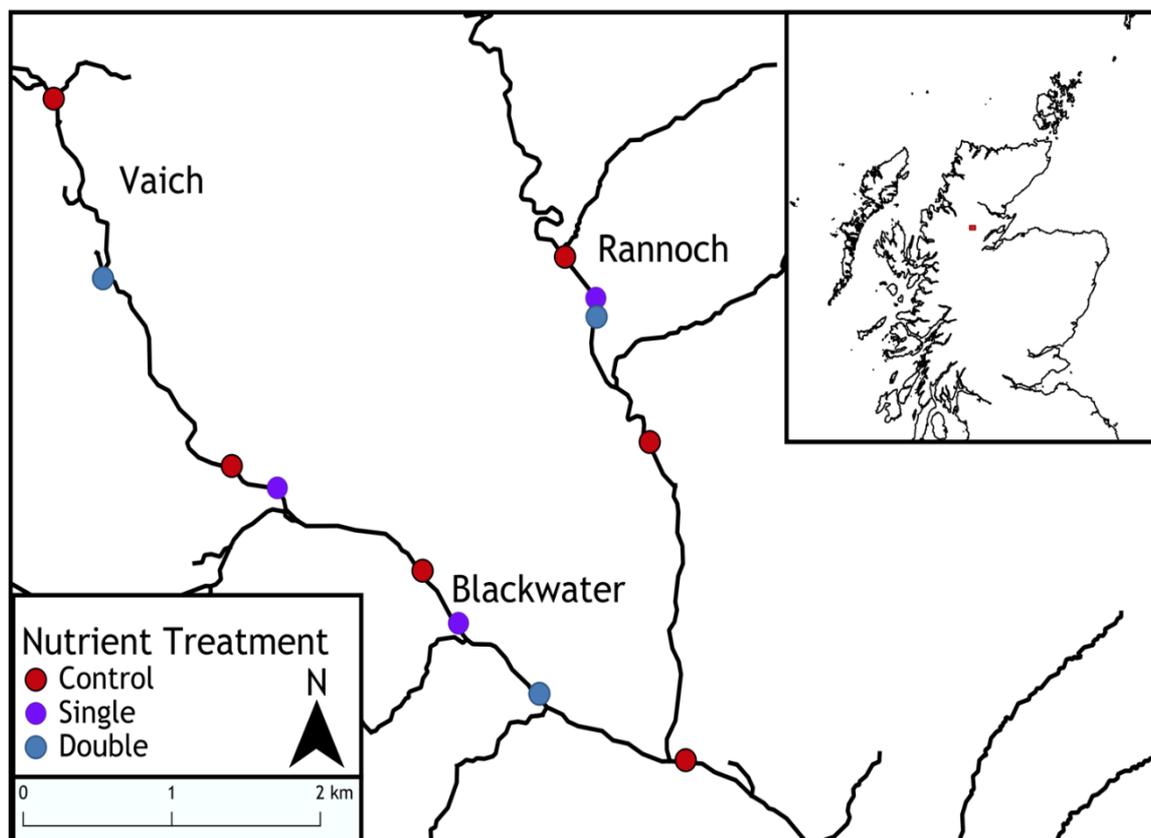
### 4.2.1 Site selection

Experimental zones were located across the main stem of the River Blackwater in northern Scotland, UK, and two of its tributaries, the Rannoch and Vaich (Figure 4.1, Table A.7). These tributaries were some of the same streams used for the experiment detailed in Chapter 3, and some of the same zones and datasets were used as in the second year of that experiment. The Allt' a Bhealaich Mhoir and the Garbat Burn were not used in this current experiment since their size and topography was rather different from the other two (and they were found to hold relatively low densities of juvenile salmon; Chapter 3). They were replaced by sites in the main stem of the Blackwater, which provided a more similar environment for 0+ salmon to the Rannoch and Vaich; the control and single dose treatment zones in the Rannoch and Vaich are the same as those used in the previously-described experiment.

Four experimental zones were identified in each of the Blackwater, Rannoch and Vaich. Each experimental zone comprised an area of approximately 500m<sup>2</sup> of suitable juvenile Atlantic salmon habitat and was located at least 360m downstream of the next closest site (apart from the single and double treatment

sites in the Rannoch, which were separated by 125m due to the more limited availability of suitable habitat in this stream).

Within each stream, the uppermost experimental zone was designated as a control treatment, as was an additional experimental zone at the most downstream section of the stream (except in the Vaich where this was the penultimate downstream zone, so as to follow the experimental zones set out in Chapter 3). These control zones received no additional nutrients. The other two zones per stream received nutrient supplementation following the scattered method detailed in Chapter 3. Each nutrient dose consisted of 15kg of fish food pellets (LR Ignite 51 2000 53pn, BioMar Ltd, Grangemouth, UK) being hand scattered over the experimental zone. All pellet treatment zones received a dose of pellets between 25<sup>th</sup> February - 1<sup>st</sup> March 2021, and one of these pellet treatment zones per stream received an additional dose of 15kg of pellets scattered on 3<sup>rd</sup> June 2021. As a result, there were two control, one single dose and one double dose treatment zones per stream (Fig. 4.1).



**Figure 4.1** | Locations of the 12 experimental zones located across the main stem of the River Blackwater and two of its tributaries, Northern Scotland. Within each stream, the two uppermost experimental zones were considered the ‘upper’ site, and the two downstream as the ‘lower’ site, making a total of six sites (see Data analysis section of main text).

#### 4.2.2 Atlantic salmon egg rearing and planting

The Atlantic salmon eggs for this study were conceived by IVF according to the methods detailed in Chapter 3, using returning anadromous wild fish that had spent one winter at sea and that were caught downstream on the River Blackwater in early winter 2020. These were used to create 25 full sibling families. Eggs were reared in the SSE hatchery at Contin until the eyed stage, at which point all the eggs were pooled together, mixed, and then sorted into batches of 2500 eggs (one per experimental zone).

Eggs were planted out between 25<sup>th</sup> February - 1<sup>st</sup> March 2021, simultaneously with the scattering of nutrient pellets in the single and double treatments. They were planted within artificial redds so as to achieve a density of 5 eggs m<sup>-2</sup> across the experimental zone. Vibert boxes, each containing 100 of the 2500 eggs, were placed in the same manner as in Chapter 3 at the upper and lower limits of each experimental zone. These were checked on 3 June 2020 by staff of the Cromarty Firth Fisheries Trust, and showed no evidence of any hatch failure or alevin mortality. HOBO temperature loggers (-20 to 70 ± 0.53°C; Onset Computer Corporation, Bourne MA, USA) were included in the Vibert boxes at the upper control zones, zones which received the double dose treatment, and the downstream site (control sites in the Blackwater and Vaich, and an experimental 'bagged' site from Chapter 3 in the Rannoch, for which only temperature data was used in this study). Loggers recorded water temperature every two hours for the duration of the study, and temperatures showed a ranged between 0.1-28.3°C, with the highest temperatures occurring in the Rannoch (see Chapter 7).

#### 4.2.3 Sampling and habitat surveys

Sampling of fish populations was undertaken between the 15-20<sup>th</sup> August 2021, using triple-pass electrofishing and following the same protocol as detailed in Chapter 3. The fished area comprised the bank-to-bank wet width, and was subdivided into sections of equal length, the number of which depended on the total area of the stream surveyed. Data collection focused on age 0+ salmon, as these were known to initially be present at equal densities in all experimental zones. However, data was also collected on age 1+ salmon and any captured brown trout (33 in total). Minnows (*Phoxinus phoxinus*) were also captured in low

numbers but data were not recorded for this non-target species. Captured fish were lightly anaesthetised with benzocaine, their fork lengths and body masses were recorded, and they were then allowed to recover from anaesthesia before being returned to their site of capture once electrofishing had ceased. Fin clips and macroinvertebrate samples were not taken during this experiment, in contrast to the first year of the experiment described in Chapter 3. Instream habitat surveys measuring flow and substrate score within the experimental zones were conducted following the same methods as detailed in Chapter 3.

#### 4.2.4 Data analysis

As in Chapter 3, frequency histograms were generated for salmon within each site to determine age classes and to exclude non-focal fish. Body condition was calculated using Le Cren's Index (Le Cren, 1951; Froese, 2006) as detailed in Chapter 3, and relative mass (i.e. body mass relative to that predicted for a fish on *ad libitum* food experiencing the same temperature regime) was determined using a model of salmon growth (Elliott & Hurley, 1997), as described in Chapter 3 (equation 2). Fish density (individuals/m<sup>2</sup>) and biomass (g/m<sup>2</sup>) were calculated by dividing the number or weight of fish caught within each section of a zone divided by the area of that section.

A principal component analysis using the R package 'stats' of the habitat variables collected was conducted following the method described in Chapter 3 in order to reduce the habitat variables to a single composite variable. Those variables used in the analysis were substrate score, flow score, stream width and stream depth. Positive values for PC1 were associated with wider streams and slower flow, whilst negative values were associated with narrow streams and faster flow.

Linear mixed effects models with R (v4.2.0) were used to examine the impacts of a single or double additions of nutrients on the fork length, body mass, body condition, relative mass, density and biomass of age 0+ Atlantic salmon. Experimental zones within the same stream were grouped into either an 'upper' or 'lower' site, each containing a control zone and the closest adjacent experimental zone (either a single or double nutrient application zone). Site was then used as a random effect in the same manner as in Chapter 3. Potential

impacts of temperature were accounted for using this site variable, since there was data available from a temperature logger in each site. Models for fork length, body mass, body condition and relative mass also used fished section as a random effect, which was nested within site. As in Chapter 3, sections in the control zones were labelled as A1, B1 *et cetera*, whilst those in the two nutrient treatments (single or double dose) were labelled A2, B2 *et cetera*. Models analysing the effect of treatment on density or biomass did not contain section as a random effect since only a single measure for density or biomass existed for each section. Fixed effects included the treatment variable and the habitat variable PC1 from the principal component analysis.

## 4.4 Results

A total of 603 age 0+ Atlantic salmon fry were captured through triple-pass electrofishing, alongside 785 Atlantic salmon parr (i.e. fish from older years classes, identified on the basis of size) and 33 resident brown trout. A small number of minnows were captured but data on these was not recorded. The number of nutrient pellet applications had differing impacts on Atlantic salmon fry. The mean fork length of fry was significantly (2.9%) smaller on average in the single dose treatment (49.1mm) when compared to the control (50.6mm). However, in the double dose treatment, mean fry fork length was significantly (on average 6.9%) greater (54.1mm) than in the control treatment (Fig. 4.2A, Table 4.1). There was no effect of the habitat variable PC1 on fish length.

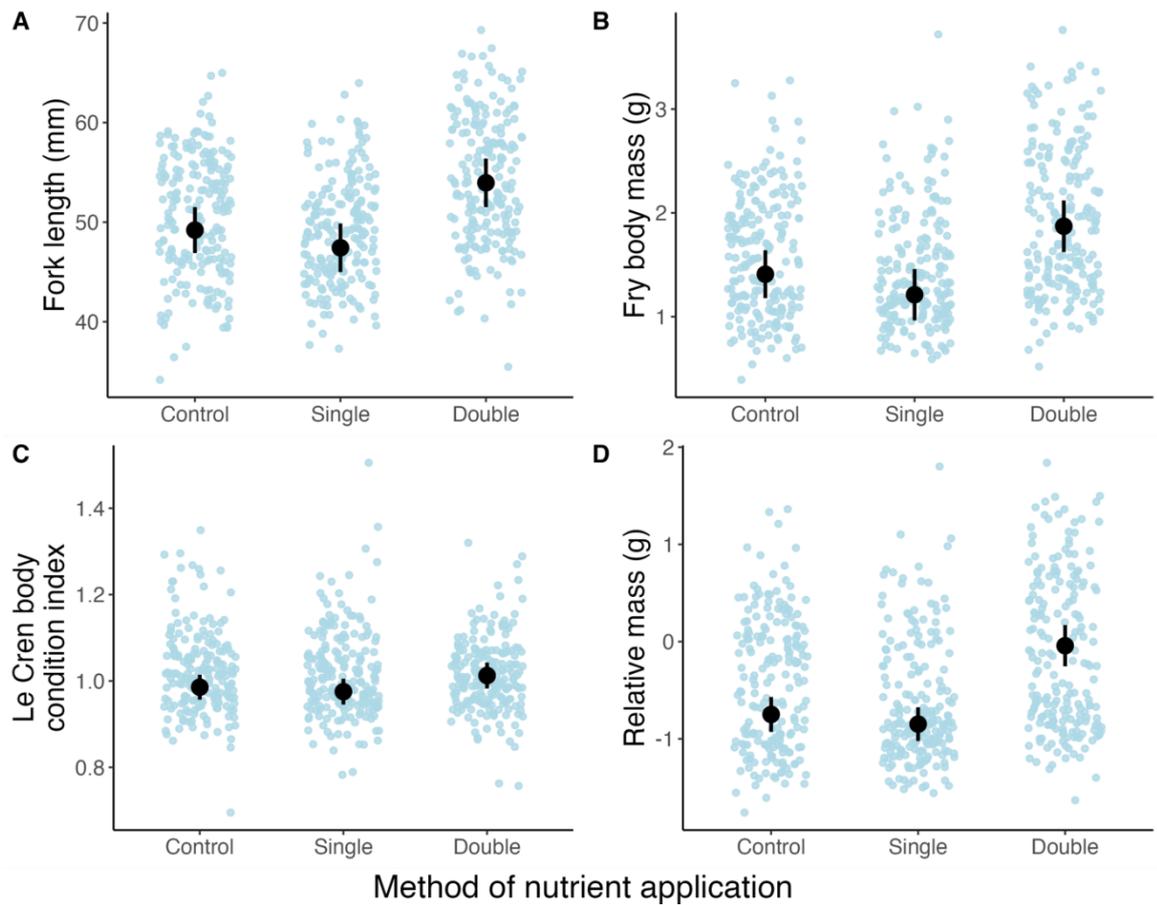
The body mass of Atlantic salmon fry was also affected by the number of nutrient additions. Concomitant with the shorter fork lengths of fish, fry body mass was significantly lower in the single dose treatment than in the controls (1.42 vs 1.58g; 10.1% difference), and correspondingly significantly higher in the double dose treatment (1.91g) than in the control (a 20.8% increase; Fig. 4.2B, Table 4.1). Again there was no significant effect of the composite habitat variable PC1.

There was no significant difference in the Le Cren body condition index of salmon fry from either the single or the double treatment compared to the control, and no significant effect of PC1 (Fig. 4.2C, Table 4.2). However, the relative mass of Atlantic salmon differed across treatments, in line with the results for absolute mass. Thus in the single dose treatment, the mean relative

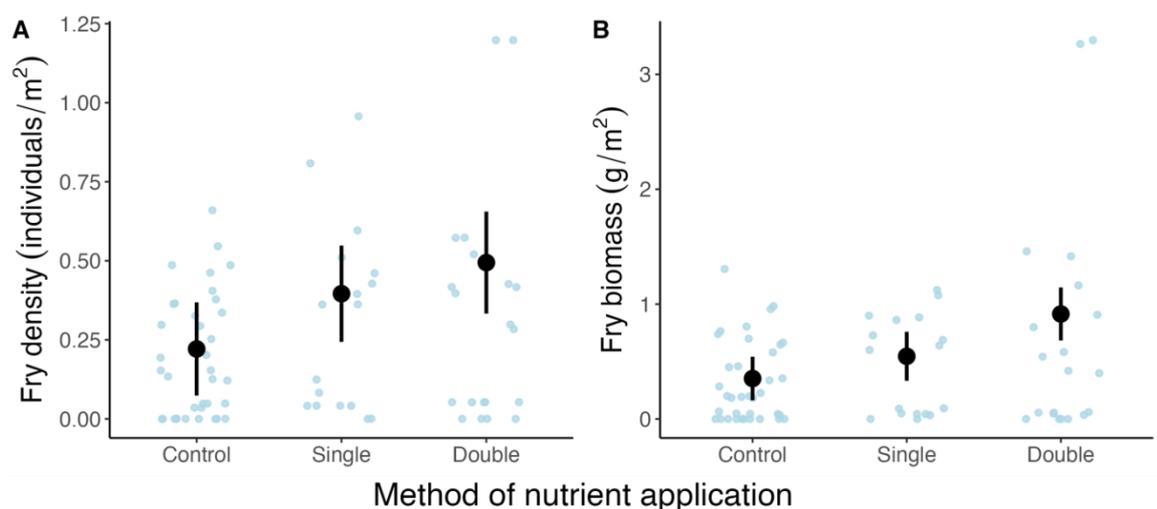
mass of fry (i.e. that compared to the growth predicted on *ad libitum* food) was 43.9% lower (-0.645g) than the relative mass of fry in the control treatment (-0.448g), while in the double dose treatment the mean relative mass (-0.125g) was 72% higher than in the control treatment (Fig. 4.2D). Again, there was no significant effect of PC1 (Fig. 4.2D, Table 4.2).

Both nutrient treatments produced significant increases in fry density compared to the control zones. The single dose treatment led to a 60.1% significant increase in fry density (0.309 individuals/m<sup>2</sup>) compared to the control (0.193 individuals/m<sup>2</sup>), with a similar effect for the double dose treatment (0.328 individuals/m<sup>2</sup>, 69.9% higher than the control) (Fig. 4.3A). There was also a significant negative effect of PC1, meaning that the density of fry was lower in narrower and faster flowing streams (Table 4.3).

There was a non-significant trend for fry biomass to be higher in the single dose treatment (0.462g/m<sup>2</sup>) compared to the control (0.318g/m<sup>2</sup>). This trend was both more pronounced and significant in the double dose treatment, where the fry biomass (0.725g/m<sup>2</sup>) was 127% higher than the control (Fig. 4.3B). There was no significant effect on biomass of the habitat variable PC1 (Table 4.3).



**Figure 4.2** | Size and condition metrics of 0+ Atlantic salmon fry in the control and nutrient treatments applied to 12 sites across the main stem of the River Blackwater and two tributary streams in August 2021 (data plotted as model predictions  $\pm$  SE),  $n = 603$  fry). A) Fork length, B) body mass, C) Le Cren body condition index and D) relative mass (where a value of zero indicates a body mass equal to that expected for fish on *ad libitum* food and experiencing the observed temperature regime).



**Figure 4.3** | Atlantic salmon fry density (A) and biomass (B) across the sections of control experimental zones ( $n = 36$ ) and sections of nutrient treatment zones ( $n = 17$  single,  $n = 20$  double) applied to 12 sites across the main stem of the River Blackwater and two tributary streams in 2021 (data plotted as model predictions  $\pm$  SE).

**Table 4.1** | Results of linear mixed effects models analysing effects of nutrient treatment and habitat (PC1 score) on fork length and body mass of 0+ Atlantic salmon fry. Single and double dose treatments are compared to the control (no nutrients added).

<i>Predictors</i>	Fork length					Body mass				
	<i>Estimates</i>	<i>std. Error</i>	<i>t value</i>	<i>p</i>	<i>df</i>	<i>Estimates</i>	<i>std. Error</i>	<i>t value</i>	<i>p</i>	<i>df</i>
(Intercept)	49.17	2.30	21.42	<0.001	596.00	1.42	0.23	6.19	<0.001	596.00
Treatment [Single]	-1.77	0.81	-2.18	<0.05	596.00	-0.20	0.09	-2.21	<0.05	596.00
Treatment [Double]	4.75	1.18	4.03	<0.001	596.00	0.46	0.13	3.62	<0.001	596.00
PC1	0.16	0.87	0.18	0.857	596.00	-0.05	0.10	-0.49	0.623	596.00
<b>Random Effects</b>										
$\sigma^2$	12.72					0.11				
$\tau_{00}$	1.49 <sub>section:site</sub>					0.02 <sub>section:site</sub>				
	30.35 <sub>site</sub>					0.30 <sub>site</sub>				
Observations	603					603				

## 4.5 Discussion

The addition of a second dose of nutrient pellets appeared to result in differences in both the growth of juvenile Atlantic salmon, and their population performance (in terms of fry density and fry biomass) when compared to both the single dose treatment and to the control. Fish from the double dose treatment zones were both longer and heavier compared to their counterparts in the single dose treatment and the control, and there was both a greater density and biomass of Atlantic salmon fry, meeting the predictions of the experiment for the double dose.

The effect of the single dose treatment was very similar to the results presented in Chapter 3, with a decrease in fork length and body mass compared to the control treatment. Fish showed a significant increase in density when streams were treated with a single dose of scattered pellets, as previously shown in Chapter 3 as the ‘scattered’ treatment in 2021, but not for 2020, where there was no significant increase in density. There was no difference in the biomass of juvenile Atlantic salmon from the single dose treatment to the control, which

conformed to the findings of the previous experiment. Most of the predictions were met for the single dose, except for the lack of effect on fry biomass.

**Table 4.2** | Results of linear mixed effects models analysing effects of nutrient treatment and habitat (PC1 score) on Le Cren body condition and relative mass of 0+ Atlantic salmon fry. Single and double dose treatments are compared to the control (no nutrients added).

<i>Predictors</i>	Le Cren body condition index					Relative mass				
	<i>Estimates</i>	<i>std. Error</i>	<i>t value</i>	<i>p</i>	<i>df</i>	<i>Estimates</i>	<i>std. Error</i>	<i>t value</i>	<i>p</i>	<i>df</i>
(Intercept)	0.99	0.03	34.60	<0.001	596.00	-0.56	0.24	-2.35	0.019	596.00
Treatment [Single]	-0.01	0.01	-0.95	0.342	596.00	-0.21	0.09	-2.29	<0.05	596.00
Treatment [Double]	0.03	0.02	1.73	0.084	596.00	0.48	0.13	3.70	<0.001	596.00
PC1	-0.01	0.01	-1.07	0.286	596.00	-0.06	0.10	-0.61	0.540	596.00
<b>Random Effects</b>										
$\sigma^2$	0.01					0.11				
$\tau_{00}$	0.00 <sub>section:site</sub>					0.02 <sub>section:site</sub>				
	0.00 <sub>site</sub>					0.33 <sub>site</sub>				
Observations	603					603				

**Table 4.3** | Results of linear mixed effects models analysing effects of nutrient treatment and habitat (PC1 score) on the density and biomass of 0+ Atlantic salmon fry. Single and double dose treatments are compared to the control (no nutrients added).

Predictors	Fry density					Fry biomass				
	Estimates	std. Error	t value	p	df	Estimates	std. Error	t value	p	df
(Intercept)	0.19	0.15	1.26	0.212	67.00	0.32	0.19	1.65	0.103	67.00
Treatment [Single]	0.17	0.05	3.21	<0.01	67.00	0.19	0.14	1.38	0.172	67.00
Treatment [Double]	0.27	0.08	3.48	<0.01	67.00	0.56	0.17	3.31	<0.01	67.00
PC1	-0.21	0.07	-2.96	<0.01	67.00	-0.22	0.13	-1.72	0.089	67.00
<b>Random Effects</b>										
$\sigma^2$	0.03					0.17				
$\tau_{00}$	0.13 <sub>site</sub>					0.18 <sub>site</sub>				
Observations	73					73				

Overall, the results showed that the number of nutrient applications can make potential differences to Atlantic salmon fry populations. Fry growth has been shown to be strongly influenced by food supply (Jones *et al.*, 2002), and Ward *et al.* (2009) demonstrated that a high prey biomass may have a stronger effect on growth than factors such as density-dependent competition, as Atlantic salmon fry experienced faster growth rates at sites with high prey biomasses regardless of fry density. The single dose of nutrients may have helped to increase the initial survival rate by providing first-feeding fish with more prey than would be present in the control zones, thus increasing the density of fish, however the nutrient additions will have degraded over time, and prey density may have returned to levels more like that of the control. As a result, the remaining fish in the single dose treatment, which were present at a high density relative to the control may have had fewer prey resources available during times of peak growth, resulting in the decrease in fork length and body mass compared to the control due to higher levels of competition because of high fry densities. Though invertebrate samples were not taken during this experiment, the results shown in Chapter 3 demonstrate that although there was no significant increase in invertebrate biomass or abundance, the average mass of individual invertebrates

was increased in the scattered treatment (equivalent to the single dose in this study), meaning these may have represented a higher quality resource.

In contrast, the 2<sup>nd</sup> dose in the double dose treatment may have provided an important increase to prey density, which appears to have allowed for faster growth resulting in greater fork lengths and body masses compared to the control, despite increased densities of fish, consistent with the findings of Ward *et al.* (2009). Juveniles may have also fed directly on the nutrient pellets as fish would have been feeding by the time of the second dose, unlike in the single dose treatment where pellets were applied at the time of egg planting. Direct consumption on the pellets may represent a high quality food source, with Martin *et al.* (2010) demonstrating that juvenile coho salmon (*Oncorhynchus kisutch*) in streams treated with nutrient pellets had significantly greater body condition compared to fish in control streams, which may have been down to both direct and indirect consumption of the nutrient pellets. However, in the present study there was no significant increase in body condition in either treatment, but fish may have still fed directly on nutrient pellets. The relative mass of fish in the double dose (around 0g) section was significantly greater than both the single dose and the control, suggesting that the provisioning available to fish was potentially closer to that of fish fed *ad libitum* (Elliott & Hurley, 1997), resulting in a body mass closer to that which would be expected based on *ad libitum* feeding at the temperatures fish experienced over the duration of the study.

However, fish within the double dose treatment, which experienced a 6.9% increase in fork length, did not reach the same increases in length as previously demonstrated by Guyette *et al.* (2014, 2013), who also used a dual-application of nutrients to mimic two spawning events from anadromous fish. In the Guyette *et al.* (2014, 2013) studies, the fork length of 0+ fish increased by 10-11%, although in those studies nutrient pellets were applied in July and October, rather than late February/early March and June. This could be a result of factors such as local environmental conditions or variation between populations but may also be affected by the timing of the pellet application. Although fish growth is expected to slow during the summer period (Jones *et al.*, 2002), fish growth nevertheless appears to be responsive to nutrient additions, with Guyette *et al.* (2013) demonstrating an absolute growth rate increase of 0.07mm/day<sup>-1</sup> within one week of nutrient application compared to a control. The later application of nutrient pellets in October to simulate Atlantic salmon spawning could potentially help to

increase the energy reserves of juveniles prior to winter, as 0+ age salmon fry and juvenile brown trout have been recorded consuming Atlantic salmon eggs which would represent a high quality food source (Näslund *et al.*, 2015).

The double dose treatment also failed to achieve the same magnitude of increased fork length as fish treated with nutrient pellets applied in bags in the study by McLennan *et al.* (2019), in which fish in nutrient-treated areas increased by ~17%. That study took place within the same catchment as the present study, but in smaller streams, and there were no previously-stocked Atlantic salmon parr present, which may have impacted the results. However, application of a second dose in the summer of the McLennan *et al.* (2019) study may have further acted to boost the growth of fish in nutrient-treated areas. Adjustment of the timing of the first dose from late-winter/early spring to mid-spring to coincide with the peak of growth potential may result in a stronger growth response during this key period, allowing for the potential of direct consumption which is likely to be limited by the time eggs hatch and the first-feeding stage is reached. Refining the method of application by dividing the quantity of nutrients for the first dose in half and applying half at the time of egg planting, and half at the expected time of first feeding may have greater benefits than simply delaying the timing of a larger dose.

The potential for additional doses is dependent on the workload and funding available for fisheries managers, who may have limited resources for conservation action (Morton *et al.*, 2016). While it may be tempting to add further additional doses of nutrients during the year, this risks the delicate balance of upland streams, which are often oligotrophic (Chapter 2). Though eutrophication is a risk that may present itself if nutrient pellets are added consistently, evidence from previous studies suggests that a cessation of nutrient supply results in a quickly diminishing effect which returns to the baseline level (Chapter 2). For example, the growth rate of age 0+ grayling (*Thymallus arcticus*) in streams treated with nutrient additions over at least a six year period showed that after nutrient addition ceased, growth rate quickly declined to levels which were similar to or lower than control streams (Benstead *et al.*, 2007).

Another factor of importance to consider is the threat of climate change to juvenile salmon. For example, in the near future many Scottish streams are expected to reach temperatures (23°C) that are stressful for Atlantic salmon more frequently (Jackson *et al.*, 2018b), and so providing extra resources during these

periods where growth may not physiologically occur would be redundant. For this reason, targeting growth towards the spring where maximum growth occurs could be more beneficial than applying a second dose in summer, unless this is paired with other forms of management to reduce stream temperatures such as riparian tree planting (Jackson *et al.*, 2021).

Potential emigration and immigration between study zones was unavoidable in this study due to the use of open experimental reaches. Given that juvenile salmon may migrate 1.23km upstream and 2.14km downstream (Eisenhauer *et al.*, 2021), juveniles may have moved between sites, which could have led to inferences around temporally variable measurements such as density not reflecting the full period of study, as this measurement represents only a snapshot of the fish density at the time of sampling. This may have resulted in artificially greater or lesser densities in experimental zones containing habitat more or less favourable to salmon and thus being the recipient of greater immigration or subject to greater emigration. The use of passive integrated transponder tags could be implemented in future study at a point at which fish would be likely to meet the minimum tag size. However, this would not address the possibility of non-focal fish migrating into the study sites.

The second dose of nutrients led to an increased fry body size, which is likely to have been beneficial as this may result in larger smolts with a greater likelihood of marine survival. However, the impact of the timing of nutrient additions could vary with ontogeny, with fry benefitting from a summer application and parr benefitting from a winter application, providing resources for compensatory growth after the winter period (Bacon *et al.*, 2005). Potentially increasing the size of the winter dose could allow for enhanced growth of parr during the compensatory growth period in early spring. A consideration as to whether fry or parr would benefit more from nutrient additions would be beneficial for future study.

Overall, the application of two doses of nutrient pellets appears to have potential conservation advantages compared to the application of a single dose, as it resulted in juvenile fish that were significantly larger and living at higher densities. The faster growth could be expected to result in fish that may smolt earlier, and so escape the pressures of mortality in freshwater earlier, or to result in fish smolting at a larger size and thus have a greater likelihood of returning successfully from sea to spawn as adults. However, further consideration as to the

timings of the doses may help to maximise the potential of nutrient additions as a potential conservation tool, especially in the face of other pressures to salmon in fresh water.

# Chapter 5 | Predicting the effects of nutrient additions on freshwater growth rate and consequences for return rates of Atlantic salmon: an individual-based modelling approach

## Abstract

The body size of individuals can play an important role in determining the timing and probability of a variety of life history events such as ontogenetic niche shifts, maturation and breeding. In Atlantic salmon (*Salmo salar*), the early growth rate (and hence body size) of juveniles may have population-level consequences by affecting the number of fish which are likely to migrate to sea, survive the marine phase and return to breed, and hence the number of fish in the next generation. However, declining Atlantic salmon populations, resulting in a lower return rate of adults, have reduced the quantity of marine-derived nutrients imported to spawning streams. This has made them increasingly oligotrophic, which may have consequences for juvenile growth and population dynamics. The use of nutrient additions has been suggested as a conservation tool to boost juvenile growth and increase the number of returning adults. While a number of experiments have shown positive effects of added nutrients on juvenile growth, no empirical studies have followed a population from the fry stage through to spawning to assess the efficacy of nutrient additions on population dynamics. This is due to the logistical challenges in tracking the impact of faster juvenile growth on the complete lifecycle. Here I addressed this knowledge gap by developing an individual-based model to predict the effect of growth manipulations on the survival rates, life history outcomes and population size and structure of Atlantic salmon. The model was parameterised using data drawn from wild salmon populations. It predicts that increasing the early growth of juvenile salmon should lead to greater numbers of fish reaching the seaward-migrating smolt stage, surviving at sea and returning to spawn. This occurs despite a parallel increase in the number of males maturing precociously (and so never reaching the smolt stage), so that the sex ratio of smolts is predicted to become more female-biased as juvenile growth rates increase. The increased numbers of sea-run spawners

arises from a predicted reduction in time to reach the smolt stage (and hence reduced mortality in rivers prior to seaward migration); the average size of smolts should be little affected by early growth rates. These results demonstrate that the use of nutrient additions to increase the early growth rate and thus the body size of juvenile salmon has the potential to be used as a conservation tool to assist populations in recovery, even if this intervention alters population structure.

## 5.1 Introduction

Body size in fish is often a key determinant of life history events since it influences a diverse range of processes ranging from maturation and reproduction to predation risk (Allsop & West, 2003; Baird *et al.*, 2020; Goatley & Bellwood, 2016). Environmental factors, such as habitat availability, have been shown to have a positive relationship with the body size of predatory salmonid and galaxiid fish, though body size was constrained by habitat disturbance (Jellyman *et al.*, 2014). Temperature is a key factor in determining growth rates, and a meta-analysis of 74 marine fish species showed declines in body size as temperatures increased (van Rijn *et al.*, 2017). Anthropogenic effects such as fishing pressures may also lead to changes in both the population structure of fish as well as changes in body size. In the United States, pressure from angling may promote growth-stunted populations of bluegill (*Lepomis macrochirus*) characterised by smaller individuals, as the harvesting of larger fish preferred by anglers may result in changes in the social structure of populations. Jennings *et al.* (1997) demonstrated that without larger males present, smaller males which nest less frequently are more likely to mature and reproduce, which may promote stunting. Further evidence towards this was provided by Oplinger *et al.* (2013), who showed a negative relationship between size-specific growth rate and male maturation age, but also a strong negative effect on growth in the presence of gizzard shad (*Dorosoma cepedianum*), a competitor with larval bluegill.

In Atlantic salmon, body size is one of the main sources of variation in freshwater life histories, which may also be impacted by both environmental conditions and the genotype of fish (Barson *et al.*, 2015; Jonsson *et al.*, 2012). Two notable life-history events are the potential maturation of males during the freshwater phase prior to ever going to sea (known as precocious maturation), and

the physiological transition to a marine-adapted phase (smolting) at the beginning of the seaward migration (Letcher & Gries, 2003a). The ages at which precocious male maturation and smolting occur varies both within and among Atlantic salmon populations. The incidence of precocious male maturity varies through ontogeny, with greater percentages of parr maturing precociously at age 2 than age 1 (Whalen & Parrish, 1999), and may also vary spatially, with stream elevation (a measure of growth opportunity) impacting the maturation size threshold of precocious parr (Baum *et al.*, 2004). The age at smolting varies across the geographic distribution of Atlantic salmon, with salmon at the southern range of the species distribution in Spain commonly smolting at age 1 (Utrilla & Lobon-Cervia, 1999), whereas at the northern limit of their distribution in Ungava Bay, Canada, fish were recorded smolting as late as ages 7 and 8 (Power, 1961; Robitaille *et al.*, 1989). Smolts of multiple age classes may be present in rivers, with the River Teno in Finland holding smolts of six different age classes, from ages 2-7 (Englund *et al.*, 1999), though the most common age at smolting in the north-east Atlantic is age 2 (Jensen *et al.*, 2012). Understanding the relationship between body size and these processes of precocious maturation and smolting is useful to build a greater understanding of population dynamics (Metcalf, 1998).

Historically, large numbers of adult Atlantic salmon returning to spawn has imported marine-derived nutrients to streams, which may have benefitted juvenile Atlantic salmon by fertilising the streams, increasing primary productivity, invertebrate abundance, and thus increasing the body size of juvenile salmon (Chapter 2, Lenders *et al.*, 2016; Nislow *et al.*, 2010; Williams *et al.*, 2009). However, as Atlantic salmon populations have declined, fewer adults are returning to spawn, meaning that the extent to which juvenile body size may have benefitted from the import of nutrients may have declined, as the export of nutrients in the form of outgoing smolts may exceed the level at which they are being imported (Nislow *et al.*, 2004).

This has led to the use of salmon carcass analogues being applied to streams to mimic the nutrients provided by larger numbers of spawning adults. The restoration of Atlantic salmon carcasses, or their equivalent in terms of nutrients, has been demonstrated to result in increases in the body size of juvenile fish (Chapters 3 and 4, Guyette *et al.*, 2013; McLennan *et al.*, 2019). The underlying thought behind the restoration of nutrients is that increasing the body size of fish will result in either larger smolts and/or a reduction in the number of years taken

to reach the smolt stage. The latter would reduce the overall mortality rate prior to smolting, while the former would be beneficial since smolt size is positively correlated with marine survival (Armstrong *et al.*, 2018; Gregory *et al.*, 2018, Simmons *et al.*, 2021); both factors may ultimately increase the number of adults that return to spawn, increasing the Atlantic salmon population size. Simmons (2022) demonstrated that this relationship varies latitudinally, with the effect being more pronounced and beneficial in southern than more northerly populations, though a larger body size could still be expected to be positively correlated with marine survival in northerly populations.

However, both precocious maturation and smolting can have complex consequences for the population. Understanding these processes is critically important if restoration of nutrients is to be used as a possible conservation measure, as there may be potentially adverse and unintended effects arising from nutrient additions. McLennan *et al.* (2019) estimated that the application of nutrients over a two-year period may have led to the mean age of smolts in the authors' study decreasing by approximately half a year, from age 2.5 to age 2 approximately, and the authors provided alternate scenarios where fish smolting at a younger age reduced the risk of freshwater mortality by remaining in streams for less time, so resulting in an increased population size at the time of spawning; alternatively, by smolting at a younger age, meaning often a smaller body size, they may be more at risk of mortality during smolt migration or at sea due to their smaller body size, and might remain at sea for longer (so as to compensate for their smaller size at the time of seaward migration), which may result in no change in spawning population size.

The precocious maturation of male parr is also linked to body size (Baum *et al.*, 2004; Whalen & Parrish, 1999), and it has been demonstrated that males that mature precociously have a reduced likelihood of subsequently smolting (Letcher *et al.*, 2002; Whalen & Parrish, 1999); note, however, that there is also evidence that this effect may not hold generally for all Atlantic salmon, and that there is a strong genetic component (Debes *et al.*, 2020). By increasing juvenile body size using nutrient additions, it is possible that a greater number of males might mature precociously, and this in turn may have population-level consequences by reducing the numbers of male smolts, which may result in fewer anadromous fish, with a skewed sex ratio towards females.

Hence, it is vital to understand how the life history processes of precocious maturation and smolting are impacted by changes in the freshwater growth rate of Atlantic salmon. To build a complete picture of these processes we must also understand how these changes in body size are linked to marine survival in order to estimate the potential numbers of fish that will return to spawn.

To address these areas of interest using field studies is logistically very challenging and would take considerable time, and therefore the use of modelling approaches provides the possibility of testing various scenarios. To that end, the use of individual-based models, such as 'IBASAM' (Individual-Based Atlantic SALmon Model, Piou & Prévost, 2012), 'IB-salmon' (Hedger *et al.*, 2013) and 'IBSEM' (Individual-Based Salmon Eco-genetic Model, Castellani *et al.*, 2015), which have been used to simulate demographic, environmental, genetic and evolutionary processes in modelled river systems, such as hydropeaking in the case of IB-salmon (Hedger *et al.*, 2018), represent a useful tool to address the questions of how changes to the freshwater environment (such as changes in nutrient levels) may affect both the life history and population dynamics of Atlantic salmon.

Here I devise an individual-based model which aims to simplify parameters for ease of assessing the impacts of altering early freshwater growth in Atlantic salmon as a result of potential nutrient inputs. This model therefore does not include environmental parameters such as temperature, and nor is it spatially explicit, except that the model is divided into the freshwater and marine phases, similar to IBASAM (Piou & Prévost, 2012). The model begins with 0+ fry in late autumn (at the end of their growing season), and only includes density-dependent processes in the stock-recruitment relationship that links the number of (female) spawners to the number of 0+ offspring present at the end of the first growth season, since the fry period is the time when density-dependence acts most strongly (at least in the closely related sea trout *Salmo trutta* that has a very similar ecology in fresh water (Elliott, 1985), although Glover *et al.* (2020) demonstrated the strong influence of stocking level on Atlantic salmon recruitment). The effects of density-dependence are thus not applied during the rest of the freshwater phase of the model, unlike the IBASAM, IB-salmon and IBSEM models (Castellani *et al.*, 2015; Hedger *et al.*, 2013; Piou & Prévost, 2012). However, the model does consider the effect of parr age on both the precocious male maturation and smolting processes, which are not included in the IBSEM model (Castellani *et al.*, 2015). There are no genetic or heritable components

within the model, in common with IB-salmon (Hedger *et al.*, 2013). The model considers only a single cohort of fish and the reproductive output of females in terms of 0+ fry, making the model circular and allowing an assessment of whether changes in freshwater growth should lead to declines or increases in population size in future generations. While the model was motivated by experimental studies of the impact of nutrient additions to Scottish streams, and is parameterised using Scottish data where possible, its structure is generic and the results should be broadly applicable to any Atlantic salmon population, and indeed the lessons are applicable to other anadromous species that exhibit variable life histories under environmental control.

## 5.2 Methods

### *Development of an individual-based model*

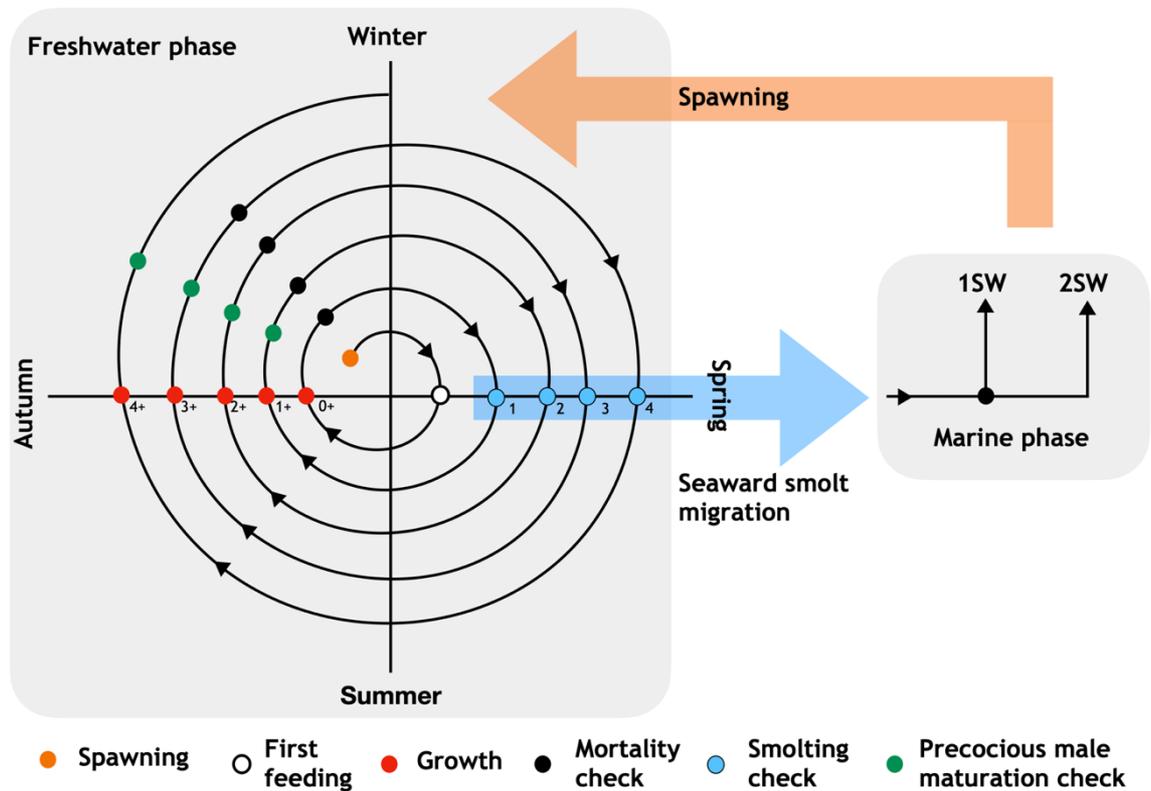
An individual-based model approach was developed using R Statistical Software (v4.2.0; R Core Team, 2022). The model was designed to predict the relative numbers of fish adopting different life histories based on their freshwater growth (with size measured in terms of fork length, since this has been the most frequently used measure of body size in both lab and field studies). The metrics of interest for this model were the numbers of fish smolting, the numbers of males maturing in freshwater as precocious parr, the number of smolts subsequently returning from the marine migration to spawn, the sex ratio of smolts and of returning spawners (number of males per 100 females), and in which year of life these life history events occurred, and finally the production of fry for the subsequent generation.

### *Growth rate of fry and parr*

The baseline model (Figure 5.1) starts with a population of 15,000 0+ fry in late autumn, at the end of their first growth season. The population size of the model was selected as being in the mid-range of fry numbers from the historical stock-fry relationship for the Girnock Burn, northeast Scotland (Gurney *et al.*, 2008) and is thus representative of a large tributary stream of approximately similar size (the Girnock Burn is approximately 9km long, has a maximum width of

15m, drains a catchment of 30km<sup>2</sup> and has an annual mean discharge of 0.5 m<sup>3</sup> s<sup>-1</sup> (Moir *et al.*, 1998)). Fry were allocated a body size (fork length, *L*) through random sampling of a truncated normal distribution of values using the function 'rtruncnorm' in the package 'truncnorm' (Mersmann *et al.*, 2022), with a mean of 52mm and standard deviation (SD) of 9.9mm, based on the mean fork length of 0+ Atlantic salmon fry in two tributaries of the River Thurso, northern Scotland (Allen, 1941). The values obtained by Allen (1941) were selected since fish were captured at the end of each growth season in October. Though other studies (Egglishaw & Shackley, 1980) have detailed size at the end of the growing season, these were measured as body weights rather than body length, and so the use of data from Allen (1941) was deemed to be the most appropriate for use in this model. The minimum size for the truncated normal distribution was set at 30mm; this was selected so as to be slightly larger than that of alevins at hatching, to prevent impossibly small fish being drawn from the normal distribution. No upper size limit was set.

After the initial body size of the 15,000 fry is generated, their size is calculated at the end of each subsequent growth season (i.e. at ages 1+, 2+, 3+ and 4+). Growth between the end of the 0+ summer and end of the 1+ summer is calculated by multiplying an individual's 0+ body size by 1.894. This value was obtained from the mean size of 1+ Atlantic salmon fry in the Thurso study divided by the mean value for 0+ fish, in both cases the measurements being taken at the end of the growth season (Allen, 1941). Body size at ages 2+, 3+ and 4+ are calculated according to Table 4.1, such that fish varied in growth rate but a given individual maintained a similar growth trajectory throughout its freshwater life, and mean size-at-age approximately matched that of fish in the Thurso River (Allen, 1941).



**Figure 5.1** | Depiction of processes within the individual-based model. Each fish commences life at the time of spawning (near the centre of the spiral). Growth is applied on an annual basis, as is the check on whether it has died or not (mortality check), migrated to sea as a smolt or (in the case of males) become precociously mature. At each ‘check’, a binomial deviate is generated based on the probability of the event occurring. At the smolting ‘check’, fish have the opportunity to smolt at ages 1, 2, 3 or 4, and in doing so leave the freshwater phase of the model and are then considered to be ‘at sea’. Within the marine phase, there is a single ‘check’ for marine survival, which accounts for the probability of surviving two sea winters (SW). The probability for fish to be 1SW or 2SW is determined after the determination of marine survival. The ‘check’ for precocious male maturation occurs each autumn once a male reaches the age of 1+, but each male may only successfully mature once.

**Table 5.1** | Body size varies with age, and the mechanism of body size determination is illustrated for each individual in the manner depicted in this Table.

Age class	Name of body size parameter	Body size determination mechanism
0+	Size0plus	Drawn from truncated normal distribution
1+	Size1	1.894(Size0plus)
2+	Size2	Size1 + (Size1-Size0plus)
3+	Size3	Size2 + ((Size2-Size1)/2)
4+	Size4	Size3 + ((Size3-Size2)/3)

Individuals are then assigned a sex by generating a deviate of a binomial distribution using the function ‘rbinom’ (0 = female, 1 = male) using a probability of 0.5. All binomial deviates hereafter are generated using this function (with the exception of the generation of the number of winters a fish spends at sea).

To determine survival between the end of the 0+ and 1+ growth seasons, a deviate of the binomial distribution (0 = mortality, 1 = survival) is generated with a probability of 0.41 for survival, being an average value for survival in the second year of life drawn from several studies (Cunjak & Therrien, 1998; Letcher *et al.*, 2002; McMenemy, 1995; Symons, 1979; see Table 5.2).

### *Probability of smolting*

The probability of a fish smolting each spring, based upon its body size (fork length  $L$  cm), is calculated following equation 1:

$$P(\text{smolting}) = 1/1(1 + e^{-x}) \text{ where } x = b(L) + c \quad (1)$$

Values for  $b$  and  $c$  in equation 1 were determined through the following method. Using the R function ‘sigmoid’ in the R package ‘sigmoid’ (Quast, 2022), the standard logistic function was calculated for a range of probabilities (0.99, 0.75, 0.5, 0.25, 0.01). Body size at each of the listed probabilities of smolting was visually estimated using Figure 1d from Jonsson *et al.* (2016), which used a

very large dataset of salmon in the River Imsa, southern Norway, to derive relationships between fork length in spring and probability of smolting for fish of different ages. Values for  $b$  and  $c$  were then determined using simultaneous equations (Table 5.3). For example, taking a fish at age 1 and using the body sizes where the probability  $P$  of smolting is 0.5 (12.8cm) and 0.1 (9.1cm) (as detailed in Table 5.3) gives:

$$0 = 12.8b + c \quad (2)$$

$$-4.595 = 9.1b + c \quad (3)$$

$$-12.8b = -4.595 - 9.1b \quad (4)$$

$$4.595 = 3.75b \quad (5)$$

$$\text{Therefore } b = 1.24, \text{ and so } c = -15.87 \quad (6)$$

For fish at age 1, equation 1 uses the 0+ body size ( $L$ ) plus 2cm, since Jonsson *et al.* (2016) found that fish gained on average 2cm between the end of the previous season of growth and the time of the smolt migration in the spring. Values for  $b$  and  $c$  used in equation 1 differ for each age of smolt (Table 4.3), since the probability of smolting is dependent on age as well as size (Jonsson *et al.*, 2016). Equation 1 is then used to calculate the probability of smolting. This is calculated for all individuals regardless of survival status.

**Table 5.2** | List of parameters and variables used in the construction of the model, along with the number of the equation where they first feature. *i* is used to signify where an individual's values (or for A, the value for that simulation of the model) is used, and the value is not fixed.

Parameter or variable	Description	Value	Equation	Reference
<i>Growth</i>				
<i>L</i>	Fork length (mm, converted to cm for equations 1,12, 13, 16 and 17)	<i>i</i>		
0+ body size	Mean value for October length of 0+ fish, based on mean from the Sinclair Burn and Sleach Water (mm)	52	-	Allen, 1941
<i>Parr survival</i>				
1 <sup>st</sup> - 2 <sup>nd</sup> summer survival	Survival probability, based on mean of 0.50 (from Symons), 0.40 (from Letcher <i>et al.</i> ), 0.33 (from Cunjak & Therrien), and 0.42 (from McMenemy)	0.41	-	Cunjak & Therrien, 1998; Letcher <i>et al.</i> , 2002; McMenemy, 1995; Symons, 1979
2 <sup>nd</sup> - 3 <sup>rd</sup> summer survival	Survival probability, based on mean of published values (0.60 (Symons), 0.33 (Cunjak & Therrien), 0.43 (McMenemy))	0.45	-	Cunjak & Therrien, 1998; McMenemy, 1995; Symons, 1979
<i>Precocious male maturation</i>				
Effect of precocious male maturation on probability of smolting	Probability that male maturation reduces probability of smolting, based on mean of published values (0.36 (Whalen and Parrish), 0.33 (Letcher <i>et al.</i> ))	0.345	-	Letcher <i>et al.</i> , 2002; Whalen & Parrish, 1999
<i>v</i>	Elevation (m)	300	12	Baum <i>et al.</i> , 2004
<i>w</i>	Weight (g)	<i>i</i>	12	
<i>t</i>	Age (1 or 2)	<i>i</i>	12	
<i>d</i>	Parr density (parr m <sup>-2</sup> )	0.6	12	

<i>Smolting</i>				
Smolting at 1:	Probability of smolting aged 1			Values estimated from Jonsson <i>et al.</i> , 2016
<i>b</i>	Coefficient for fish length	1.24	1	
<i>c</i>	Constant	-15.87	1	
Smolting at 2:	Probability of smolting aged 2			
<i>b</i>	Coefficient for fish length	0.753	1	
<i>c</i>	Constant	-8.89	1	
Smolting at 3 or 4:	Probability of smolting aged 3 or 4			
<i>b</i>	Coefficient for fish length	0.517	1	
<i>c</i>	Constant	-7.02	1	
<i>Marine survival</i>				
<i>mL</i>	Increment of increase in marine survival per unit increase in smolt length	0.0045	13, 16	Mangel, 1996
<i>S</i> <sub>1</sub>		-0.024	16	Armstrong <i>et al.</i> , 2018
<i>S</i> <sub>2</sub>		0.146	16	
<i>Expected fry production</i>				
<i>A</i>	Number of returning females	<i>i</i>	18	Adapted from Gurney <i>et al.</i> , 2008.
<i>p</i>		5.613825	18	
<i>q</i>		1.309254	18	
<i>r</i>		688.496733	18	
<i>F</i>	Number of 0+ fry in the autumn	<i>i</i>	18	
<i>F</i> <sub>max</sub>	Asymptotic population size (in thousands)	28.266534	18	

**Table 5.3** | Smolt sizes corresponding to different probabilities of smolting at given ages, based on data extracted from Figure 1d in Jonsson *et al.* (2016).

Probability	Smolt at 1 (cm)	Smolt at 2 (cm)	Smolt at 3 or 4 (cm)
0.01	9.1	5.7	4.4
0.25	11.8	10.3	11.2
0.5	12.8	11.8	13.6
0.75	13.7	13.3	15.5
0.99	16.5	17.4	22.2
Value for <i>b</i>	1.24	0.753	0.517
Value for <i>c</i>	-15.87	-8.89	-7.02

#### *Spring of the 1+ year*

For fish that survive the first year, the probability of their smolting at age 1 is determined by generating a binomial deviate of 0 or 1 based on their size at the time of the smolt migration (approximately May). This size is estimated by adding 2cm (Jonsson *et al.*, 2016) to their body size at the end of the previous growth season (Size0plus), the new size being termed Size0plus\_2cm. Fish that are classified as smolting are assigned a 1 for the Smolt1 variable in the dataframe, whilst fish not smolting are assigned a 0. Non-smolting fish have the 2cm size update removed.

#### *Probability of male maturation*

In the autumn of the 1+ year, males that have not smolted may mature in the river as precocious parr. The most appropriate empirical relationship that predicts precocious maturation for Scottish salmon is based upon body weight. Therefore to calculate the probability of this happening, fork length is converted to body weight using an equation detailed by Sutton *et al.* (2000), using 284 wild parr with a size range of 5.5-14.5cm ( $R^2 = 0.96$  for the relationship between weight and length):

$$\text{Log}_{10}W = 2.78(\text{log}_{10}L) - 1.76$$

(7)

Therefore:  $2.78\log L = \log W + 1.76$

( 8 )

And so:  $\log L = (\log W + 1.76)/2.78$

( 9 )

Baum *et al.* (2004) describe a logistic regression for the probability of captured parr at the end of the growing season in Scotland being a precocious parr as follows ( $v$  = elevation of site above sea level (m),  $d$  = fish density (parr m<sup>-2</sup>),  $w$  = fish weight (g) and  $t$  = fish age (1 or 2):

$$P(\text{mature}) = X/(1 + X) \text{ where } X = e^{(0.00253(v.w) - 0.0118(a.w.t) + 3.452t + 0.09(d.w) - 9.524)}$$

( 10 )

This equation was simplified using mean values for elevation and density (Table 5.2) given in Baum *et al.* (2004).

$$\text{So that } X = e^{(0.759w - 0.354(w.t) + 3.452t + 0.054w - 9.524)} = e^{(0.813w - 0.354(w.t) + 3.452t - 9.524)}$$

( 11 )

The probability of this precocious maturation is then calculated for male fish within the model using equation 12. The equation for predicting precocious maturation of male parr at age 3+ and 4+ uses the age value of 2, since Baum *et al.* (2004) only describe the relationship for parr at ages 1+ and 2+. As parr were not sexed in the study by Baum *et al.* (2004), in order to correct for this the probability of males to precociously mature was doubled in equation 12, assuming an equal sex ratio:

$$P(\text{mature}) = (2 \times (1/(1 + e^{-x}))) \text{ where } x$$

$$= 0.813w - 0.354(w.t) + 3.452t - 9.524$$

( 12 )

### *Autumn of the 1+ year*

For the surviving males which have not emigrated as smolts, a binomial deviate is generated using each individual's probability of maturing precociously, with 1 signifying maturation while fish receiving a 0 value remain immature. These values are applied to each individual in the Mature1 column. Females are automatically assigned a 0. Precocious maturation may only occur once for each fish, and so any males that mature are exempted from future checks for maturation, and will mature precociously in each subsequent breeding season that they remain a parr.

In order to progress to age 2+, survival over the 1+ year is calculated in the same manner as survival over the 0+ period, using a value of 0.45 (Table 5.2). Fish that smolted at age 1 are not included in this survival calculation and are assigned a 2 in the Survive1 column, signifying their at-sea status.

### *2+ year*

The probability of surviving fish smolting at age 2 is calculated in a similar way to the previous year, this time after adding 2cm to the 1+ body size. Precocious male maturation has been shown to reduce the likelihood of parr subsequently smolting (Letcher *et al.*, 2002; Whalen & Parrish, 1999), so for males that had matured at 1+ the probability of smolting at age 2 is multiplied by 0.345 (Table 5.2). A binomial deviate is applied to this revised probability to determine whether each individual then smolts at age 2. If fish do smolt, they are assigned a 1 in the Smolt2 column of the database, and 0 if they do not, with the 2cm size increase removed for these non-smolting fish.

The surviving males that have not smolted or previously matured precociously then have a binomial deviate calculated to determine whether they mature as precocious parr at age 2+. If yes, they are assigned a 1 in the Mature2 column of the database, and 0 if not; all females are also assigned 0.

Survival from age 2+ to age 3+ is determined in the same manner using the 0.45 value as in the 2+ year, with fish smolting at age 2 assigned a 2 in the Survive2 column to remove them from the pool of fish in the stream system.

### *3+ year*

The probability of smolting aged 3 is calculated using the 2+ body size plus 2cm; as before, the reduction in smolt probability is applied for all previously mature males. The binomial deviate is then applied to each individual's (revised) smolt probability to determine which fish smolt at age 3. Smolts are assigned a 1 if they smolt at this age in the Smolt3 column, and receive 0 if they do not, and then the 2cm size increase is removed from fish that are not predicted to smolt.

Precocious maturity is determined as before for the remaining male parr that have not previously matured, and maturing fish at age 3+ receive a 1 in the Mature3 column.

Fish survival from age 3+ to 4+ uses the same 0.45 value as the 2+ year, and any fish that smolt at age 3 are assigned a value of 2 in the Survive3 column to signify their seaward migration.

### *4+ year*

The probability of fish smolting aged 4 is calculated based on the 3+ body size plus 2cm. The probability is multiplied by 0.345 for males which matured precociously in the previous years and have not yet smolted, after which the binomial deviate is generated to determine which fish will smolt, and then the 2cm size increase is removed for fish not smolting.

The probability of maturing precociously is calculated in the same manner as previous years for the remaining male parr, with any maturing fish designated as 4+ maturing fish. The freshwater phase of the model ends here, since the number of fish predicted to still be remaining as parr is trivial, which matches the empirical finding that very few salmon smolt at ages greater than 4 years old except in the most northerly populations in the world (Metcalf & Thorpe, 1990).

### *Marine survival*

The marine phase of the life cycle is simplified for the purpose of this study as the focus is more on the dynamics in fresh water; here the emphasis is to see how size at the time of the smolt migration influences the probability of surviving at

sea through to returning to spawn. Smolt size has been shown to impact marine survival for Atlantic salmon (Armstrong *et al.*, 2018; Gregory *et al.*, 2018). Mangel (1996) details an equation relating smolt size  $L$  to the probability of surviving the  $i$ th year at sea ( $i= 1$  or  $2$ ) using the value  $m$ , which is the increment in marine survival per unit increase in smolt length. The value chosen for  $m$  in the following equations was  $0.0045\text{cm}^{-1}$  (Table 5.2) derived from values given in Armstrong *et al.* (2018).

$$S_i(L) = s_i + mL \tag{13}$$

Using an example value of a 12cm smolt, based on the average size of smolts from the River Conon, northern Scotland (Armstrong *et al.*, 2018), and assuming 1<sup>st</sup> year marine survival is 0.03 and for 2<sup>nd</sup> year marine survival is 0.20:

$$S_1(L = 12) = 0.03 = s_1 + 0.0045(12); \text{ therefore } s_1 = -0.024 \tag{14}$$

$$S_2(L = 12) = 0.20 = s_2 + 0.0045(12); \text{ therefore } s_2 = 0.146 \tag{15}$$

Values for 1<sup>st</sup> year marine survival of 0.03 and 2<sup>nd</sup> year marine survival of 0.20 are estimated based on the assumption that current survival rates have declined and are likely to be lower than previously published values (Chaput, 2012). However, this is only a rough estimate, since the extent to which marine survival rates have declined is currently unknown; in a later section I explore the consequences of this uncertainty in a sensitivity analysis. It is difficult to determine the relative proportion of smolts that are destined to be one sea-winter fish (1SW) or 2SW fish - this is not the same as the ratio of 1SW to 2SW fish in those that return to the river, since an unknown number of fish destined to adopt the two life history strategies will have died at sea before returning. The simplifying assumption is therefore made that 50% of fish will adopt the 1SW and 50% the 2SW strategy. The proportion of fish of a given smolt size that return will then be:

$$\begin{aligned}
P(\text{returning}, L) &= (0.5 * (-0.024 + (0.0045 * L))) + (0.5 * (0.146 + (0.0045 * L))) \\
& * (-0.0024 + (0.0045))
\end{aligned}
\tag{16}$$

This generates a return probability for each smolt based on its size at smolting. A binomial deviate is then generated using the return probability calculated for each smolt to determine whether it returns, with 1 signifying marine survival through to spawning and 0 indicating mortality at sea or on the return migration. The proportion of marine survivors that will be 1SW fish is given by equation 17.

$$\begin{aligned}
\text{Proportion of 1SW fish in spawners} &= [0.75 * S_1(L)] / [[0.75 * S_1(L)] + [0.25 * S_1(L) * S_2(L)]]
\end{aligned}
\tag{17}$$

This determines the probability for each returning fish to be a 1SW fish. A binomial deviate using the R function ‘sample.int’ (using a value of 2 in place of 0, or 1) is performed using each individual’s probability calculated in equation 17. The probability of a 1 being generated (meaning a 1SW fish) is the probability generated in equation 17 for each individual, and the probability of a 2 being generated (for a 2SW fish) is the probability generated in equation 17 subtracted from 1. Survival across multiple sea winters is incorporated into equation 16, so there is no additional mortality check for a second sea winter if fish have the binomial deviate of 1 for returning to spawn.

#### *Determining mean fry production*

To determine the reproductive output of the model, I consider all returning fish together as one generation, regardless of the year in which they smolted or how many winters were spent at sea. Gurney *et al.* (2008) provide a stock-recruitment relationship for the Girnock Burn, NE Scotland, that relates the total number of returning females ( $A_y$ ) to the number of 0+ fry in the stream in their first autumn. This relationship has the following form (equation 18):

$$F = F_{max}(p * A)^q \div (r + (p * A)^q * 1000) \quad ( 28 )$$

This equation predicts the number of 0+ fry in the autumn ( $F$ ) from the number of spawning females ( $A$ ), and captures the density-dependent nature of early fry survival (such that there is an upper limit to fry numbers ( $F_{max}$ )). Parameter values are given in Table 5.2. Since the outcome of this equation is an estimation of the number of 0+ fry at the end of the first season of growth, this takes us back to the starting point of the model for the next generation. This value is pasted into the ‘FryProduction’ column of the model; a value greater than 15,000 (the starting point for 0+ population size) indicates an increasing population, and one less than 15,000 indicates a shrinking population.

### *Sensitivity analysis*

Many of the parameter values chosen for the model are based on multiple and/or large datasets (Table 5.2) and so are likely to be robust. This is especially true for the freshwater phase of the life cycle, where data are easier to obtain and there have consequently been more published studies from which data can be drawn. There is less evidence for the exact values for the marine phase, not least because shifts in marine ecosystems caused by climate change and/or overfishing have led to alterations to salmon marine growth and survival rates in recent decades (Chaput, 2012; Dadswell *et al.*, 2021). A sensitivity analysis was therefore undertaken to determine the effect of changing the slope relating smolt size to marine survival, to test how sensitive model outputs were to the exact value of this parameter. This was done by testing the impact of changing the steepness of the smolt size-survival slope from the baseline value of 0.0045; this required parallel changes in  $S_1$  and  $S_2$  (Table 5.4), with all other parameter values held constant. A second sensitivity analysis was then conducted to assess the impact of changing mean marine survival independently of smolt size (Table 5.5). The baseline condition in this analysis was for all smolts to have a marine survival probability of 0.03 for their first sea winter and 0.2 for their second winter. Of the fish that survived their first sea winter, 25% were selected to be at sea for this second sea winter. As there is little information regarding how many 2SW fish

die prior to returning to sea, and uncertainty surrounding the reasons that some fish spend more than one winter at sea (although this might be related to the need for females to accumulate reserves for spawning (Tréhin *et al.*, 2021)), a value of 25% was selected for the second sensitivity analysis, recognising the inherent uncertainty surrounding this value. Both sensitivity analyses were conducted with a seed of 1 (using the `set.seed` function in R), ensuring that whilst values differed between runs of the model, values obtained across the simulations were equal, meaning that the only change was due to the change in marine survival values, and not as a result of random variation in fish size between runs. However, the values manipulated for the sensitivity analysis (a maximum of  $\pm 20\%$ ) may not be large enough to detect the potential effects that could arise at more extreme fluctuations in marine conditions.

**Table 5.4** | Ranges of values used for sensitivity analysis exploring the impact of changing the slope relating smolt size to marine survival. The baseline values for the slope were decreased or increased by 5, 10, 15 or 20%;  $S_1$  and  $S_2$  were recalculated as in equations 14 and 15 assuming the same mean smolt size and survival.

Percentage change from baseline	Slope (baseline = 0.0045)		$S_1$ (baseline = -0.0024)		$S_2$ (baseline = 0.146)	
	Decrease (-%)	Increase (+%)	Decrease (-%)	Increase (+%)	Decrease (-%)	Increase (+%)
5%	0.004275	0.004725	-0.0213	-0.0267	0.1487	0.1433
10%	0.00405	0.00495	-0.0186	-0.0294	0.1514	0.1406
15%	0.003825	0.005175	-0.0159	-0.0321	0.1541	0.1379
20%	0.0036	0.0054	-0.0132	-0.0348	0.1568	0.1352

**Table 5.5** | Ranges of values used for sensitivity analysis testing the impact of alterations to mean marine survival independent of body size. Baseline values were decreased or increased by 5, 10, 15 or 20%.

Percentage change from baseline	First year mean marine survival (baseline = 0.03)		Second year mean marine survival (baseline = 0.2)	
Direction of change	Decrease (-%)	Increase (+%)	Decrease (-%)	Increase (+%)
5%	0.0285	0.0315	0.19	0.21
10%	0.027	0.033	0.18	0.22
15%	0.0255	0.0345	0.17	0.23
20%	0.024	0.036	0.16	0.24

### *Manipulating growth rate to simulate nutrient inputs*

After the development of the baseline model, four different models were produced which matched the baseline model with the single exception of altering growth rates in fresh water, in order to simulate the effect of nutrient input to streams. These models represented a theoretical 5, 10, 15 and 20% increase to size at the end of the first season of growth, and growth rate in fresh water thereafter. These percentage increases were selected to cover the range of values that previous nutrient supplementation studies have demonstrated in terms of changes in length-at-age. For example, application of a double dose of nutrients increased the mean size of Atlantic salmon fry by 6.9% (Chapter 4), McLennan *et al.* (2019) demonstrated a 17.4% increase in age 0+ salmon fry after the application of carcass analogues, whilst Guyette *et al.* (2013) found a 11-12% increase. In the model, the size increases were applied by increasing the mean of the normal distribution of 0+ fish sizes and the growth between the 0+ and 1+ year by the appropriate percentage growth increase (Table 5.6). Growth in subsequent years was unchanged from the baseline model.

**Table 5.6** | Increases in mean body size at age 0+ and growth multiplier for differing nutrient growth simulations.

<b>Growth percentage increase</b>	<b>Mean size at 0+ (mm)</b>	<b>Growth multiplier between 0+ and 1+</b>
0% (baseline)	52	1.894
5%	54.6	1.9887
10%	57.2	2.0834
15%	59.8	2.1781
20%	62.4	2.2728

### *Running the model*

To determine an appropriate number of simulations of the model, a range of simulation numbers were tested using the baseline version of the model. These ranged from 20 simulations to 200 simulations and were assessed using selected model outputs that were shown to be sensitive to change during testing. These were the mean number of age 1 smolts, the sex ratio of smolts, the sex ratio of spawners, and the mean production of fry. The outputs of the selected metrics rapidly stabilised as the number of simulations increased above 100 (Fig. A.4), and therefore 200 simulations for each growth percentage scenario was selected. The sensitivity analyses were run for 100 simulations for each increase or decrease in marine survival.

The models were executed in R using the cloud computing service DigitalOcean (New York, USA). Each of the growth variations of the model was run with 200 simulations with parallel processing using the R package ‘parallel’ (R Core Team, 2022) alongside the use of the ‘bettermc’ package from GitHub (<https://github.com/gfkse/bettermc>) for ease of reproducibility. The random number generator used in R was set to ‘L’Ecuyer-CMRG’. A seed of 200 was set for the 200 simulation version of the baseline program, and for the 5%, 10% 15% and 20% different seeds were set (201, 202, 203, 204 respectively). When testing the number of simulations, a seed was set according to the number of simulations (so that the test of 20 simulations had a seed of 20), in order to prevent the same numbers being drawn randomly.

## 5.3 Results

### 5.3.1 Sensitivity analyses

In the first sensitivity analysis examining the effect of changing the slope of the relationship between smolt size and marine survival, the mean body size of smolts that were predicted to return to spawn increased as the survival penalty for being small increased (Fig. 5.2A). At the -20, -15 and -10% versions of the slope relationship, the mean body size of smolts returning to spawn was 144mm. At -5, the baseline scenario, and +5% versions of the relationship, the mean size was 145mm, and this increased to 146mm for the +10, +15 and +20% versions of the slope relationship. This equated to around a reduction of three fish returning to spawn in the -20% scenario compared to the baseline, and an increase of three of fish returning to spawn in the +20% scenario, where the baseline scenario had 33 returning fish (Fig. 5.2B). Plausible variations in the steepness of the smolt size-survival relationship therefore had predictable but relatively small effects on the number of returning spawners.

In the second sensitivity analysis, which examined percentage changes in marine survival independently of body size, the mean smolt size of fish successfully returning to spawn was barely affected, being 136mm at the -20, -15, +15 and +20% versions of the model, and 137mm at the -10, -5, baseline, +5 and +10 versions (Fig. 5.3A). However, varying mean marine survival predictably had a strong impact on the number of adults successfully returning to spawn, with the baseline number of 36.8 returning adults falling to 29 when marine survival was reduced by -20%, and increasing to 44.7 fish when it was increased by +20% (Fig. 5.3B).

### 5.3.2 Impacts of nutrient additions on the number of smolts

The model predicted that increases in freshwater body size and growth rate would result in an increase in the mean smolt production (Figure 5.4A). The baseline scenario predicted that 15,000 0+ fry would generate 1524 smolts. Smolt production was increased by 10.1% if early growth and body size were increased by 5%. With a 10% increase in body size, there was a corresponding 18.5% increase

in smolt production compared to the baseline. At a 15% body size increase, the rise in smolt production was 24.9%, which rose to a 29.5% increase at the 20% increase in body size. There was also a change in the age at smolting, with an increase in the number of fish that smolted at age 1 (Fig. 5.5A). The main increase in the number of smolts occurred as a result of the number of fish that smolted at age 2 (Fig. 5.4A), the age at which the greatest number of fish smolted, although this trend appeared to have a saturating relationship with body size. By age 3, the number of smolts decreased linearly as body size increased (Fig. 5.5C). For fish smolting at age 4, there was an inverse relationship with body size (Fig. 5.5D). The fork length of smolts increased linearly as fry/parr body size increased (Fig. 5.6). The number of fish smolting varied by sex. For male smolts, as body size increased so did the number of fish smolting, though this was of a much lower magnitude than the increases seen in the number of female smolts (Fig. 5.7A). Female smolts increasingly outnumbered male smolts as mean early growth rate increased (Fig. 5.7B). The mean sex ratio (males per 100 females) of smolts (Fig. 5.9A) gradually declined as body size increased.

### 5.3.3 Impacts of nutrient additions on the number of salmon surviving to spawning

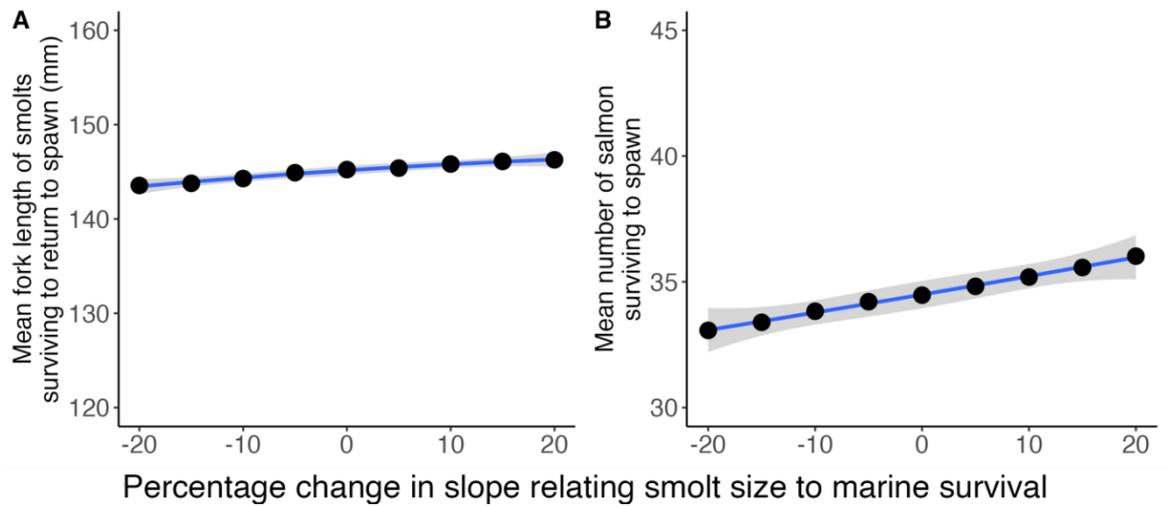
There was a linear increase in the number of salmon surviving to spawning as fry/parr body size increased (Fig. 5.4B). At the baseline size level, the mean number of returning salmon was 34. At a 5% size increase, there was an 18.5% increase in the number of returning spawners; this trend continued so that at a 20% increase in body size, there was an 89.7% increase in the number of spawning salmon in comparison to the baseline. Only one salmon on average returned out of the age 1 smolts (Fig. 5.8A) across all the body size increases. Most spawning salmon were fish that had smolted at age 2, and there was a linear increase in the number of salmon surviving to spawning that had smolted at age 2 as body size increased (Fig. 5.8B). For salmon which smolted age 3, there was a slight hump-shaped relationship with body size (Fig. 5.8C). Very few fish were predicted to smolt age 4, leading to a correspondingly small number of returning fish regardless of early growth scenario (Fig. 5.8D).

The number of male salmon returning to spawn increased linearly with body size (Fig. 5.7C), but was always lower than the number of females, which increased more steeply as early growth conditions improved (Fig. 5.7D). The number of returning females was used to calculate fry production; this increased with early growth rate of the spawners but showed signs of levelling off at high rates of early growth due to the density-dependent effect on fry survival (Fig. 5.4C). Both the baseline level of mean fry production and mean fry production at a 5% body size increase was below the initial population size (15,000 fry), and so these levels represent a declining population. However, at juvenile body size increases of 10% or above, the mean fry production was greater than that of the number of fry at the start of the model, so represented a population increase. The sex ratio (males per 100 females) of salmon returning to spawn exhibited a shallow U-shaped relationship as early body size increased (Fig. 5.9B), though the sex ratio was less female-biased in spawners than in smolts. The number of salmon spending one winter at sea increased linearly with early body size (Fig. 5.10A). A 20% increase in body size only resulted in two more fish spending two winters at sea in comparison to the baseline growth scenario (Fig. 5.10B).

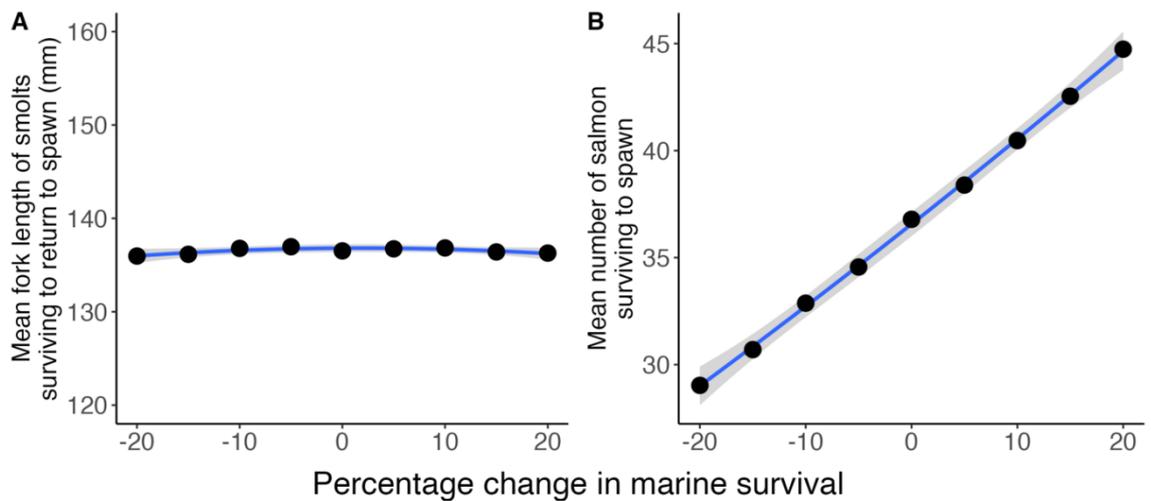
#### 5.3.4 Impacts of nutrient additions on the number of male parr maturing precociously

As early body size increased, so did the percentage of male parr that were predicted to mature precociously, in an initially linear fashion with a slight rate of decline at the higher end of the body size scale (Fig. 5.4D). At the baseline level, there were predicted to be 185 male parr out of the original 15,000 0+ fry which would mature precociously. When early body size was increased by 5%, the number of mature male parr increased by 24.3%, and at the most extreme growth scenario (20% above baseline) the number of male parr maturing precociously increased by 60.2%.

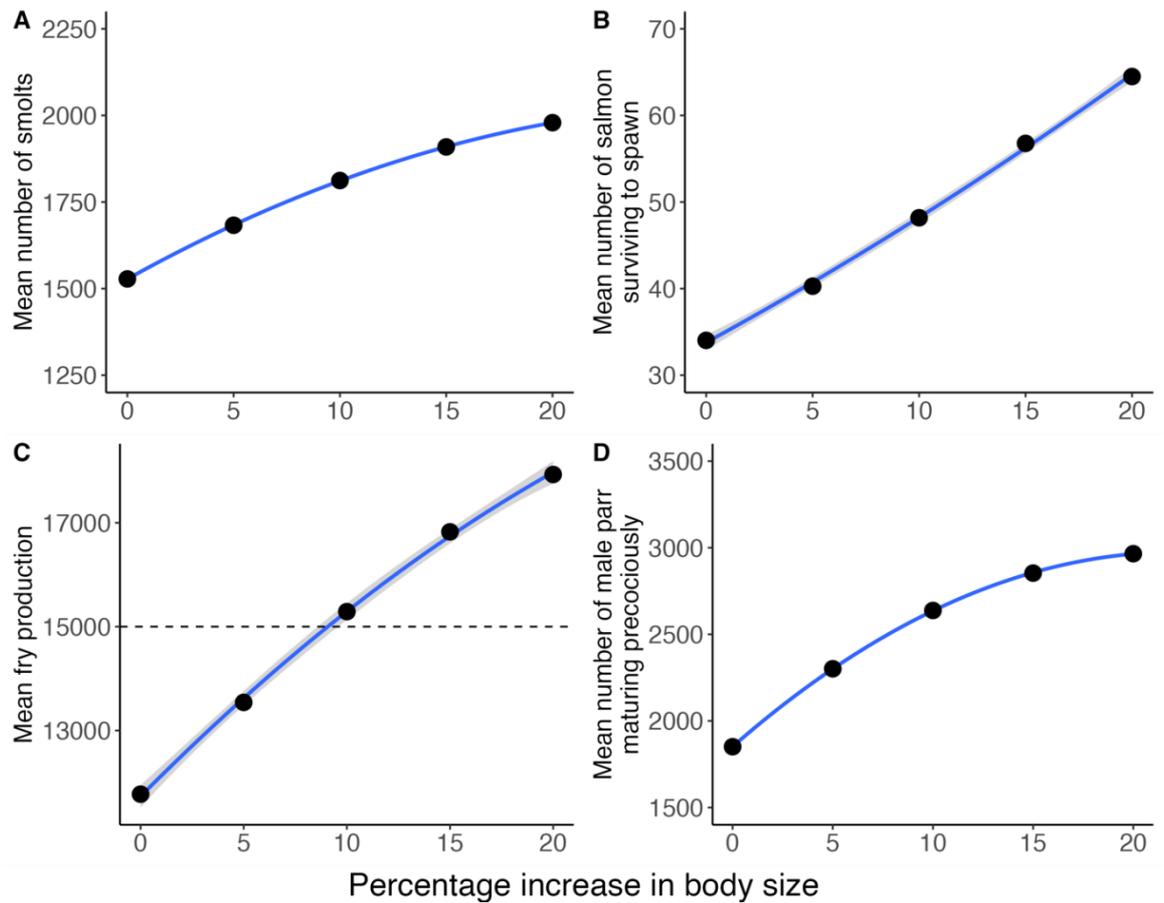
Faster juvenile growth was predicted to result in an increasing proportion of the males maturing aged 1+ but a decreasing proportion first maturing at older ages (Fig. 5.11). As a result, increases in early growth were predicted to result in virtually all of the precocious males first maturing aged 1+ and almost none first maturing when older than 2+.



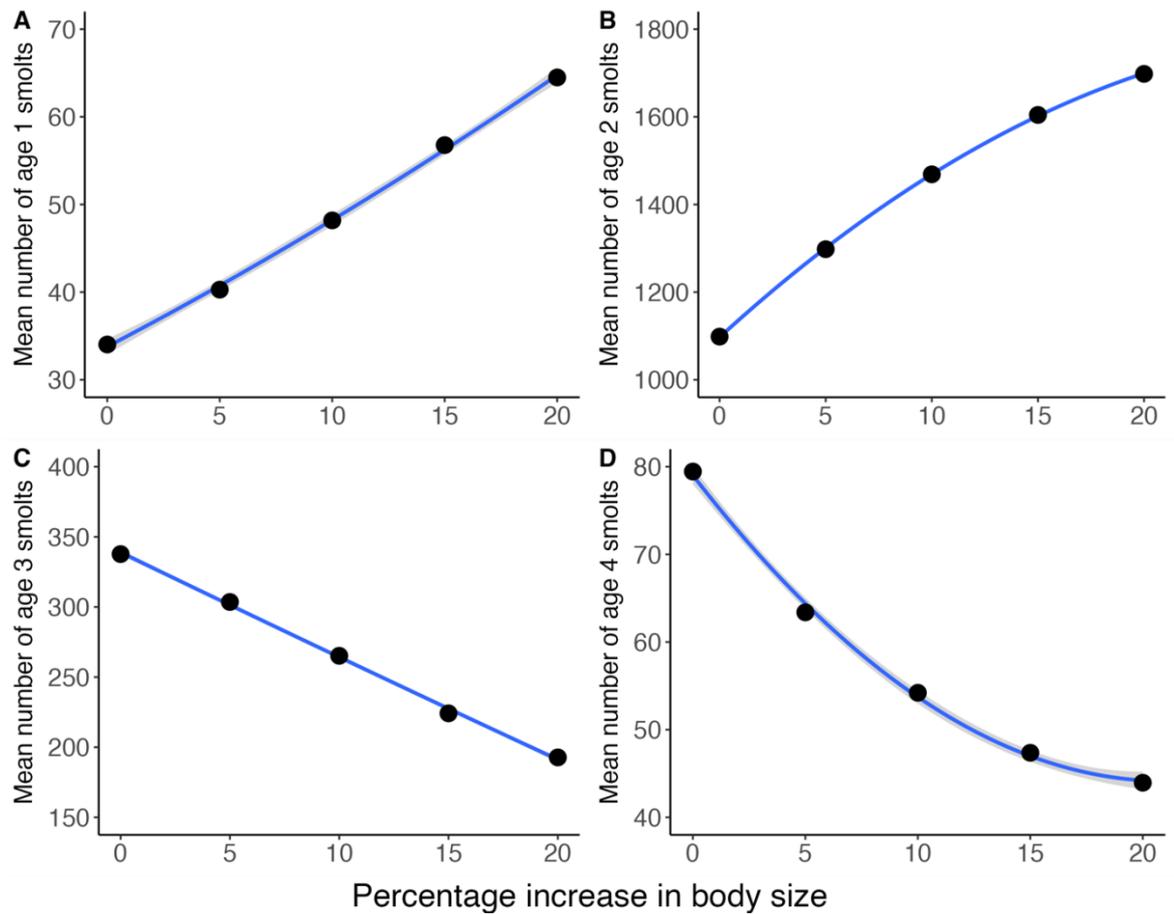
**Figure 5.2 |** Sensitivity analysis detailing the impact of increasing or decreasing the slope that relates smolt size to marine survival, in comparison to the baseline value. A) Fork length of smolts which go on to successfully survive the marine phase and return to spawn. B) Mean number of smolts that survive the marine phase and return to spawn. Both are based on a simulation of 100 model runs for each percentage change, using fixed values for each run so that only the slope relating smolt size to marine survival is altered between simulations (shaded area denotes 95% confidence interval which may not be visible on all plots).



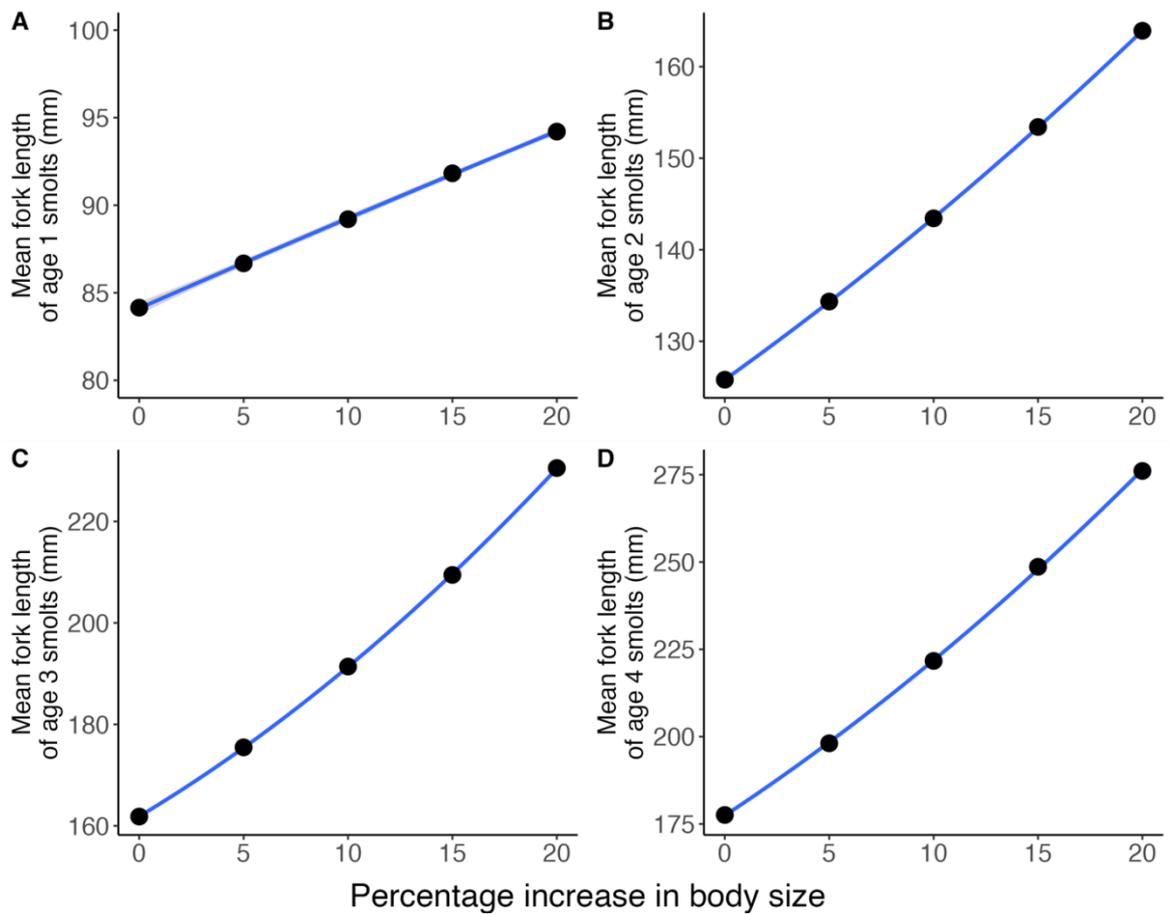
**Figure 5.3 |** Sensitivity analysis detailing the impact of increasing or decreasing the mean marine survival rate independent of body size, in comparison to the baseline value. A) Fork length of smolts which go on to successfully survive the marine phase and return to spawn. B) Mean number of smolts that survive the marine phase and return to spawn. Both are based on a simulation of 100 model runs for each percentage change, using fixed values for each run so that only marine survival is altered between simulations (shaded area denotes 95% confidence interval which may not be visible on all plots).



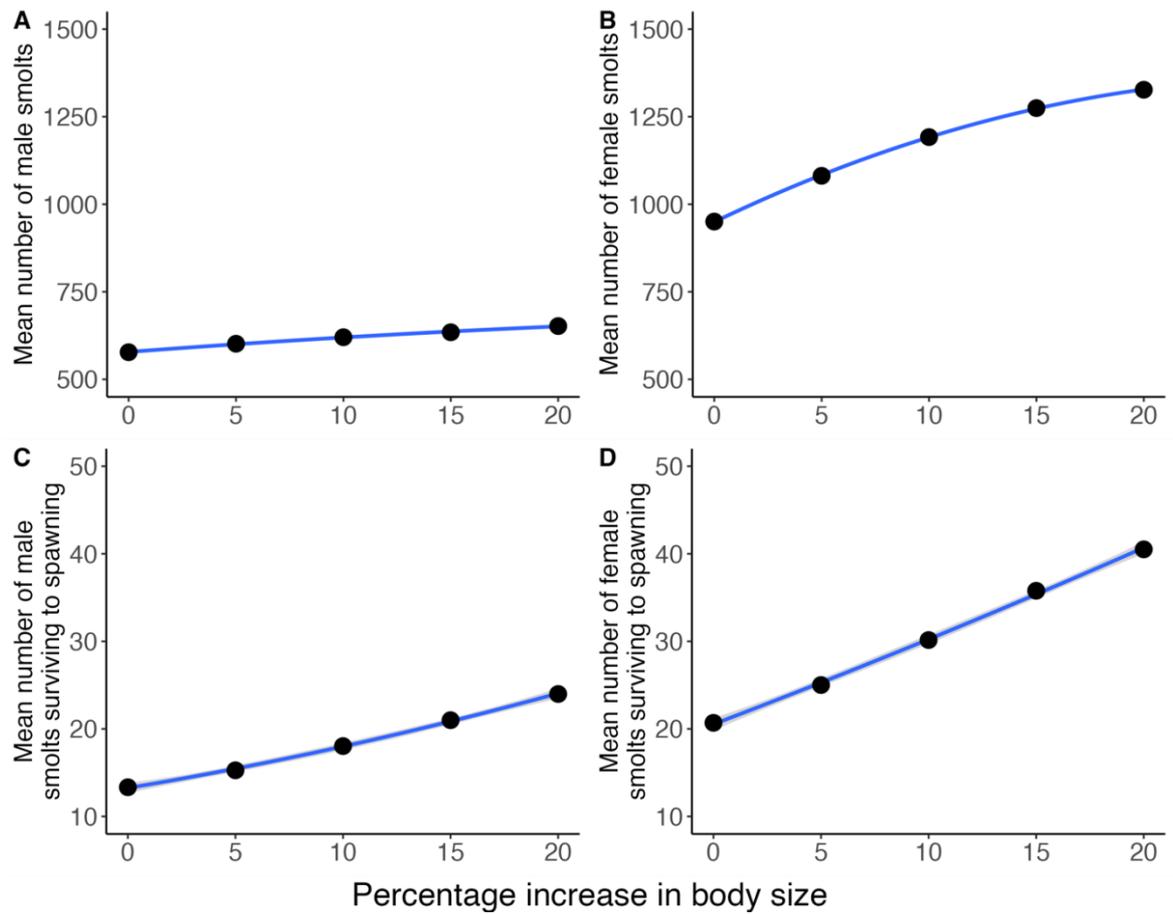
**Figure 5.4 |** Mean numbers of Atlantic salmon at different life history stages in relation to simulated changes in body size in early life, as might be caused by nutrient supplementation. Results are based on 200 model runs for each percentage increase in size (shaded area denotes 95% confidence interval which may not be visible on all plots). A) Mean number of salmon which smolt. B) Mean number of fish surviving the marine phase to return to spawn. C) Mean number of fry produced by females that survive to spawn. The dotted line represents the 15,000 fry at the inception of the model, so below this line represents a declining population. D) Mean number of male parr that mature precociously.



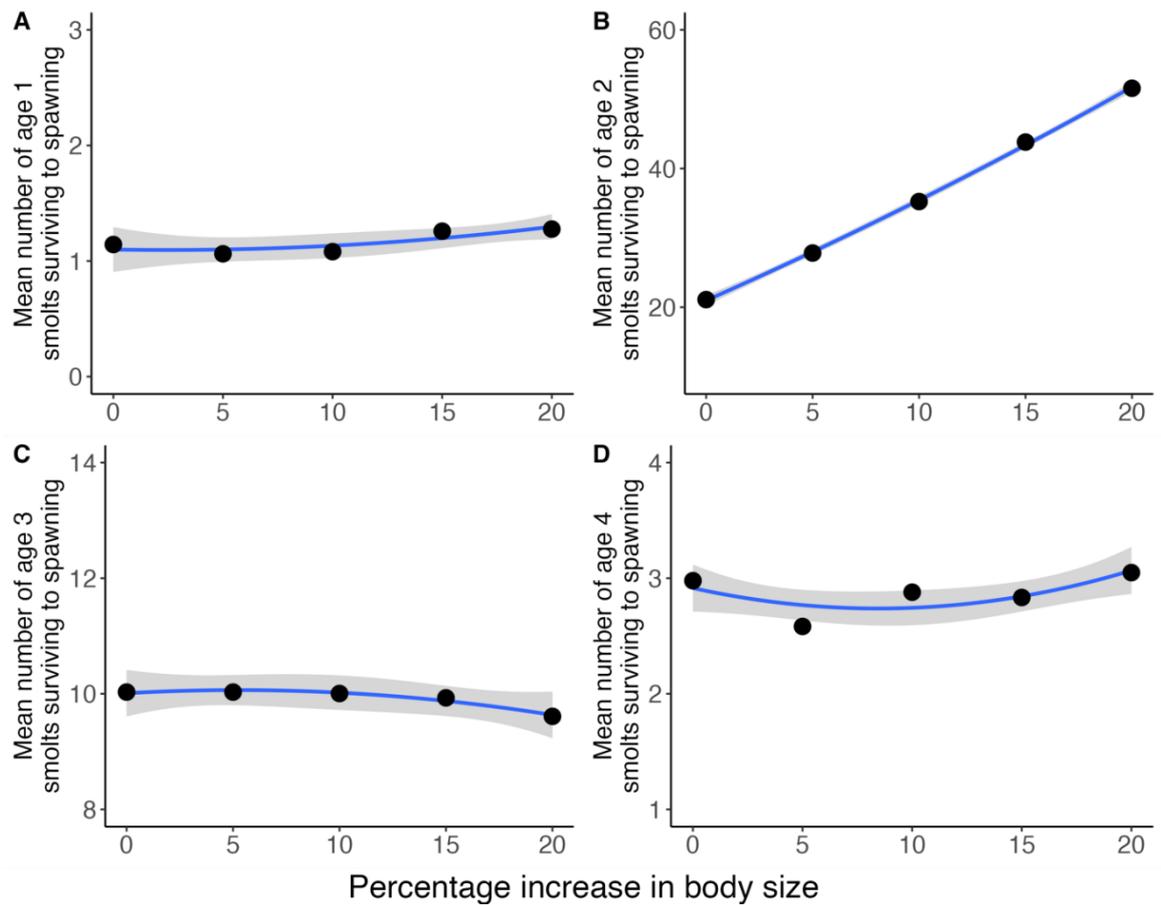
**Figure 5.5 |** Mean numbers of Atlantic salmon smolts at different life history stages in relation to simulated changes in body size in early life, as might be caused by nutrient supplementation. Results are based on 200 model runs for each percentage increase in size (shaded area denotes 95% confidence interval which may not be visible on all plots). Plots A-D show the mean number of fish predicted to smolt aged 1-4 respectively.



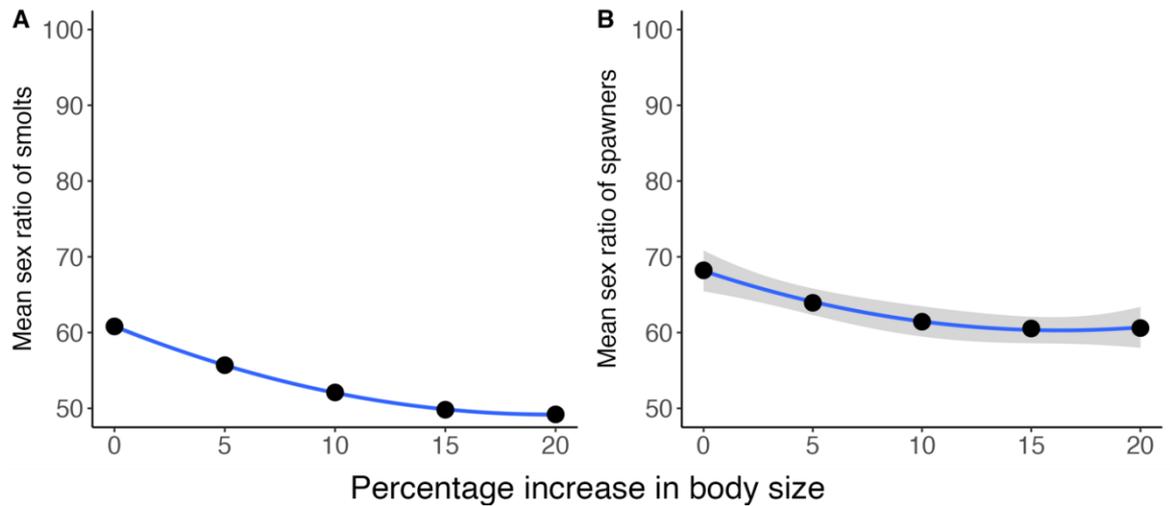
**Figure 5.6** | Mean fork length of Atlantic salmon smolts at different life history stages in relation to simulated changes in body size in early life, as might be caused by nutrient supplementation. Results are based on 200 model runs for each percentage increase in size (shaded area denotes 95% confidence interval which may not be visible on all plots). Plots A-D show the mean fork length of fish predicted to smolt aged 1-4 respectively.



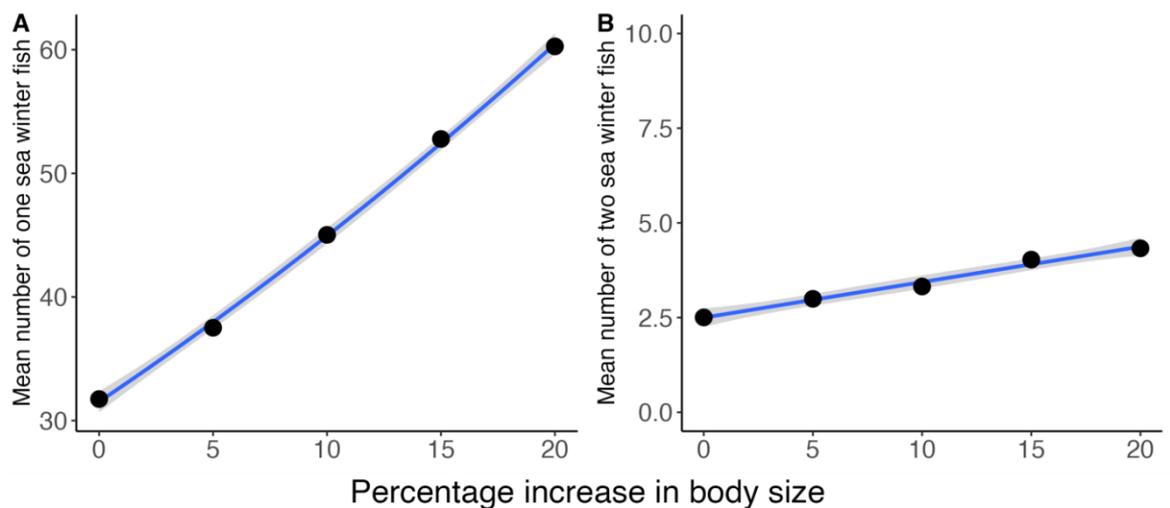
**Figure 5.7** | Mean numbers of Atlantic salmon reaching the smolt phases, and surviving the marine phase to reach spawning at different life history stages in relation to simulated changes in body size in early life, as might be caused by nutrient supplementation. Results are based on 200 model runs for each percentage increase in size (shaded area denotes 95% confidence interval which may not be visible on all plots). A) Mean number of male smolts. B) Mean number of female smolts. C) Mean number of male smolts surviving to spawning. D) Mean number of female smolts surviving to spawning.



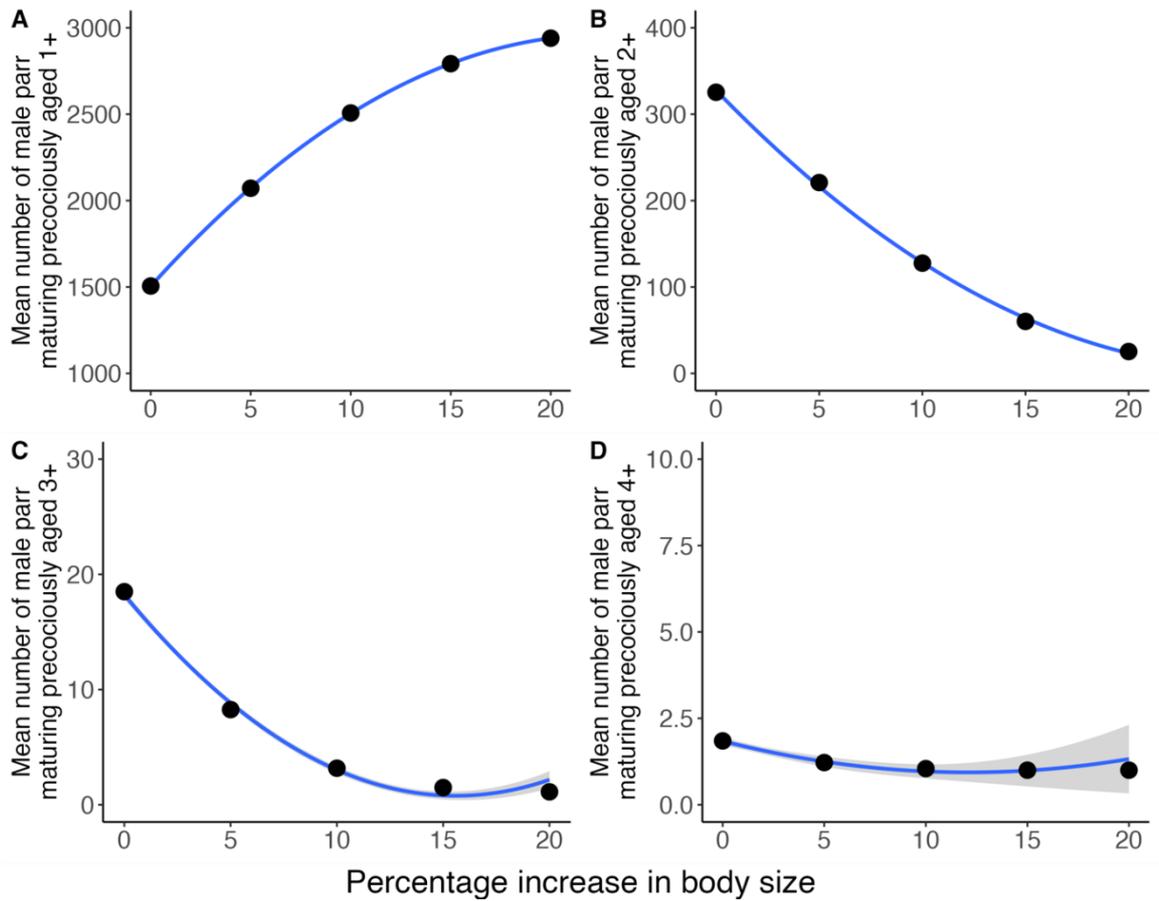
**Figure 5.8** | Mean numbers of Atlantic salmon surviving the marine phase to reach spawning, in relation to simulated changes in body size in early life, as might be caused by nutrient supplementation. Results are based on 200 model runs for each percentage increase in size (shaded area denotes 95% confidence interval which may not be visible on all plots). Data are plotted separately in panels A-D for fish smolting aged 1-4 respectively.



**Figure 5.9** | Mean sex ratio (males per 100 females) of Atlantic salmon smolts (A) and spawners (B) in relation to simulated changes in body size in early life, as might be caused by nutrient supplementation. Results are based on 200 model runs for each percentage increase in size (shaded area denotes 95% confidence interval which may not be visible on all plots).



**Figure 5.10** | Mean numbers of returning Atlantic salmon in relation to simulated changes in body size in early life, as might be caused by nutrient supplementation. Results are based on 200 model runs for each percentage increase in size (shaded area denotes 95% confidence interval which may not be visible on all plots). Data are plotted separately for salmon that had spent A) one winter and B) two winters at sea.



**Figure 5.11** | Mean numbers of male Atlantic salmon parr predicted to mature precociously in relation to simulated changes in body size in early life, as might be caused by nutrient supplementation. Results are based on 200 model runs for each percentage increase in size (shaded area denotes 95% confidence interval which may not be visible on all plots). Numbers are plotted separately in panels A-D for male parr predicted to first mature precociously when aged 1+ to 4+ respectively.

## 5.4 Discussion

Individual-based modelling of the effects of potential increases in body size as a result of nutrient additions indicates the potential benefits of such nutrient additions as a possible conservation tool. By testing the impact of increases in body size in early life that cover the range previously demonstrated experimentally (Chapter 4, Guyette *et al.*, 2013; McLennan *et al.*, 2019), the model demonstrates a high degree of sensitivity in the number of fish reaching different life history stages as a response to changes in body size. Based on the parameters used within the model, the baseline version suggests that current growth and survival rates would produce a declining population of Atlantic salmon, fitting with current population trends (Chaput, 2012). The model outputs further suggest that increasing body size in early life by 5% is insufficient to offset this trend. However, a 10% increase in body size appears to result in a stable level of fry production, while an increase in early growth by 15 or 20% may result in increased fry production after one model cycle, although this may not necessarily result in an increased population due to external factors not included within the model and feedback controls such as density-dependence and competition. Previous research has indicated that a 10-11% increase in age 0+ Atlantic salmon fry body size as a result of nutrient additions is possible (Guyette *et al.*, 2013), though this study was conducted in Maine, USA, and the parameter values used in the model are based on Scottish data where possible. In Chapter 4, the double dose experiment resulted in a 6.9% increase in body size, and the results from the model indicate that this would be insufficient to create a stable or growing population. However, McLennan *et al.* (2019) demonstrated a 17.4% increase 0+ Atlantic salmon fry body size in streams treated with nutrient pellets in experiments undertaken in Scotland. Although the model developed here aims to help illustrate the effects of potential nutrient additions, the model may also be used in the context of any intervention or change that might result in increased early freshwater growth rates, such as habitat restoration.

The increase in both the number of smolts and the number of returning adults as growth in freshwater is increased appears to be mainly driven by increases in the number of fish smolting at age 2. Under the baseline scenario few fish smolted aged 1 and most smolted at age 2 or 3. However, under the scenarios of an increase in freshwater growth rate there would be an increased number of fish

smolting at age 1 and (especially) at age 2. Due to the fact that a large number of fish have then smolted and left the river population, the number of fish smolting at age 3 and age 4 would decline as freshwater growth rate increased.

Nutrient supplementation may result in an increased number of precocious parr, which may be subjected to higher mortality pressures as they may remain in fresh water for longer as smolting is often delayed (Letcher *et al.*, 2002). From a management perspective, an increase in the number of precocious parr may not be ideal, as it may lead to a reduction in the total number of smolts. However, the outputs of the individual-based model used here indicates that although the number of precocious parr increases as body size increases, so too does the corresponding number of smolts and thus the number of fish predicted to successfully return to breed as anadromous adults.

The greater the percentage increase in body size, the more males mature precociously at age 1, which is the most common age of first precocious maturation. As very few fish in the environmental conditions modelled here are predicted to smolt at age 1, an increase in the number of precocious males leads to a reduction in the number of males smolting relative to females, due to the fact that precociously maturation reduces the likelihood of then smolting in a subsequent year (Letcher *et al.*, 2002; Whalen & Parrish, 1999). This in turn has the potential to impact upon the spawning behaviour of Atlantic salmon (though this is not modelled), as the sex ratio of anadromous fish is thus biased towards females. However, the sex ratio becomes slightly less skewed when marine mortality is accounted for. This may be due to the fact that there is a size discrepancy between male and female smolts (Table A.11) which begins with fish smolting age 2. At age 2, male smolts are smaller than female smolts (122mm and 128mm respectively in the baseline scenario) due to larger male parr having matured precociously at 1+; amongst 2-year old smolts males may have a higher mortality rate in the marine phase due to their smaller mean size. However, the complexities of size-dependent precocious maturation result in males that smolted at age 3 or 4 (166mm and 188mm respectively) being larger than females smolting at these ages (159mm and 163mm respectively), so at these ages males may have a lower mortality rate than females during the marine phase. This may explain the shift in the sex ratio (males per 100 females) between smolts and fish returning to spawn. Marine growth has also been demonstrated to have differential sex effects, with females taking longer to reach maturity, leading to

a greater proportion of females in 2SW fish (Tréhin *et al.*, 2021). This was not considered in the model, but may further alter the shifting sex ratio, and could be considered in future iterations.

Within the model, there are aspects that have been simplified, and adding further complexity to these parts may lead to different outputs to the model's current version. For example, within the model an individual's growth is based entirely on the body size it is assigned at the end of the first growth season; thus individuals that grew relatively fast in their first summer continue to grow faster than average. These relative differences among fish are not unrealistic, given the consistent differences in relative growth rates of individual wild Atlantic salmon parr over periods of at least two years (Letcher & Gries 2003). However, the model does not capture variation in growth conditions over time (e.g. between years). Piou & Prévost (2012) showed that within the IBASAM model, changes in the speed of growth whilst in the freshwater phase altered population structure, and this may have been apparent within the current individual-based model if growth was parameterised in a more flexible manner. In a more true-to-life version of the model, including environmental parameters such as temperature and flow regime may provide a more accurate estimate of growth, rather than the assumption made of a fixed value dependent on initial body size. For example, the IBASAM model (Piou & Prévost, 2012) parameterises flow data and temperature within the model, whilst river temperature and river size is parameterised within the IB-salmon model (Hedger *et al.*, 2013) and the IBSEM model (Castellani *et al.*, 2015). However, no studies have been conducted where the interactions between flow, temperature and nutrient supplementation have been measured concurrently, and so flow and temperature were not included within the individual-based model used in this chapter. However, nutrient supplementation could help to increase growth during periods of higher temperatures when energy demand may be high, but conversely high flows may lead to nutrient supplementation being washed away and may not impact growth in the same manner as during lower flow when nutrient supplementation may be more easily accessible and retained within the system. Birkel *et al.* (2013) modelled the net ecosystem respiration of the Gironck Burn, on which many parameters for this model are based, and showed that net ecosystem respiration was higher over the summer period, indicating that demand for nutrients may be high. Nutrient supplementation during this time, when coupled with parameterising the effect of temperature on growth, may have led

to fish experiencing higher growth than the baseline version of no nutrient supplementation, though this effect differed across moorland and forested sites (Birkel *et al.*, 2013). Temperature may also affect precocious male maturation, with a lifelong increase in mean temperature leading to a higher rate of precocious male maturation, presumably acting through its effect on growth rates (Åsheim *et al.*, 2023).

Additionally, making the model spatially explicit and factoring in density-dependent competition may lead to different results from the current model, which only applies density-dependence at the stage of the model where fry production is generated from the number of salmon predicted to return to spawn. Other aspects of the model may be considered less robust. The freshwater phase of the model is based on data gathered from large datasets (Table 5.1), but the marine phase of the model is based on a very rough estimate of current marine survival and as such there may be a wider margin of error surrounding values obtained for fish returning to spawn successfully and other metrics derived from this value, such as mean fry production. Other factors such as the latitudinal impact of smolt size on marine survival, where the effect of smolt size is more pronounced in more southerly populations (Simmons, 2022) could also be further considered, and may drive much more pronounced impacts and changes to the marine phase of the model if modelling southerly populations.

The model also does not address any genetic components that may contribute towards smolting or maturation. For example, the *vgll3* gene has been demonstrated to play an important role in the timing of maturation (Barson *et al.*, 2015) and may contribute up to 40% of the variation towards this, with an early (*vgll3\*E*) and late allele (*vgll3\*L*) for maturation affecting activity in migrant fish in a sex-dependent manner (Niemelä *et al.*, 2022). However, within the individual-based model presented here, all smolts which have not matured as precocious male parr are assumed to mature within the marine phase, so the model does not take into account the possible implications of early or late marine maturation, either on a life-history basis or a genetic basis.

Though this model considers a single cohort of fish and pools their reproductive output regardless of the year in which they spawn, other modelling techniques such as time lagging would allow for the consideration of multi-cohort processes present in natural systems, such as density-dependent interactions between cohorts, as well as determining a more accurate annual spawning level

considering cohorts returning from sea at different ages and hence in different spawning years.

Due to a lack of experimental data on the impacts of nutrient additions over the life cycle of a generation of salmon, it was not possible to validate every aspect of the model against empirical data from real life. However, as the majority of model parameters are sourced from large datasets covering a range of geographic distributions (though these are centred on Scottish populations where possible), the model is expected to be relatively robust.

The outputs shown here demonstrate that the use of individual-based models may help to understand the potential impacts of the addition of nutrients may have on the life history and population dynamics of Atlantic salmon, and whether such interventions may be suitable as a conservation measure. They demonstrate the level at which body growth over the first years of life may alter change the population from a population in decline to a stable or growing population, and reveal that population growth may occur despite potential adverse effects such as an increase in precocious male maturation.

# Chapter 6 | High summer temperatures are associated with poorer performance of underyearling Atlantic salmon in upland streams

## Abstract

Future warming scenarios are predicted to result in an increased frequency of high, and potentially stressful, temperatures in aquatic ecosystems. Here I examined whether the performance of wild underyearling Atlantic salmon (*Salmo salar*) in Scottish streams stocked with identical egg densities was influenced by thermal stress. Biomass and density declined with degree hours exceeding 23°C, indicating apparent mortality or emigration as a possible result of exposure to high temperatures. These results strengthen the need for further action such as riparian tree planting to reduce stream summer temperatures.

## 6.1 Introduction

In aquatic ecosystems, water temperature is one of the most important variables that governs the activity of organisms across multiple levels of biological organisation, from cells to populations (Caissie, 2006). As a result of climate change, water temperatures are rising alongside increased precipitation and more variable discharge, and these impacts are expected to be particularly pronounced in northerly latitudes (Schneider *et al.*, 2013). Climate change is thus predicted to disproportionately affect cold-adapted species such as the Atlantic salmon (Thorstad *et al.*, 2021). The optimal temperatures for growth of juvenile Atlantic salmon are between 16-20°C (Jonsson & Jonsson, 2009), whereas temperatures above 23°C are widely recognised to induce heat stress, resulting in the cessation of growth and the initiation of behavioural avoidance strategies (Breau *et al.*, 2011; Lund *et al.*, 2002); the ultimate lethal temperature has been estimated between 30-33°C (Elliott 1991).

Important Atlantic salmon rivers are already experiencing temperatures that are likely to result in thermal stress to Atlantic salmon (Cunjak *et al.*, 2013)

across the species' range: Jackson *et al.* (2021) estimated that in 2018 around 70% of streams in Scotland experienced temperatures stressful to salmon. The impact of high summer temperatures on fish populations is likely to depend on the duration of a hot spell as well as its peak temperature, but there have currently been few attempts to test if this is the case.

Here I test for relationships between the extent of high temperatures and the performance of underyearling Atlantic salmon in neighbouring streams with contrasting temperature regimes. The data for this study were incidentally obtained as part of a set of wider experiments investigating the effects on juvenile Atlantic salmon of manipulating nutrient levels in oligotrophic streams; here I only analyse data from unmanipulated control sites in three adjacent streams that did not receive additional nutrients, allowing the effect of temperature to be investigated independently of any impacts of nutrient supplementation.

## 6.2 Methods

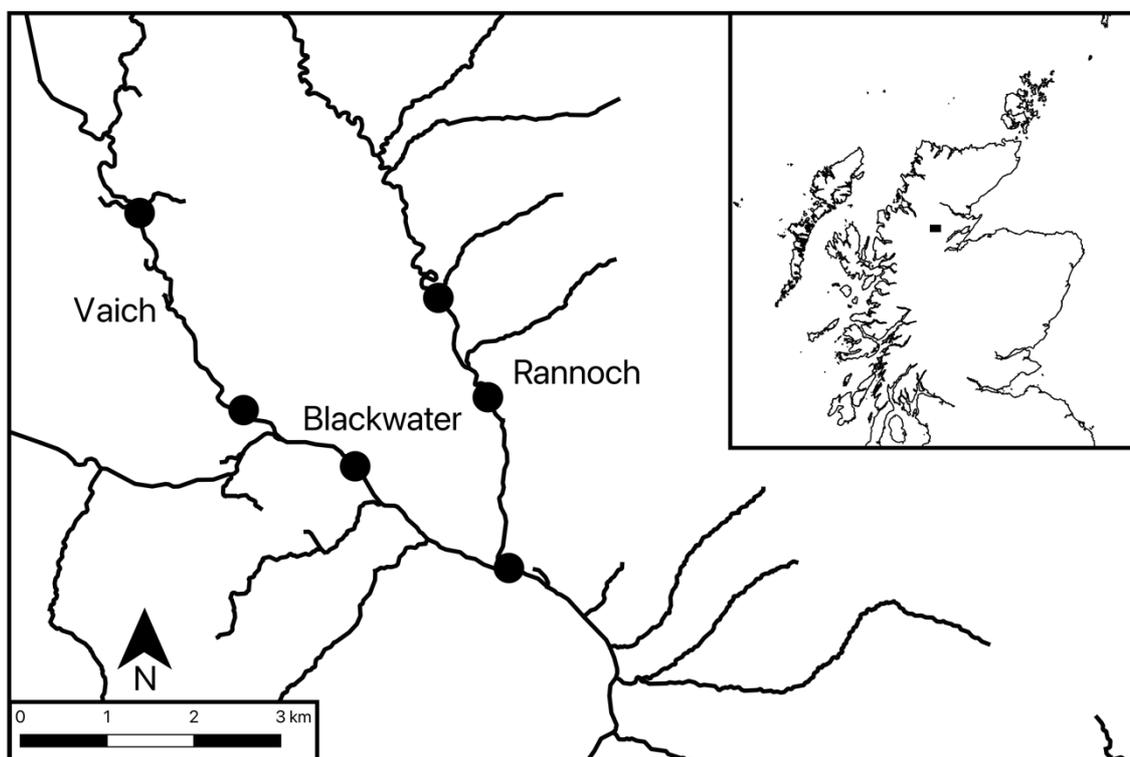
The streams were two tributaries of the upper reaches of the River Blackwater (Rannoch and Vaich) in northern Scotland, and the section of the Blackwater itself between the junctions of these tributaries (Fig. 6.1). Owing to the presence of hydropower dams there is no natural spawning of Atlantic salmon in the Blackwater or its tributaries, but since the 1960s they have been stocked with eggs or first-feeding fry derived from wild parents captured in the same catchment. All three streams contain extensive areas of suitable rearing habitat (in terms of substrate, water depth and flow) for young salmon. The Rannoch runs through moorland and is mostly unshaded, the Vaich is regulated, being fed from an upstream reservoir; it is also unshaded and runs through rough grassland. The Blackwater runs through rough grassland and is shaded in places by riparian trees. The three streams thus have different risks of high summer temperatures despite being at similar elevations and a maximum of only 6 km apart.

Six experimental sites (two per stream, at least 1 km apart) were chosen over the three streams, four of which were used in both 2020 and 2021, with a further two sites (on the Blackwater) added in 2021 (Table A.12). Each site comprised an approximately 500m<sup>2</sup> area of suitable habitat. Within each site, 2500 eggs (100 from each of the same 25 families, which differed between years) at

the eyed stage of development were planted across three artificial redds. All sites thus started with the same density, number and genetic composition of salmon eggs, despite these being of wild origin. At each site, a temperature logger (HOBO Pendant, Onset Computer Corporation, Bourne MA,  $-20-70^{\circ}\text{C} \pm 0.53^{\circ}\text{C}$ ) was placed in a plastic lattice box to allow through-flow at the time of egg planting and buried in the stream substrate. Loggers were programmed to record water temperatures hourly in 2020 and every 2h in 2021, and were retrieved at the time of sampling fish by electrofishing in late summer. On three occasions the logger at the site could not be found, and so temperature data from the nearest located logger were used (in each occasion this was for a nutrient addition site, 340-450 m downstream). Temperature profiles confirmed that streams differed in exposure to stressful temperatures (Fig. 6.2), with the number of degree hours per year exceeding  $23^{\circ}\text{C}$  ranging between 0-195 (Table A.12). Surviving fry were captured between 21-25/9/2020 and 15-20/8/2021, several weeks after the stream temperatures had last exceeded  $23^{\circ}\text{C}$ , by triple-pass electrofishing (E-fish Ltd, Grange-over-Sands, UK; 350V, 60Hz with a 10% duty cycle) covering the whole channel width. Each fished area was subdivided using bankside markers into 4-9 sections (dependent on stream width) with a separate tally kept of fish caught per section; surveyed areas contained similar habitats in each stream (see supplementary information). Fish were lightly anaesthetised (MS-222, 30 mg/L) for measurement of fork length and body mass, before being returned to the stream at the site of capture.

All data were analysed using R (v4.2.0). Fish were assigned to the underyearling fry age class based on size frequency distributions within each site. Degree hours exceeding  $23^{\circ}\text{C}$  were quantified for each site by first removing values below  $23^{\circ}\text{C}$ . The remaining values then had  $23^{\circ}\text{C}$  subtracted, and values were then summed (as Dugdale *et al.*, 2016). Since temperatures were recorded every two hours in 2021, the values for this year were then multiplied by two (this correction had no effect on the results - see supplementary information). Calculated degree hours exceeding  $23^{\circ}\text{C}$  for each site were applied to every section within a site. Fish density (individuals/m<sup>2</sup>) and biomass (g/m<sup>2</sup>) were calculated by dividing the number or weight of fish caught per section of a site by the section area. The effect of temperature on density and biomass was analysed using separate linear mixed effects models using the package “glmmTMB”. Density and biomass were logged to produce linear relationships, after having added 0.02 to each density

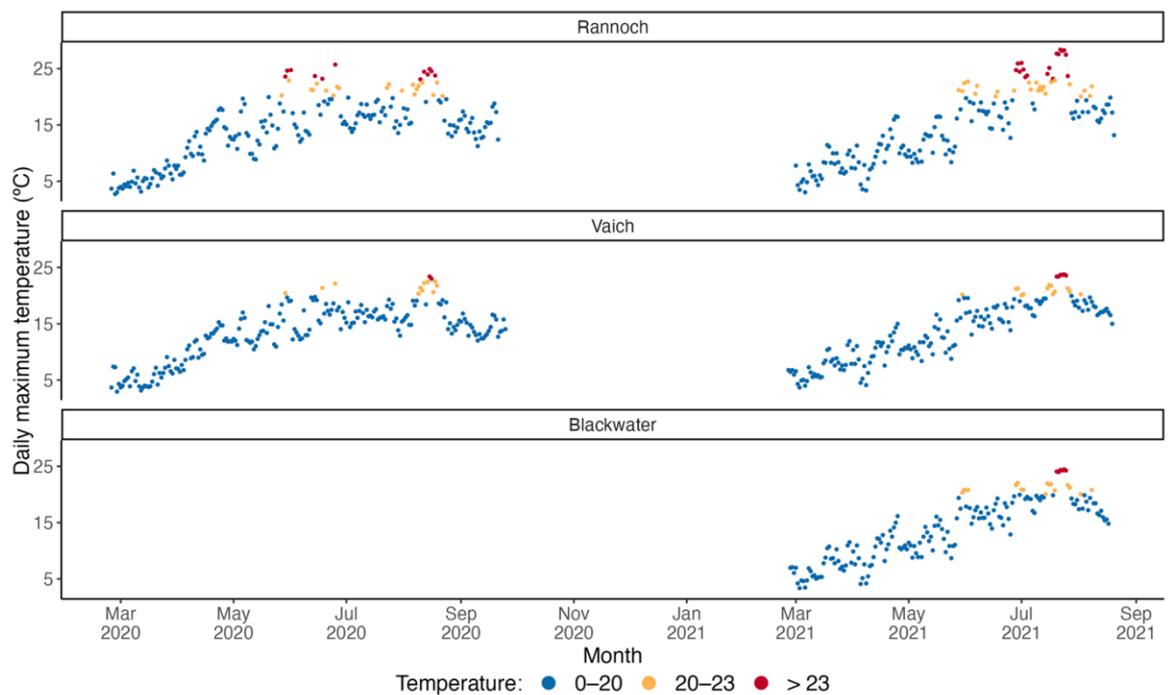
and biomass value to remove zeroes from the density and biomass data, but this was not applied to the temperature data. Degree hours exceeding 23°C, year and stream were used as fixed effects. Site and section within site were used as random effects, to control for the non-independence of sections within a site. The Blackwater stream was used as the reference level. Moran's I ( $P = 0.387$ ) showed no spatial autocorrelation between sampling sites, and temporal autocorrelation was discounted using visual residual plots and Durbin-Watson tests (for density  $P = 0.922$ , for biomass  $P = 0.926$ ).



**Figure 6.1** | Locations of sampling sites (circles) in the river Conon catchment, Northern Scotland. The map depicts the area within the black box in the inset map.

## 6.3 Results

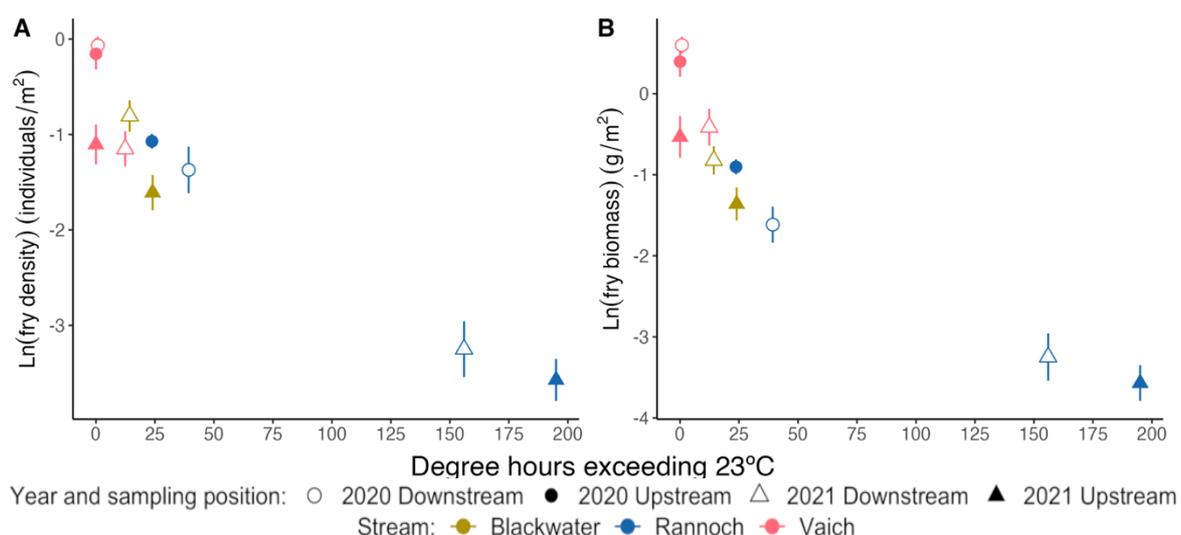
Log density of Atlantic salmon fry differed among streams and was lower in 2021 than 2020 and, after controlling for these effects, was negatively correlated ( $P < 0.001$ ) with degree hours exceeding 23°C (Figure 6.3A, Table 1a). Similarly, biomass of salmon was negatively correlated with degree hours exceeding 23°C independently of the significant differences among streams and years (Figure 6.3B, Table 1b). These effects were independent of habitat differences among sites (see supplementary information).



**Figure 6.2** | Daily maximum temperatures recorded in each stream during the study period (points represent the daily highest temperature for the entire stream, so may be either from the upper or lower sampling sites). Red values indicate temperatures > 23°C, considered stressful to Atlantic salmon, while yellow values indicate temperatures between 20°C and 23°C, and blue values indicate temperatures < 20°C.

**Table 6.1** | Model coefficients for log density and log biomass with degree hours exceeding 23°C. The Blackwater river and 2020 were the reference stream and year; bold indicates significance at  $P < 0.05$ .

Predictors	Log density				Log biomass			
	Estimates	std. Error	Z value	p	Estimates	std. Error	Z value	p
(Intercept)	-0.10	0.25	-0.40	0.691	-0.06	0.28	-0.20	0.839
Degree hours exceeding 23°C	-0.01	0.00	-5.02	<b>&lt;0.001</b>	-0.01	0.00	-4.72	<b>&lt;0.001</b>
Year [2021]	-0.94	0.19	-5.02	<b>&lt;0.001</b>	-0.86	0.21	-4.15	<b>&lt;0.001</b>
Stream [Rannoch]	-0.85	0.32	-2.71	<b>0.007</b>	-0.92	0.35	-2.60	<b>0.009</b>
Stream [Vaich]	-0.02	0.24	-0.08	0.935	0.53	0.27	1.96	<b>0.050</b>
<b>Random Effects</b>								
$\sigma^2$	0.21				0.25			
$\tau_{00}$	0.09 <sub>section:site</sub>				0.07 <sub>section:site</sub>			
	0.00 <sub>site</sub>				0.01 <sub>site</sub>			
Observations	63				63			



**Figure 6.3** | A) Density and (B) biomass of underyearling Atlantic salmon (both on a natural logarithmic scale,  $\pm$  SE) in relation to duration of peak temperatures (degree hours above 23°C) at sites in the River Conon catchment ( $n = 63$  sections sampled across six sites in two years, 589 fish). All sites had the same initial density and genetic composition of eggs.

## 6.4 Discussion

Despite the limitations of this study in addressing areas of variability such as flow regime, potential egg mortality and unknown levels of emigration, the strong negative correlations between related measures of performance or population persistence and temperatures known to induce heat stress suggest that juvenile salmon fry in these northern Scottish streams were experiencing adverse effects of high temperatures. As temperatures in Scottish streams are expected to increase (Hrachowitz *et al.*, 2010), these effects are likely to become more pronounced. Previous work has demonstrated the importance of density, stocking level and discharge on fry production, but showed minimal impacts of temperature (Bal *et al.*, 2011; Glover *et al.*, 2020). In spite of this, the declines in density and biomass seen in the present study may indicate apparent mortality at sites experiencing longer durations of high temperatures. Though factors such as density have been shown to have greater impacts on growth and production than temperature (Bal *et al.*, 2011; Glover *et al.*, 2020), the precise threshold and stress response to high temperature within a population may differ due to natural variability, and thus the impacts of high temperatures may be more pronounced in some populations.

Low densities of juveniles at the warmest sites may be explained by movement of salmon to locate thermal refugia (Dugdale *et al.*, 2016). However, the formation of aggregations of individuals in thermal refugia has been shown to be age-structured, with underyearling fish being much less likely than older cohorts to form such aggregations (Breau *et al.*, 2007). The possibility of juveniles dispersing between sites cannot be discounted, since Atlantic salmon stocked as eggs have been shown to move a mean distance of 403 m both upstream and downstream, with a maximum mean dispersal distance of 1.23 km upstream and 2.14 km downstream (Eisenhauer *et al.*, 2021). In the present study I was unable to separate migration and mortality using the data available, but there was no evidence for sites further downstream to have higher densities (Fig. 1C), suggesting that any such effect was minimal. The sampling date between years varied, however this was taken into account by including year as a fixed effect in the models used, and the impact of this difference is considered to be negligible.

The adverse effects of temperature on cold-adapted fish shows a need for potential mitigation measures. For example, planting riparian vegetation can

reduce the impacts of high summer temperatures through increased canopy shading (Imholt *et al.*, 2013), especially in areas of open grassland or moorland (Dugdale *et al.*, 2018; Malcolm *et al.*, 2008), with extensive modelling indicating areas where it may be most effective (Jackson *et al.*, 2018b, 2021). Riparian tree planting may help to reduce the effects of high summer temperatures on a species already subject to numerous threats.

# Chapter 7 | General Discussion

## 7.1 Summary

Understanding the effectiveness and impacts of conservation practices is vitally important, in order to reduce any potential adverse effects. In this thesis, I have combined experimental approaches to assessing various ways of practically implementing nutrient additions as a potential conservation tool to benefit Atlantic salmon with an individual-based modelling approach to look beyond short-term experimentation to the possible impacts on life history of a whole population from changes in early growth rate. I have also demonstrated the need for the conservation of vital habitat against the threat of climate change, as the process of nutrient remediation would not be effective without sustainable, viable habitat.

Previous research has demonstrated the viability of salmon feed pellets as an effective nutrient replacement for stream salmonids (Guyette *et al.*, 2014; Kohler *et al.*, 2008; Pearsons *et al.*, 2007). Relatively few studies have addressed this in a potential conservation context for Atlantic salmon; they have primarily demonstrated that adding nutrient pellets to salmon streams has generally increased the body size of juvenile salmon, as well as increasing the abundance and biomass of their macroinvertebrate prey (Auer *et al.*, 2018; Guyette *et al.*, 2014, 2013) (McLennan *et al.*, 2019). However, no research has been undertaken to address the practicalities of implementing nutrient remediation using salmon feed pellets, importantly whether the benefits gained from any nutrient additions outweigh any unintended consequences such as changes to life histories which may arise through manipulation of early growth rate. The aim of this thesis was to address these areas of uncertainty and so assess the utility of nutrient additions as a potential conservation tool for Atlantic salmon.

## 7.2 Main findings and their significance

### Impacts of nutrient additions on macroinvertebrate communities

Aquatic macroinvertebrates are an important component of freshwater biodiversity. These invertebrates provide food not only for aquatic predators such as salmon, but typically many aquatic invertebrates only have their larval phases restricted to freshwater, and adults leave the water to aid dispersal. This means that aquatic invertebrates are an important linkage between terrestrial and aquatic ecosystems, with many terrestrial predators such as spiders and birds benefitting from emergent aquatic insects as prey (Collier *et al.*, 2002; Larsen *et al.*, 2016). Terrestrial insects may also fall into streams and these represent a significant component of the diet of many salmonid fishes, particularly as juveniles, as part of the 'drift', which may also contain aquatic invertebrates such as elmid beetles, Ephemeroptera such as baetids, as well as Plecoptera and other taxa (Elliott, 2008; Naman *et al.*, 2022).

The importance of macroinvertebrates in the juvenile diet of Atlantic salmon, particularly Chironomidae and Ephemeroptera (Martinussen *et al.*, 2011), makes understanding how any nutrient additions may affect the macroinvertebrate community in streams useful. For example, if there was a decrease in the abundance or biomass of macroinvertebrates in streams treated with nutrient additions, it would be questionable as to whether nutrient additions may be a useful conservation tool, as the aim is to work alongside natural processes rather than convert juvenile salmon to solely feeding directly on pellets, which would be unsustainable and time-costly. I quantified the biomass, abundance and diversity of aquatic invertebrates in streams treated with either bagged or scattered pellets in Chapter 3, predicting that these three metrics would increase relative to the control treatments. Previous research has suggested that using nutrient pellets in streams as a nutrient remediation method generally leads to invertebrates becoming isotopically enriched with marine-derived nutrients found in the pellets (Guyette *et al.*, 2014; Kohler & Taki, 2010; Kohler *et al.*, 2008), suggesting that invertebrates may feed either directly on the pellets or may become enriched indirectly through the consumption of enriched algae (Nislow *et al.*, 2010). This may have led to the increases in invertebrate biomass

and abundance demonstrated by Auer *et al.* (2018) and McLennan *et al.* (2019), though no stable isotope analysis was undertaken in those studies.

However, my results only partially conformed to the predictions, with the only increase in biomass being the increase in the log mass of individuals in the scattered treatment, with no significant differences in the overall biomass or abundance in streams treated with either the bagged or scattered treatments. This differed from previous studies undertaken in the same system (Auer *et al.*, 2018; McLennan *et al.*, 2019) using carcass analogue pellets, which showed increases in the abundance and biomass of macroinvertebrates. The use of actual salmon carcasses as nutrient remediation where they would not occur naturally due to barriers has also been shown to affect macroinvertebrate communities within the Conon study system, increasing invertebrate biomass in carcass treated streams by around 75%, with invertebrates sampled on the carcasses being particularly enriched with marine-derived nutrients (Nislow *et al.*, 2010). The increases in biomass observed by Nislow *et al.* (2010) were mainly driven in increases in the abundance of larval chironomids, an important food source for juvenile salmon (Martinussen *et al.*, 2011).

Although the results presented in Chapter 3 mainly did not conform to the hypotheses, the increase in the body size of individual invertebrates suggests that invertebrates in the scattered treatment may represent a higher quality food source, as they would contain a greater amount of energy compared to smaller invertebrates. However, Atlantic salmon are gape-limited predators, depending on the growth rate of invertebrates and the age of juveniles, larger invertebrates as a result of nutrient additions could be more difficult to handle and more energy intensive to consume (Nunn *et al.*, 2012). Evidence from the diet of the closely related juvenile brown trout shows that dietary shifts occur dependent on the state of yolk absorption. Sánchez-Hernández *et al.* (2011) showed that 21% of fry began feeding when the yolk was at 0-10% of wet yolk weight, and these fry consumed fewer prey, and did not consume larger items such as the imago stage prior to invertebrates leaving streams. Yolk absorption increases locomotive ability, allowing dietary breadth to increase, with juveniles to better handle and capture prey such as the imagoes of chironomids (Sánchez-Hernández *et al.*, 2011). In the present study, even though there was no increase in the abundance of invertebrates, there was still an increase in prey as each prey item was significantly larger than those found in the control or bagged treatment.

There were also differences between the experimental zones and invertebrate samples taken 500m downstream from the two pellet treatments (bagged and scattered). The individual log mass of invertebrates in both the scattered treatment and 500m downstream of it was greater than those in the control, bagged treatment and 500m downstream of the bagged treatment. There were also differences in the individual log mass of Diptera, Plecoptera and Trichoptera, with increased mass in dipterans in the zone in which pellets were scattered and downstream of both pellet treatments. Plecopterans had decreased mass compared to the control in the bagged treatment, whilst trichopterans were significantly smaller downstream of the scattered treatment. The exact processes leading to these changes in the individual log mass are not known. Pellets in the scattered treatment might have been dislodged 500m downstream in the pelleted treatment, but this could not have happened in the bagged treatment; a more likely route is by the leaching of nutrients into the water column, which were then taken up by autotrophs. Nislow *et al.* (2010) demonstrated enrichment with marine-derived nutrients in both periphyton and invertebrates up to 350m downstream of Atlantic salmon carcasses, so it may be possible that the nutrient effect could extend further than the 350m measured to at least 500m downstream, as there was a detectable effect of the nutrient treatments in the study presented in Chapter 3 (though not through direct measurement of stable isotopes). Sampling directly on the bagged pellets may have shown increased mass or abundance in Diptera, as previous research has shown salmon carcasses to be readily colonised by chironomid larvae and Simuliidae larvae (Nislow *et al.*, 2010).

The results in Chapter 6 indicate that higher stream temperatures affect the abundance and biomass of juvenile salmon. Climate change is likely to impact not only salmon, but entire Scottish stream communities including invertebrates. A consequence of the changing climate may be changes in invertebrate life histories. As temperatures increase, the possibility for greater voltinism among invertebrates such as chironomids may increase as warmer temperatures may increase invertebrate development time (Braune *et al.*, 2008; Drake, 1985), in turn providing more prey items for juvenile salmon. The density of larval chironomids has been demonstrated to be greatest in the spring, followed by winter, with summer densities the lowest (Berg & Hellenthal, 1992). This indicates that the first application of carcass analogue in the early spring could represent a beneficial additional resource for invertebrates, as chironomid growth patterns

show the greatest increases in mean weight over the spring period (Berg & Hellenthal, 1992). This may support the results shown for the scattered/single dose of higher densities of fish but with poorer growth: the pellets could have result in a higher density of chironomid larvae in early summer, so improving the survival of salmon fry in the period immediately after their emergence. This could lead to a greater density of fish, but may result in increased density-dependent competition for food by late summer, as a result of the effects of the nutrient supplementation having worn off (see below for a discussion of density-dependent growth in salmon).

Additional impacts on invertebrate communities may result from an early summer nutrient application. Nislow *et al.* (2010) recorded a greater number of individual chironomids present on salmon carcasses in May and June compared to the January-April period in the Conon experimental system, which may indicate further capacity for growth within this period with additional nutrient supply from a summer application. Indeed, this may support a greater abundance of other invertebrates such as Ephemerellidae, which increased dramatically in abundance in June on carcasses compared to the previous month in the same study. Nislow *et al.* (2010) also showed high abundances of Simuliidae and Leptophlebiidae larvae in the January-March period, giving further support for the potential of an early spring application to support invertebrate communities, although these increases were not shown in my own work. Nutrient additions therefore may have the potential to influence invertebrate populations forming part of the salmon diet across multiple seasons, though this was not tested experimentally within this thesis. It should be borne in mind that the invertebrate sampling was not a core part of this project and could have been done in more detail; potential limitations of my sampling methodologies are discussed in section 7.3.

Overall, I have demonstrated that the method of nutrient application affects the extent to which macroinvertebrate communities are impacted by the nutrient additions. Though my initial predictions were not met, my results did partially conform to those found in previous studies. Further research would be required to fully understand the impacts on macroinvertebrate communities when introducing nutrient remediation using carcass analogues on a larger scale.

## Impacts of nutrient additions on the growth of juvenile Atlantic salmon

Ultimately one of the most important metrics when assessing the use of nutrient pellets as a conservation tool for Atlantic salmon is whether their use has a positive effect on the growth of juvenile fish. As the goal is to produce more high quality smolts (Simmons *et al.*, 2021; Thorstad *et al.*, 2021), where greater body length (but also body mass and condition factor) is the standard of quality, assessing whether juvenile salmon demonstrated increased growth as a result of nutrient additions may be considered as the key marker of success.

In Chapter 3, I compared two approaches of implementing nutrient additions, application of pellets in mesh bags (as used by Auer *et al.*, 2018; Guyette *et al.*, 2014, 2013; McLennan *et al.*, 2019), or through hand-scattering pellets across the area of stream to achieve an even density (as in Collins *et al.*, 2016; Kohler & Taki, 2010). In previous studies, the only application method for carcass analogue pellets used in the context of Atlantic salmon was using mesh bags, which were found to result in significant increases in the length of juvenile salmon (Auer *et al.*, 2018; Guyette *et al.*, 2013; McLennan *et al.*, 2019). Here I contextualise the results of the nutrient addition experiments presented in this thesis in terms of the effects on the growth of juvenile salmon.

In the experiment presented in Chapter 3 of this thesis, there were different effects on growth in the two years of the study. Differences between study years may be explained by environmental factors such as temperature or flow rate. The effect of temperature plays an important role (Chapter 6, also see Elliott & Elliott, 2010) and may have accounted for some of the inter-year variation. Flow, particularly in the summer, is a key determinant of growth for juvenile Atlantic salmon, with fish able to achieve twice the growth in high summer flow streams compared to low summer flow streams (Nislow *et al.*, 2004b). Excess flow during periods such as spring floods can also play a structuring role in Atlantic salmon populations, with alevins and recently emerged fry being vulnerable to high levels of discharge which may result in mortality (Jensen & Johnsen, 1999). Flow rates were not quantified throughout the study period, and it is possible that spring floods could have reduced the population size by increasing mortality before or soon after emergence, or that low summer flow may have constrained growth, leading to the variability in the results between the years.

The bagged treatment only positively affected growth in the second year of the study (2021), with significant increases in fork length, body mass, body condition and relative mass when compared to the control. The salmon that were age 1+ when captured in 2021 would have been subjected to the nutrient treatments as 0+ fry in 2020; these fish did not show a greater 1+ length in the bagged treatment, but did have a significantly greater body condition. This may align with the fact that in 2020 0+ fry saw no increase in fork length as a result of the bagged treatment. McLennan *et al.* (2019) showed significant increases in the fork length of 1+ parr which were subject to nutrient restoration through bagged pellets as both 0+ fry and 1+ parr. However, the higher temperatures shown in Chapter 6 may have impacted the growth of 1+ parr, as high summer temperatures have been shown to result in decreased fork length in Atlantic salmon parr (Swansburg *et al.*, 2002). The results of the bagged treatment did not conform to the predictions set out in Chapter 3, except for the increase in 0+ fork length in 2021 and the increase in 1+ body condition.

Previous research using actual salmon carcasses, which may be more similar to the bagged than the scattered treatment, have mainly demonstrated positive effects on the growth of fish, particularly in Pacific salmon where the abundance of carcasses is greater (Kaylor *et al.*, 2019). Indeed, Wipfli *et al.* (2010) demonstrated that the use of carcasses provides more of a boost of growth to coho salmon and enriches more trophic levels than the addition of inorganic fertiliser pellets, though the use of organic fertiliser pellets made from fishmeal could be expected to differ from inorganic pellets. However, Harvey & Wilzbach (2010) did not show any increased growth in juvenile salmonids (mainly steelhead) in streams treated with carcasses anchored to the stream substrate, indicating that the addition of nutrients in the form of carcasses may not always positively impact the growth of juvenile fish.

In comparison, the scattered treatment presented in Chapter 3 showed significant negative effects on growth when compared to the control. In both years of the study, 0+ fry were significantly smaller than their control counterparts, and this reduction in size was also followed by a significant reduction in body mass and in relative mass, indicating that these fish deviated more from their maximal growth (Elliott & Hurley, 1997) when compared to the control. 0+ fry in the scattered treatment also did not significantly differ in body condition compared to the control, though in juvenile coho salmon, the use of scattered carcass

analogue resulted in increased body condition (Martin *et al.*, 2010). There was a significant increase in the density of fish in the scattered treatment in 2021, and the potential impacts of density on growth are discussed later in this chapter.

When the results of the experiment presented in Chapter 3 are considered in isolation, it would be difficult to judge either pellet treatment as a ‘success’, despite the increase in body length shown in 0+ fish from the bagged treatment in 2021. However, when considered together with the results from Chapter 4, the impact on growth is clearer. In Chapter 4, I presented an experiment comparing the impact of one single dose of the scattered pellet treatment to a double dose of the scattered treatment, with the second dose applied during the summer. In general, the results from the single dose treatment followed those shown in the scattered treatment in Chapter 3, with a significant decrease in the fork length of 0+ salmon. However, in the double dose treatment, there was a significant increase in the fork length of 0+ salmon, indicating that a second dose is important in generating the increase in length desired as the conservation outcome. The growth performance of juvenile salmon using relative mass as a metric showed that fish in the double dose treatment grew much closer to their maximal predicted growth potential than fish in the control treatment, as the relative mass of double dose fish was 72% higher. Fish in the single dose treatment performed more poorly, as these fish were furthest from their maximal growth potential, with a relative mass that was 43% lower than the fish in the control treatment.

However, the increases in growth in terms of body length were lower in magnitude than in previously reported studies (a 6.9% increase in the double dose treatment in this study, compared to 9-15% observed by Guyette *et al.* (2013) and 17% observed by Auer *et al.* (2018) and McLennan *et al.* (2019)). This may have been due to differences in environmental conditions (e.g. baseline nutrient levels, temperature etc) but also in the experimental designs. The Auer *et al.* (2018) and McLennan *et al.* (2019) studies took place within the same catchment as the experimental data presented in this thesis, but not in the same streams. The aforementioned studies used 3000 eggs from 30 families planted over a 300m<sup>2</sup> area, whilst the experimental design in Chapters 3 and 4 used 2500 eggs from 25 families over a 500m<sup>2</sup> area, making the stocking density of eggs in my studies 50% lower than those presented by Auer *et al.* (2018) and McLennan *et al.* (2019).

The growth of juvenile salmon may also have been impacted by the presence of brown trout, which are also likely to have been affected by additional

nutrient inputs. The salmonid communities within the experimental reaches are likely to have been altered in some way by nutrient additions, and further research would benefit from an assessment of the responses of brown trout to nutrient additions, in order to more fully understand the potential impacts on salmon conservation outcomes and how these may be altered by the presence of competing species. Brown trout abundance was particularly high in some sites in 2020, which may have led to more intense interspecific competition, so reducing the size juvenile Atlantic salmon could have attained. In turn, resident brown trout may have increased in size as a result of the nutrient additions, though this was not measured.

The streams used in the experimental chapters of this thesis are also used by fisheries managers for the stocking of Atlantic salmon as both eggs and first feeding fry. Though areas around the experimental zones were not stocked with non-focal fish during the study period, fish that may have been stocked in previous years may have still been resident prior to smolting, and there is the possibility for the immigration of non-focal fry to the experimental zones. Juvenile Atlantic salmon stocked as eggs have shown a maximum dispersal distance of 1.23km upstream and 2.14km downstream (Eisenhauer *et al.*, 2021), so emigration to experimental zones from non-focal fry is possible, but the extent of this occurrence within my experimental sites is unknown.

## Impacts of nutrient additions on the density and biomass of juvenile Atlantic salmon and density-dependent effects on growth

Density has strong structuring effects in Atlantic salmon populations, affecting both the growth and survival of fish, and this is most pronounced in the juvenile freshwater phase where habitat is limited (Imre *et al.*, 2005). In Chapter 3, which compared the addition of nutrients from either bagged or scattered pellets, there was no effect of the bagged pellets on the density of fry in either year, or in parr in 2021. However, the scattered pellet treatment in 2021 showed a significant increase in 0+ salmon density, though this effect was not apparent in 2020 or for 1+ parr measured in 2021. These results conform to the subsequent data presented in Chapter 4, where a comparison was made between the application of scattered pellets singly at the time of egg planting or as a double

dose, applied first at the time of egg planting with the second dose applied at the beginning of June. This study showed that the density of 0+ fish in the single treatment (which is analogous to the scattered treatment in the experiment described in Chapter 3, as this was the same quantity of nutrients applied in the same manner and timing) increased significantly by 60%, whilst the double dose treatment showed a 69% increase in density, both compared to the control. In both the scattered treatment and the single dose treatment, a higher density was accompanied by poorer growth. In underyearling brown trout, increased density has been shown to be accompanied by a reduction in the body mass of fish as a result of greater intra-cohort competition (Kvingedal & Einum, 2011), and a similar pattern may have driven the results observed in Chapters 3 and 4.

Previous studies using carcass analogues as nutrient additions have not demonstrated changes in the density of juvenile Atlantic salmon (Auer *et al.*, 2018; McLennan *et al.*, 2019), or did not record data on density after nutrient additions (Guyette *et al.*, 2013). The results presented in Chapter 4 are the first to report not only a significant increase in the growth of 0+ Atlantic salmon, but also an increase in their density. However, the processes that govern this increase in density seem to depend on the addition of the second dose of nutrients, as a single dose (and the scattered treatment from Chapter 3) increased juvenile density at the cost of a reduction in growth. Jenkins *et al.* (1999) demonstrated that in brown trout the impacts of density-dependence on growth is strongest at low densities, and Imre *et al.* (2005) demonstrated this in juvenile Atlantic salmon. Though increased density has not previously been shown in salmon as a result of carcass analogue additions, density has increased where actual carcasses have been used, such as in juvenile coho salmon (*Oncorhynchus kisutch*) (Bilby *et al.*, 1998). Dunkle *et al.* (2021) showed that adding carcasses to experimental mesocosms did not affect the growth rate of juvenile coho salmon, but led to higher densities of fish as fewer emigrated downstream. Though the single dose treatment in Chapter 4 produced a negative effect on growth, density was increased, which may have been through more fish either surviving or remaining in the experimental zone rather than dispersing downstream. In the results presented in Chapter 4, the control treatment had the lowest density of salmon, though the fork length of fish in the control treatment was significantly greater than those in the single treatment. Management measures other than nutrient additions may also have effects on density: in juvenile coho salmon, the addition

of wood bundles in order to provide in-stream refuges led to greater increases in density than did the addition of either carcass analogue pellets or wood bundles together with pellets (Martin *et al.*, 2010).

There were inconsistent effects of the nutrient applications on the overall biomass of juvenile Atlantic salmon. In Chapter 3, I hypothesised that nutrient supplementation would lead to increases in the biomass of juvenile salmon, but that the extent of the increase would be greater in the bagged treatment than in the scattered treatment. However, there were no significant differences in the biomass of fry or parr to the control for either application method, contrary to the results of previous studies (Auer *et al.*, 2018; McLennan *et al.*, 2019). In contrast, in Chapter 4 the effect of nutrient additions on biomass partially conformed to the hypothesis that there would be increases in both the single and the double application, with only the double dose showing a significant increase in biomass. The results from the double dose in Chapter 4 are similar to the results shown by Williams *et al.* (2009), who demonstrated that the increasing addition of Atlantic salmon carcasses resulted in higher parr biomass, as a consequence of both a greater density of fish and of those fish being a larger size. This suggests that a double dose of carcass analogue pellets may be as beneficial as the application of actual salmon carcasses.

## Impacts of manipulating early growth rate on the life histories and population size of Atlantic salmon

As no study has previously examined the impact of nutrient additions over a single generation of Atlantic salmon from fry to adult (either experimentally or through modelling), the potential effectiveness of nutrient additions as a beneficial conservation tool has not been thoroughly interrogated. Many studies have used either actual salmon carcasses (Williams *et al.*, 2009) or carcass analogues (Auer *et al.*, 2018; Guyette *et al.*, 2014, 2013; McLennan *et al.*, 2019) to demonstrate changes in the growth, density or biomass of juvenile salmon, with the expectation that this could result in benefits to Atlantic salmon, but these benefits have not always been clearly defined. Hence, the understanding of impacts of the nutrient additions beyond the juvenile stage, and beyond the effects of growth, density and biomass, have been mainly speculative thus far. In

Chapter 5, I aimed to provide clarity on the potential impacts that manipulating early freshwater growth could have on the population size and life histories of Atlantic salmon. Though this was presented in the context of nutrient additions, the results are more generalisable to any intervention such as habitat restoration that may result in increased early freshwater growth.

The outputs of the model indicate that increasing the early freshwater growth of juvenile salmon results in a greater output of smolts that are also of larger body size at the time of smolting. This latter finding was not inevitable, given that the salmon can potentially smolt at a younger age if their growth rate is increased, and younger smolts are on average smaller than older smolts. Larger smolts have a greater likelihood to survive at sea compared to smaller smolts (Armstrong *et al.*, 2018; Gregory *et al.*, 2018; Simmons *et al.*, 2021), so that the greater the increase in early freshwater growth, the more pronounced the increase in the number of salmon successfully returning to spawn. This happens despite the fact that there is an increase in the proportion of males that mature precociously as parr; this loss of potential smolts is more than offset by the reduction in mean age at which fish become smolts (and thus are at risk of freshwater mortality for a shorter period). This reduction in mean smolt age would also result in a reduction in the number of older parr present in streams, reducing competition between cohorts, which may in turn facilitate faster growth of younger fish. The presence of younger fish may impact the growth of older cohorts, particularly at high densities, as demonstrated in Atlantic salmon (Einum *et al.*, 2011) and in brown trout (Kvingedal & Einum, 2011). The same is true for the effect of older year classes on younger cohorts, with 0+ Atlantic salmon fry having greater biomass in areas without older salmon, whilst fry raised in the presence of older salmon showed a reduction in biomass (Kennedy & Strange, 1986).

Though the model was designed to assess the impacts of nutrient additions using changes in early freshwater growth rate as a proxy, the data collected and presented in Chapters 3 and 4 were not explicitly built into the model. It is useful to consider that the double dose as presented in Chapter 4 would not be sufficient to increase the population size of Atlantic salmon, as the percentage increase in early freshwater growth required to result in a stable population is around 9%, with population expected to grow at above this value, whilst the double dose only resulted in a 6.9% growth increase. However, within the model it is expected that

Atlantic salmon parr would experience faster growth, as well as 0+ fry, which was demonstrated by McLennan *et al.* (2019) but the results for parr growth in that study were not replicated in parr growth presented in Chapter 3.

The model suggests that the increase in the number of precocious male parr, which are less likely to smolt (Letcher & Gries, 2003b; Whalen & Parrish, 1999), leads to a female-biased sex ratio in anadromous spawners. This conforms to previous research demonstrating a female bias in the sex ratio of returning spawners (Fleming, 1996). However, this differs from the operational sex ratio (the number of sexually active males to sexually active females on the spawning grounds). Here, the increased number of precocious male parr may have more of an impact on spawning, potentially countering the impact of the lower number of anadromous males relative to females by increased fertilisation of eggs by precocious male parr, as has been demonstrated in a Canadian stream where the sex ratio changed from female-biased to male-biased when taking precocious male parr into account (Richard *et al.*, 2013).

A further complication is that females may be more at risk of angling. For example, sport angling in Spain has resulted in a greater number of females being captured than males due to females entering rivers sooner than males (Pérez *et al.*, 2005). In many rivers salmon must be released after capture by anglers (Gargan *et al.*, 2015). However, even when best-practice catch and release guidelines are followed there can still be adverse effects: salmon that have been stressed as a result of being caught may produce fewer offspring (Papatheodoulou *et al.*, 2022), and this effect is strongest in large females (Richard *et al.*, 2013). Given that nutrient additions may result in returning spawners having a larger body size, this may make them more vulnerable to the impacts of catch and release angling.

In order to support greater numbers of larger fish emigrating, it is also important to consider the role of nutrient dynamics within oligotrophic freshwater systems. If greater numbers of fish are emigrating, but few are returning, as would theoretically be the case at the start of an interventionist conservation programme, it might be possible that streams would become net exporters of nutrients such as P and N (Nislow *et al.*, 2004a). Considering that Atlantic salmon have shown rapid decreases in body size as a result of adaptation to regulated river flows, the potential for nutrient import by adults may be even more reduced when they return at a smaller weight than they may have historically (Jensen *et*

*al.*, 2022). As such conservation programmes progressed (according to the outputs of the model in Chapter 5), it would be possible that the flux of nutrients would shift to a net import of nutrients by returning adults, so long as there was adequate habitat for nutrient retention to occur. Nutrient additions therefore may provide an opportunity to allow headwater streams, which are often nutrient-limited (Jarvie *et al.*, 2018), to increase their productivity of Atlantic salmon, but these must be accompanied by sufficient habitat management to allow nutrients to be retained within the system. This of course may risk eutrophication of what some may consider a pristine system (Boon *et al.*, 2002), despite the likelihood that cultural oligotrophication has contributed to the perception of pristineness; it is important to consider the implications over time of such nutrient additions which may impact the ecological status of streams (as measured by such as the Water Framework Directive (Council of the European Communities, 2000) and the European Habitats Directive (Council of the European Communities, 1992)).

## Impacts of high temperatures on the population performance of juvenile Atlantic salmon

High stream temperatures can negatively impact the growth of Atlantic salmon, in which heat stress begins at around 23°C (Lund *et al.*, 2002). Salmon change their behaviour in an attempt to avoid high temperatures (Breau *et al.*, 2011), and areas of cooler water within the environment can provide thermal refuges for salmon parr, shielding them from stressful or potentially lethal high temperatures (Corey *et al.*, 2023). However, the availability and extent of these cool refuges may be limited in many nursery streams. In Chapter 6, I demonstrated the impacts of exposure to high temperatures in terms of degree hours above 23°C on 0+ Atlantic salmon density and biomass, showing a negative relationship between degree hours and density/biomass. Atlantic salmon with higher body condition have been shown to have a greater thermal tolerance (Gallant *et al.*, 2017), which may indicate that the provision of carcass analogues, which in Chapter 3 were shown to increase body condition of fry and parr in 2021 in the bagged treatment, may help to mitigate the effects of heat shock. Although estimates of mortality and dispersal were not possible in Chapter 6, the declines in density and biomass in warmer sites/years suggest that juvenile Atlantic salmon

probably experienced heat stress, and may have either experienced higher mortality or migrated away from the sampling sites. The sampling sites mainly focused on riffles, and fry may have moved to deeper water to escape higher temperatures, such as has been shown in brown trout that move to pools in drought periods (Elliott, 2000).

Predictions show that Scottish streams are likely to become warmer as a result of climate change, with those in the northwest and west of the country particularly sensitive (Loerke *et al.*, 2023). It is likely that in summer these streams will reach stressful temperatures for Atlantic salmon, and indeed many already are (Jackson *et al.*, 2018a). One management option to try to cope with these increased temperatures is riparian tree planting, which has the aim of reducing the peak summer stream temperatures through increased shading (Jackson *et al.*, 2021). Many Scottish streams currently have limited riparian tree coverage (Imholt *et al.*, 2013), contributing to poorer thermal resilience (O’Briain *et al.*, 2017) which may negatively impact salmonids. Increased riparian planting may have other beneficial impacts for Atlantic salmon which may all help to increase juvenile growth, and potentially reduce the extent to which nutrient additions are required, as the goal would be to restore streams to a level where artificial nutrient intervention is not necessary. Riparian trees and bushes are likely to have overhanging branches that can increase the number of terrestrial invertebrates entering rivers, providing food for salmonids (Bridcut, 2000). Dineen *et al.* (2007) demonstrated that when the input of terrestrial invertebrates is significant, dietary partitioning may occur between Atlantic salmon and brown trout (*Salmo trutta*), with brown trout consuming more terrestrial invertebrates than Atlantic salmon. This may reduce the level of intraspecific competition between the two species, which may potentially result in increased growth. This is likely to be especially important if nutrient additions result in increased densities of juvenile salmon (as shown in Chapters 3 and 4), since this can lead to greater intraspecific and intercohort competition; any reduction in interspecific competition would therefore be welcome.

Riparian planting is also likely to reduce the level of soil erosion around stream banks (Purvis & Fox, 2016). High levels of soil erosion can lead to greater suspended sediment, which may have behavioural impacts on Atlantic salmon such as an alarm reaction (Robertson *et al.*, 2007), and may also increase mortality of embryos (Sear *et al.*, 2016). Increased riparian planting may also lead to a greater

abundance of large woody material in streams, which has been shown to provide shelter for Atlantic salmon and may result in increased spawning densities (Floyd *et al.*, 2009). Martin *et al.* (2010) added woody material alongside carcass analogue pellets in streams with juvenile coho salmon, and showed that the mass of invertebrates in the diet of juvenile coho in the wood and analogue treatment was three times greater than that of those in the control treatment, indicating that these impacts may be synergistic. This indicates that despite the threat of climate change on juvenile salmon (Thorstad *et al.*, 2021), conservation measures such as habitat restoration and nutrient additions may work in conjunction to provide successful conservation outcomes.

### 7.3 Justification of methodology and limitations of study

The experiments presented in this thesis were carried out in wild, but anthropogenically impacted, systems. This allowed for the experimental approaches taken in this thesis, using sites where no natural spawning of Atlantic salmon occurred due to migratory barriers preventing the movement of adults upstream, thus allowing for more direct control over initial egg densities and genetic diversity. However, as the Conon system is subject to human alteration, management dictates that Atlantic salmon eggs are stocked within the system. Where the conservation of a threatened species is concerned, experimental approaches should not aim to hinder current conservation practices. In my studies, this meant that the streams available for experimental purposes within the Conon catchment were fewer than ideal, as other streams with prime habitat were being used for higher-density stocking of eggs from wild adults stripped at the local hatchery. Ideally, streams which were not stocked in the same year as the studies took place would have been used; while fisheries managers did not stock in the vicinity of study sites, movement of non-focal fish into study sites was possible. As a result of the restricted availability of streams for experimental use, multiple treatments in both Chapters 3 and 4 had to be applied within the same stream. Wherever possible, I used a 500m buffer between treatments to reduce the possibility of upstream or downstream migration, as has been used in previous studies (Guyette *et al.*, 2014, 2013). However, in some cases due to the availability of prime riffle habitat for juvenile salmon, the buffer was shorter than

500m, which may have made some experimental zones more accessible through the upstream or downstream movement of juvenile salmon (Eisenhauer *et al.*, 2021). Nislow *et al.* (2010) demonstrated that in the Conon system, periphyton and invertebrates 350m downstream from the site of carcass additions may become enriched with marine-derived nutrients, indicating the possible effect of nutrients downstream from the site of application. This may have meant that upstream treatments which received nutrient applications could have contributed nutrients from those experimental zones to downstream experimental treatments, which may particularly have impacted the control sites. This would be most relevant in 2021, where the second year of the nutrient application method experiment detailed in Chapter 3 occurred alongside the dosage experiment in Chapter 4, leading to a greater number of nutrient treatments in the Rannoch and Vaich streams than in the previous year. Ideally, in order to reduce the possibility of treatments upstream impacting downstream treatments, one treatment would have been applied per stream, with a greater number of streams used. However, this was not possible as other streams within the catchment, as well as areas within the Rannoch and Vaich streams further upstream, were needed for the planting of eggs by fisheries managers.

The choice of streams may also have had different impacts on the results of the experiments. For instance, the experimental area of the Rannoch was located close to land used for forestry (but had negligible riparian planting), whilst the experimental section of the Vaich was adjacent to pasture land used for pastoral sheep and cattle farming, from which there may have been some nutrient run-off. This may have led to differences within the initial nutrient profiles of the two streams, with the Vaich potentially being less nutrient-limited than the Rannoch, which did not have an adjacent source of nutrients. Agriculture and nutrient enrichment may impact Atlantic salmon populations (Heaney *et al.*, 2001), and high levels of nutrient input has been shown to increase the growth of three-spined stickleback *Gasterosteus aculeatus* (Bell & Magnus Huss, 2022), so it is possible that the greater nutrient input in the Vaich may have led to larger fish. However, when testing the efficacy of nutrient additions as a possible conservation measure, assessment of a variety of streams with different levels of nutrient status would be important in order to create a more targeted approach.

One limitation arose from a sampling mistake with the macroinvertebrate samples collected in Chapter 3. Although multiple samples were taken within each

experimental site, these samples were then pooled into a single sample bag. This had the effect of reducing the statistical power of the analyses conducted, reducing the number of bagged and scattered samples to three each, and controls to six samples each, as per the number of sites, rather than having six samples per site for a total of 18 samples per treatment, with 36 samples for the control. Other research in the Conon system has used this approach of composited invertebrate samples (Nislow *et al.*, 2010), though in the present study using composited samples may have limited the statistical power of the analysis of the invertebrate data when considering data on the overall biomass, abundance and diversity metrics. Where invertebrates were considered individually (such as the analysis of individual log mass), I consider this to not have the same level of impact due to the high numbers of individual invertebrates. I had planned to take additional invertebrate samples in the period between the time of nutrient additions and the electrofishing surveys, but this was not possible as a result of lockdowns during the Covid-19 pandemic.

## 7.4 Scope for future research

Though the use of carcass analogues has been tested experimentally and has been used in management since at least 2004 (Compton *et al.*, 2006), much of this research has been on Pacific salmonids, with relatively few studies examining the use of these analogues as a nutrient remediation tool for Atlantic salmon streams. These studies on Atlantic salmon are limited to only two catchments, one in Maine, USA (Guyette *et al.*, 2014, 2013), and one in northern Scotland (Auer *et al.*, 2018; McLennan *et al.*, 2019), in which the experiments presented in this thesis were also conducted. Given the variability of results from nutrient addition experiments as demonstrated in Chapter 3, our understanding would be increased by an expansion in the catchments used for the study of nutrient remediation using carcass analogues for Atlantic salmon conservation. Atlantic salmon populations may differ strongly between catchments, with environmental factors such as flow influencing their morphological variation (Drinan *et al.*, 2012), whilst the landscape may isolate some populations and lead to genetic differentiation (Dillane *et al.*, 2008). Streams and rivers also differ in their nutrient status, and may experience nutrient limitation or co-limitation to

lesser or greater extents (Jarvie *et al.*, 2018). Therefore testing the effects of nutrient additions on the performance of Atlantic salmon populations over a range of catchments is likely to lead to greater understanding of the underlying processes involved.

Even within a single catchment, environmental variation is likely to influence the effects of nutrient additions. In Chapter 6 I demonstrate the impacts of high temperatures on the density and biomass of juvenile salmon. One environmental parameter that has not been assessed alongside the application of carcass analogues is the effect of flow rate. This could be expected to be particularly important in the summer months, where low summer flows at a time when salmon density is high can reduce summer growth rates (Nislow *et al.*, 2004a; Teichert *et al.*, 2010), and may further contribute to potential heat stress as waters warm (Gallant *et al.*, 2017). Understanding how flow affects both the movement of carcass analogues, such as in periods of high spring flows where they may be washed downstream, and the rate at which pellets degrade, may lead to further understanding of the best timing for the application of nutrient pellets. An experiment combining the impacts of flow rate, temperature and nutrient additions would be enormously useful in appreciating the interaction between these important environmental variables and how they may impact the effects of nutrient additions. It may be useful to conduct such a study in a catchment with both regulated and non-regulated rivers, as the impact of flow regulation on downstream water temperature and discharge may influence the growth and population performance of juvenile salmon (Jensen, 2003), with modelling also indicating that river regulation could mitigate negative effects of climate change on salmon (Sundt-Hansen *et al.*, 2018), but that the process of hydropeaking may negatively impact growth and survival (Hajiesmaeili *et al.*, 2023).

Though modelling (as in Chapter 5) can indicate whether increased early freshwater growth is likely to result in population level changes and impact the life history of salmon, measuring this empirically would both help to validate the model and to illustrate the processes involved. Although such an experiment would require long-term study (a minimum of five years) and funding, it is the only way to fully understand the impact that nutrient additions would have on Atlantic salmon populations. The advantage of carrying this out as an empirical study, compared to modelling, is that repeated sampling would allow for a richer understanding that nutrient additions may have on the stream assemblages as a

whole. Repeated sampling of nutrient levels, periphyton and macroinvertebrates could show in detail the complex processes which may be involved, as well as reveal changes in community structure. Other measurements, such as assessment of the diet of juvenile salmon, would also help to understand how any changes in nutrient profile affect Atlantic salmon prey, rather than simply showing differences in the size or abundance of invertebrates. A study such as this would ideally require treatments to be carried out on complete streams or rivers, with as many fish being tagged as possible to allow for recapture rate and growth rate to be monitored, as well as to have the greatest chance of tagged juveniles returning in sufficient numbers as adults to provide adequate statistical power. The ultimate goal of nutrient additions as a conservation practice would be to help restore Atlantic salmon populations to such a level that nutrient additions were no longer required, as the addition of nutrients over many years is likely to result in changes to the nutrient status of a river (Slavik *et al.*, 2004).

## 7.5 Conclusions

Atlantic salmon populations have fallen dramatically over past decades, and this has strengthened the need for conservation measures which will positively impact the survival of individuals to spawning. I have demonstrated the potential use of carcass analogue additions for nutrient remediation, showing that though the impacts may vary, increasing the early freshwater growth rate of Atlantic salmon is likely to result in more individuals surviving to spawn. If undertaken, this nutrient supplementation should be in conjunction with habitat restoration to allow future populations to thrive, with the goal of nutrient additions being a short-term intervention.



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# A | Appendix

## A.1 Supplementary Material: Chapter 3

**Table A.1** | Site habitat metrics for experimental zones over four tributaries of the River Blackwater in northern Scotland. Measurements were retaken in 2021 for sites used in the previous year. Continued overleaf.

Site	Nutrient application treatment	Latitude	Longitude	Number of sections	Elevation (m)	Section area (m <sup>2</sup> )	Section length (m)	Total area (m <sup>2</sup> )	Total length (m)	Mean width (m)	Mean depth ± SD (cm)	Flow score	Substrate score
<i>2020</i>													
Allt a' Bhealaich Mhoir	Control	57.65975	-4.624667	7	373	47.52	16	332.64	112	2.97	23.8 ± 11.1	4.0	3.2
	Scattered	57.660817	-4.629000	7	361	23.64	12	165.48	84	1.97	22.5 ± 9.76	4.0	3.5
Garbat Burn	Control	57.6734	-4.642283	7	258	25.08	4	341.04	28	6.27	26.5 ± 10.5	3.9	4.1
	Bagged	57.673433	-4.64615	7	235	28.02	6	196.14	42	4.67	23.2 ± 9.81	4.0	4.35
Upper Rannoch	Control	57.712733	-4.702017	7	253	27.34	2	191.38	14	13.67	11.6 ± 2.76	4.0	3.5
	Scattered	57.7105	-4.698367	6	248	22.60	2	135.6	12	11.3	12.7 ± 10.1	3.8	3.4
Lower Rannoch	Control	57.702583	-4.691683	8	235	19.26	2	154.08	16	9.63	19.1 ± 5.30	3.8	3.5

Site	Nutrient application treatment	Latitude	Longitude	Number of sections	Elevation (m)	Section area (m <sup>2</sup> )	Section length (m)	Total area (m <sup>2</sup> )	Total length (m)	Mean width (m)	Mean depth ± SD (cm)	Flow score	Substrate score
Upper Vaich	Control	57.720333	-4.7604	6	230	24	2	144	12	12	18.6 ± 3.52	4.95	3.5
	Bagged	57.717583	-4.7587	5	227	29.94	2	149.7	10	14.97	24.8 ± 5.44	4.8	3.1
Lower Vaich	Control	57.700233	-4.73875	6	215	27.26	2	124.7	12	12.47	27.4 ± 4.20	4.95	3.25
Lower Vaich	Scattered	57.699117	-4.733517	5	211	24.94	2	163.56	10	13.63	23.7 ± 10.2	4.9	3.9
<hr/>													
<i>2021</i>													
Upper Rannoch	Control	57.712733	-4.702017	9	253	20.68	2	186.12	18	10.34	21.5 ± 7.52	3.8	3.5
	Scattered	57.7105	-4.698367	8	248	24.12	2	192.96	16	12.06	11.9 ± 4.70	3.7	3.45
Lower Rannoch	Control	57.702583	-4.691683	9	235	20.68	2	186.12	18	10.34	21.5 ± 7.52	3.8	3.5
	Bagged	57.70015	-4.688517	6	231	18.96	2	151.68	14	10.34	20.70 ± 4.67	3.9	3.7
Upper Vaich	Control	57.720333	-4.7604	7	230	24.66	2	172.62	14	12.33	26.3 ± 5.03	4.95	3.5
	Bagged	57.717583	-4.7587	6	227	21.12	2	126.72	12	10.56	23.70 ± 7.67	4.6	3.1
Lower Vaich	Control	57.700233	-4.73875	6	215	23.80	2	142.80	12	11.90	26.6 ± 8.04	4.95	3.25
	Scattered	57.699117	-4.733517	5	211	30.40	2	152.00	10	15.20	25.3 ± 5.72	4.9	3.9

**Table A.2 | Family level length-mass equations (dry mass (mg) =  $aL^b$  where  $L$  is total body length (mm) with  $a$  and  $b$  as constants).**

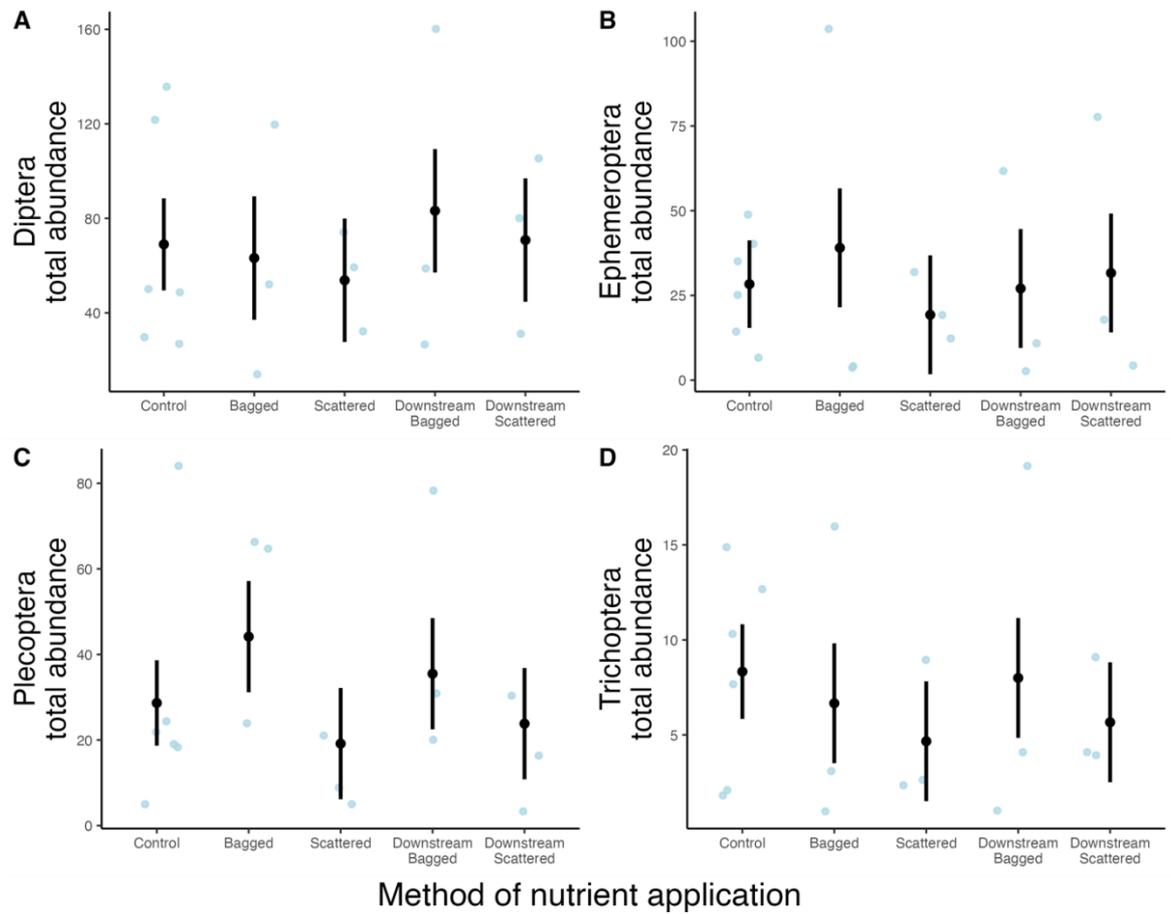
Family/taxonomic group	$a$	$b$	Reference
Acari	2.33	4.23	Baumgärtner & Rothhaupt, 2003
Baetidae	0.0053	2.875	Benke <i>et al.</i> , 1999
Brachycentridae	0.0083	2.818	Benke <i>et al.</i> , 1999
Caenidae	0.0054	2.772	Benke <i>et al.</i> , 1999
Capniidae	0.0049	2.562	Benke <i>et al.</i> , 1999
Ceratopogonidae	0.0025	2.469	Benke <i>et al.</i> , 1999
Chironomidae	0.0018	2.617	Benke <i>et al.</i> , 1999
Chloropertidae	0.0065	2.724	Benke <i>et al.</i> , 1999
Coenagrionidae	0.0051	2.785	Benke <i>et al.</i> , 1999
Cordulegastridae	0.0067	2.782	Benke <i>et al.</i> , 1999
Elmidae	0.0074	2.879	Benke <i>et al.</i> , 1999
Ephemerellidae	0.0103	2.676	Benke <i>et al.</i> , 1999
Ephydriidae	0.0054	2.546	Benke <i>et al.</i> , 1999
Glossostomatidae	0.0082	2.958	Benke <i>et al.</i> , 1999
Gyrinidae	0.0531	2.59	Benke <i>et al.</i> , 1999
Heptageniidae	0.0108	2.754	Benke <i>et al.</i> , 1999
Hydropsychidae	0.0019	2.89	Benke <i>et al.</i> , 1999
Hydroptilidae	0.0122	2.57	Baumgärtner & Rothhaupt, 2003
Leptophlebiidae	0.0047	2.686	Benke <i>et al.</i> , 1999
Leuctridae	0.0028	2.719	Benke <i>et al.</i> , 1999
Limoniidae	0.0039	2.44	Tod & Schmid-Araya, 2009
Lumbricidae	2.394	0.373	Collins, 1992
Nemouridae	0.0056	2.762	Benke <i>et al.</i> , 1999
Ostracoda	0.1738	4.2678	O’Gorman & Emmerson, 2010
Pediciidae	0.0013	2.85	Benke <i>et al.</i> , 1999
Perlidae	0.0099	2.879	Benke <i>et al.</i> , 1999
Perlodidae	0.0196	2.742	Benke <i>et al.</i> , 1999
Philopotamidae	0.005	2.511	Benke <i>et al.</i> , 1999
Psychomyiidae	0.0039	2.873	Benke <i>et al.</i> , 1999
Rhyacophilidae	0.0099	2.48	Benke <i>et al.</i> , 1999
Scirtidae	0.0074	2.879	Used same relationship as Elmidae, Benke <i>et al.</i> , 1999
Sericostomatidae	0.074	2.741	Benke <i>et al.</i> , 1999
Simuliidae	0.002	3.011	Benke <i>et al.</i> , 1999
Taeniopterygidae	0.0072	2.665	Benke <i>et al.</i> , 1999
Tipulidae	0.0029	2.681	Benke <i>et al.</i> , 1999

**Table A.3** | Results of linear mixed effects models analysing effects of nutrient treatment on the total abundance of Diptera and Ephemeroptera sampled in 2020. Bagged and scattered treatments (and their downstream counterparts) are compared to the control (no nutrients added).

<i>Predictors</i>	Diptera total abundance					Ephemeroptera total abundance				
	<i>Estimates</i>	<i>std. Error</i>	<i>t value</i>	<i>p</i>	<i>df</i>	<i>Estimates</i>	<i>std. Error</i>	<i>t value</i>	<i>p</i>	<i>df</i>
(Intercept)	69.00	19.48	3.54	<b>0.005</b>	11.00	28.33	12.92	2.19	0.051	11.00
Treatment [Bagged]	-5.80	26.84	-0.22	0.833	11.00	10.71	18.51	0.58	0.574	11.00
Treatment [Scattered]	-15.20	26.84	-0.57	0.583	11.00	-9.05	18.51	-0.49	0.635	11.00
Treatment [Downstream of Bagged]	14.20	26.84	0.53	0.607	11.00	-1.29	18.51	-0.07	0.946	11.00
Treatment [Downstream of Scattered]	1.80	26.84	0.07	0.948	11.00	3.29	18.51	0.18	0.862	11.00
<b>Random Effects</b>										
$\sigma^2$	1253.42					605.11				
$\tau_{00}$	1022.61 <sub>site</sub>					395.91 <sub>site</sub>				
Observations	18					18				

**Table A.4 | Results of linear mixed effects models analysing effects of nutrient treatment on the total abundance of Plecoptera and Trichoptera sampled in 2020. Bagged and scattered treatments (and their downstream counterparts) are compared to the control (no nutrients added).**

<i>Predictors</i>	Plecoptera total abundance					Trichoptera total abundance				
	<i>Estimates</i>	<i>std. Error</i>	<i>t value</i>	<i>p</i>	<i>df</i>	<i>Estimates</i>	<i>std. Error</i>	<i>t value</i>	<i>p</i>	<i>df</i>
(Intercept)	28.67	9.97	2.87	0.015	11.00	8.33	2.49	3.35	0.007	11.00
Treatment [Bagged]	15.50	12.62	1.23	0.245	11.00	-1.67	2.89	-0.58	0.576	11.00
Treatment [Scattered]	-9.50	12.62	-0.75	0.467	11.00	-3.67	2.89	-1.27	0.231	11.00
Treatment [Downstream of Bagged]	6.83	12.62	0.54	0.599	11.00	-0.33	2.89	-0.12	0.910	11.00
Treatment [Downstream of Scattered]	-4.83	12.62	-0.38	0.709	11.00	-2.67	2.89	-0.92	0.376	11.00
<b>Random Effects</b>										
$\sigma^2$	269.39					13.80				
$\tau_{00}$	327.59 <sub>site</sub>					23.42 <sub>site</sub>				
Observations	18					18				



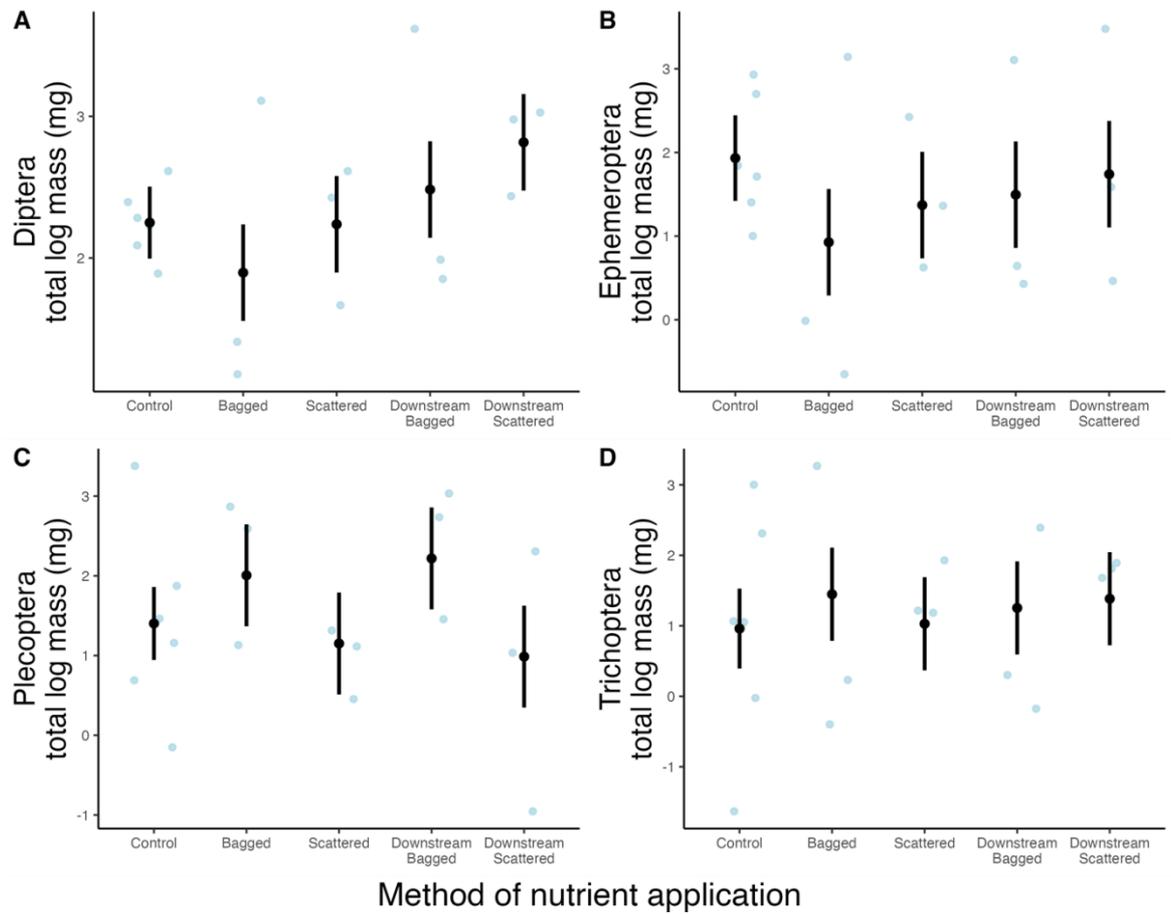
**Figure A.1** | Total abundance of Diptera (A), Ephemeroptera (B), Plecoptera (C) and Trichoptera (D) sampled across the control, nutrient treatments, and 500m downstream of the nutrient treatments over six sites across four tributaries of the River Blackwater in 2020 (data plotted as model predictions  $\pm$  SE, n= 18 samples).

**Table A.5 | Results of linear mixed effects models analysing effects of nutrient treatment on the total log mass of Diptera and Ephemeroptera sampled in 2020. Bagged and scattered treatments (and their downstream counterparts) are compared to the control (no nutrients added).**

<i>Predictors</i>	<b>Diptera total log mass</b>					<b>Ephemeroptera total log mass</b>				
	<i>Estimates</i>	<i>std. Error</i>	<i>t value</i>	<i>p</i>	<i>df</i>	<i>Estimates</i>	<i>std. Error</i>	<i>t value</i>	<i>p</i>	<i>df</i>
(Intercept)	2.25	0.25	8.86	<0.001	11.00	1.93	0.51	3.78	0.003	11.00
Treatment [Bagged]	-0.35	0.35	-1.01	0.335	11.00	-1.01	0.56	-1.79	0.101	11.00
Treatment [Scattered]	-0.01	0.35	-0.03	0.974	11.00	-0.56	0.56	-1.00	0.338	11.00
Treatment [Downstream of Bagged]	0.23	0.35	0.67	0.519	11.00	-0.44	0.56	-0.78	0.452	11.00
Treatment [Downstream of Scattered]	0.57	0.35	1.62	0.134	11.00	-0.19	0.56	-0.34	0.738	11.00
<b>Random Effects</b>										
$\sigma^2$	0.21					0.51				
$\tau_{00}$	0.17 <sub>site</sub>					1.06 <sub>site</sub>				
Observations	18					18				

**Table A.6 |** Results of linear mixed effects models analysing effects of nutrient treatment on the total log mass of Plecoptera and Trichoptera sampled in 2020. Bagged and scattered treatments (and their downstream counterparts) are compared to the control (no nutrients added).

<i>Predictors</i>	Plecoptera total log mass					Trichoptera total log mass				
	<i>Estimates</i>	<i>std. Error</i>	<i>t value</i>	<i>p</i>	<i>df</i>	<i>Estimates</i>	<i>std. Error</i>	<i>t value</i>	<i>p</i>	<i>df</i>
(Intercept)	1.40	0.46	3.06	<b>0.011</b>	11.00	0.96	0.57	1.70	0.118	11.00
Treatment [Bagged]	0.60	0.72	0.84	0.421	11.00	0.49	0.49	0.99	0.344	11.00
Treatment [Scattered]	-0.25	0.72	-0.35	0.735	11.00	0.07	0.49	0.14	0.893	11.00
Treatment [Downstream of Bagged]	0.82	0.72	1.13	0.283	11.00	0.29	0.49	0.59	0.565	11.00
Treatment [Downstream of Scattered]	-0.42	0.72	-0.58	0.577	11.00	0.42	0.49	0.86	0.409	11.00
<b>Random Effects</b>										
$\sigma^2$	0.97					0.38				
$\tau_{00}$	0.29 <sub>site</sub>					1.54 <sub>site</sub>				
Observations	18					18				



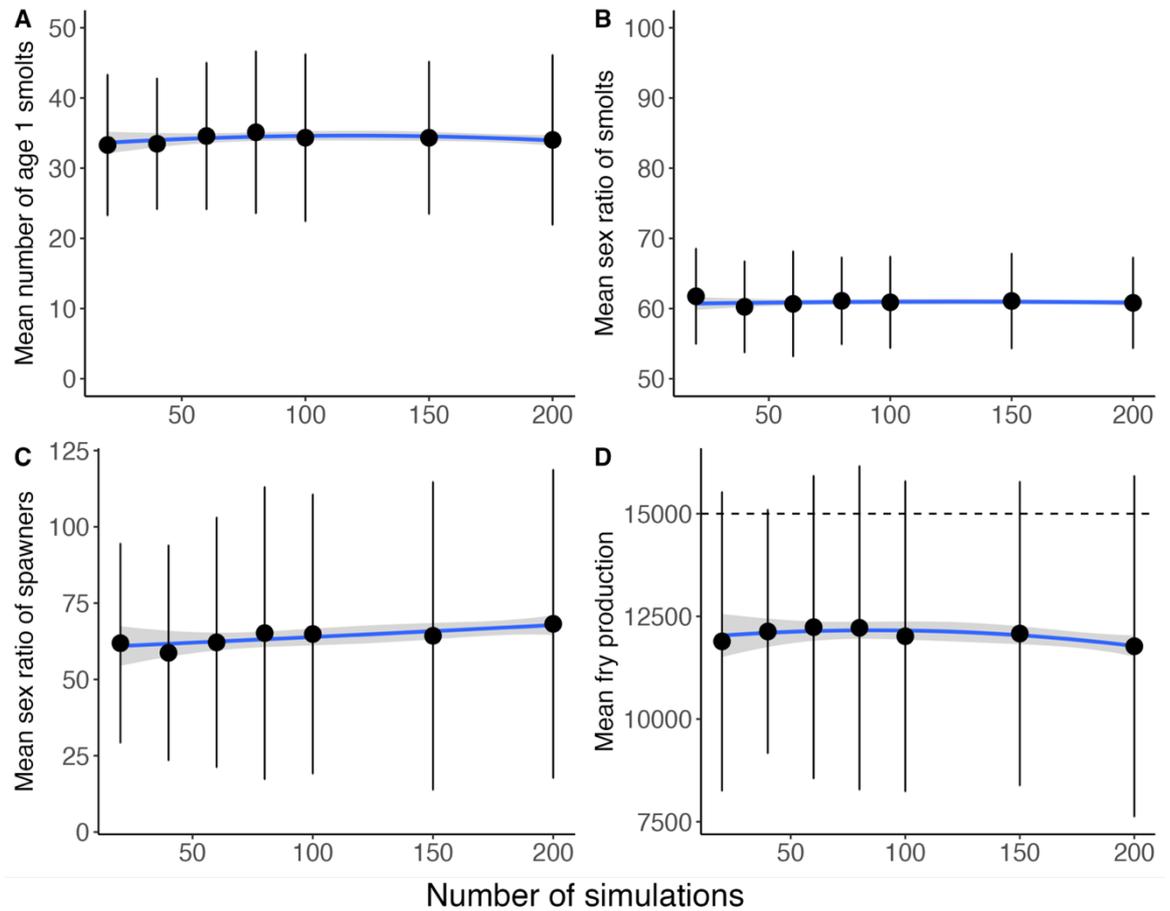
**Figure A.2** | Total log mass of Diptera (A), Ephemeroptera (B), Plecoptera (C) and Trichoptera (D) sampled across the control, nutrient treatments, and 500m downstream of the nutrient treatments over six sites across four tributaries of the River Blackwater in 2020 (data plotted as model predictions  $\pm$  SE, n= 18 samples).

## A.2 Supplementary Material: Chapter 4

**Table A.7 |** Site habitat metrics for experimental zones over the main stem of the River Blackwater and two tributaries in northern Scotland in 2021. Treatments are ordered in descending order of river flow.

Stream	Nutrient application treatment	Latitude	Longitude	Number of sections	Elevation (m)	Section area (m <sup>2</sup> )	Section length (m)	Total area (m <sup>2</sup> )	Total length (m)	Mean width (m)	Mean depth $\pm$ SD (cm)	Flow score	Substrate score
Blackwater	Upstream control	57.694946	-4.717014	4	197	52.12	2	208.48	8	26.06	27.7 $\pm$ 8.86	3.3	4.05
	Single dose	57.691765	-4.712554	4	191	47.00	2	188.00	8	23.50	19.9 $\pm$ 5.76	3.95	3.6
	Double dose	57.688835	-4.704685	4	184	70.40	2	281.60	8	35.20	17.0 $\pm$ 3.53	2.95	4
	Downstream control	57.684692	-4.685863	4	161	121.20	1	484.80	4	30.30	30.5 $\pm$ 6.13	3.45	3.7
Rannoch	Upstream control	57.712433	-4.701554	7	253	28.07	2	196.42	14	14.03	12.1 $\pm$ 2.18	7	3.5
	Single dose	57.710506	-4.698501	8	248	24.12	2	192.96	16	12.06	11.9 $\pm$ 4.70	3.7	3.45
	Double dose	57.708599	-4.698652	9	248	19.06	2	171.54	18	9.53	11.7 $\pm$ 1.06	4.1	5.6
	Downstream control	57.702332	-4.691547	9	235	20.68	2	186.12	18	10.34	21.5 $\pm$ 7.52	3.8	3.5
Vaich	Upstream control	57.720253	-4.760412	7	230	24.66	2	172.62	14	12.33	26.3 $\pm$ 5.03	4.95	3.5
	Double dose	57.709553	-4.751167	7	225	19.20	2	134.40	14	9.60	25.6 $\pm$ 6.20	4.1	3.55
	Downstream control	57.700199	-4.738966	6	215	23.80	2	142.80	12	11.90	26.6 $\pm$ 8.04	4.95	3.25
	Single dose	57.69878	-4.733026	5	211	30.40	2	152.00	10	15.20	25.3 $\pm$ 5.72	4.9	3.9

### A.3 Supplementary Material: Chapter 5



**Figure A.3** | Selected outputs of the baseline growth version of the model showing the stability of the model across an increasing number of simulations  $\pm$  SD. A) Mean number of fish predicted to smolt aged 1. B) Mean sex ratio (males to females) of Atlantic salmon smolts and spawners (C). D) Mean number of fry produced by spawning females. The dotted line represents the 15,000 fry at the inception of the model.

**Table A.8 | Mean values ( $\pm$  SD) and variances of selected outputs of increasing number of simulations of the baseline version of the model.**

Number of simulations	Mean number of age 1 smolts $\pm$ SD	Variance in number of age 1 smolts	Mean sex ratio of smolts $\pm$ SD	Variance in sex ratio of smolts	Mean sex ratio of spawners $\pm$ SD	Variance in sex ratio of spawners	Mean fry production $\pm$ SD	Variance in fry production
20	13.6 $\pm$ 2.98	8.88	61.7 $\pm$ 3.41	11.6	61.9 $\pm$ 16.4	267	11892 $\pm$ 1821	3315759
40	12.4 $\pm$ 2.96	8.75	60.2 $\pm$ 3.27	10.7	58.7 $\pm$ 17.6	311	12133 $\pm$ 1484	2203065
60	12.0 $\pm$ 3.24	10.5	60.7 $\pm$ 3.76	14.1	62.2 $\pm$ 20.5	420	12239 $\pm$ 1845	3402973
80	13.6 $\pm$ 3.48	12.1	61.1 $\pm$ 3.12	9.72	65.2 $\pm$ 24.0	575	12222 $\pm$ 1972	3888977
100	13.1 $\pm$ 3.29	10.9	60.9 $\pm$ 3.27	10.7	64.9 $\pm$ 22.9	525	12017 $\pm$ 1891	3576521
150	12.7 $\pm$ 3.63	13.2	61.1 $\pm$ 3.40	11.5	64.3 $\pm$ 25.2	637	12083 $\pm$ 1852	3429740
200	12.4 $\pm$ 3.64	13.2	60.8 $\pm$ 3.25	10.5	68.2 $\pm$ 25.3	639	11774 $\pm$ 2076	4309939

The percentage of fish smolting was calculated by summing the total of fish per run, and dividing this by the number of smolts, and then multiplying by 100. The percentage of smolts surviving to spawning was calculated by dividing the number of smolts surviving to spawn by the total number of smolts, then multiplying by 100. The percentage of salmon surviving to spawning was calculated by dividing the number of salmon surviving to spawn by the total number of fish per run, then multiplying by 100 (Table A.9).

The percentage of male parr that mature precociously was calculated by dividing the number of males that mature precociously by the number of males at the beginning of the model (before any mortality events occur), then multiplying by 100. The percentage of mature males that do not smolt was calculated by dividing the number of mature males that did not smolt by the number of mature males, then multiplying by 100. The percentage of mature males that smolt was calculated by dividing the number of mature males that smolt by the number of mature males, then multiplying by 100. The percentage of male smolts which did not survive the marine phase was calculated by dividing the number of mature

males which smolted but did not survive the marine phase by the number of mature male smolts, then multiplying by 100. The percentage of mature males that survived the marine phase and returned to spawn was calculated by dividing the number of mature male smolts that survived to spawning by the overall number of males that matured precociously, then multiplying by 100 (Table A.10).

**Table A.9** | Percentages of Atlantic salmon experiencing different life history events related to smolting and marine survival. All percentages are mean values from the 200 runs of each simulation  $\pm$  SD.

Growth percentage increase (%)	Percentage of fish smolting $\pm$ SD (%)	Percentage of smolts surviving to spawning $\pm$ SD (%)	Percentage of salmon surviving to spawning $\pm$ SD (%)
0	10.2 $\pm$ 0.25	2.23 $\pm$ 0.39	0.22 $\pm$ 0.04
5	11.2 $\pm$ 0.23	2.39 $\pm$ 0.34	0.26 $\pm$ 0.03
10	12.1 $\pm$ 0.24	2.66 $\pm$ 0.36	0.32 $\pm$ 0.04
15	12.7 $\pm$ 0.27	2.97 $\pm$ 0.36	0.37 $\pm$ 0.04
20	13.2 $\pm$ 0.27	3.26 $\pm$ 0.39	0.43 $\pm$ 0.05

**Table A.10** | Percentages of male Atlantic salmon experiencing different life history events related to precocious male sexual maturation. All percentages are mean values from the 200 runs of each simulation  $\pm$  SD.

Growth percentage increase (%)	Percentage of male parr that mature precociously $\pm$ SD (%)	Percentage of mature male parr that do not smolt $\pm$ SD (%)	Percentage of mature male smolts $\pm$ SD (%)	Percentage of mature male smolts not surviving the marine phase $\pm$ SD (%)	Percentage of mature males returning to spawn $\pm$ SD (%)
0	24.68 $\pm$ 0.49	83.23 $\pm$ 0.88	16.76 $\pm$ 0.88	97.14 $\pm$ 0.95	0.47 $\pm$ 0.16
5	30.70 $\pm$ 0.49	81.99 $\pm$ 0.79	18.00 $\pm$ 0.79	97.03 $\pm$ 0.88	0.53 $\pm$ 0.16
10	35.16 $\pm$ 0.50	80.95 $\pm$ 0.68	19.04 $\pm$ 0.68	96.81 $\pm$ 0.81	0.60 $\pm$ 0.15
15	38.07 $\pm$ 0.53	80.21 $\pm$ 0.70	19.78 $\pm$ 0.70	96.46 $\pm$ 0.76	0.69 $\pm$ 0.15
20	39.54 $\pm$ 0.59	79.52 $\pm$ 0.73	20.47 $\pm$ 0.73	96.15 $\pm$ 0.83	0.78 $\pm$ 0.17

**Table A.11** | Mean body sizes (fork length) of male and female smolts at different smolt ages from 200 simulations of the model.

Growth percentage increase (%)	Mean male smolt size $\pm$ SD (mm)	Mean male smolt size aged 1 $\pm$ SD (mm)	Mean male smolt size aged 2 $\pm$ SD (mm)	Mean male smolt size aged 3 $\pm$ SD (mm)	Mean male smolt size aged 4 $\pm$ SD (mm)	Mean female smolt size $\pm$ SD (mm)	Mean female smolt size aged 1 $\pm$ SD (mm)	Mean female smolt size aged 2 $\pm$ SD (mm)	Mean female smolt size aged 3 $\pm$ SD (mm)	Mean female smolt size aged 4 $\pm$ SD (mm)
0	137 $\pm$ 37.6	84.4 $\pm$ 10.2	122 $\pm$ 15.9	166 $\pm$ 27.1	188 $\pm$ 31.9	135 $\pm$ 45.8	83.9 $\pm$ 9.97	128 $\pm$ 16.0	159 $\pm$ 20.6	163 $\pm$ 20.7
5	148 $\pm$ 41.4	86.6 $\pm$ 9.73	130 $\pm$ 18.1	184 $\pm$ 29.4	209 $\pm$ 33.9	141 $\pm$ 50.4	86.7 $\pm$ 9.90	136 $\pm$ 17.1	169 $\pm$ 22.0	173 $\pm$ 21.4
10	160 $\pm$ 45.5	89.2 $\pm$ 9.84	140 $\pm$ 20.1	202 $\pm$ 30.8	231 $\pm$ 35.6	148 $\pm$ 54.9	89.2 $\pm$ 9.75	145 $\pm$ 18.2	179 $\pm$ 23.9	181 $\pm$ 23.3
15	172 $\pm$ 49.7	91.9 $\pm$ 9.83	151 $\pm$ 21.4	221 $\pm$ 32.3	255 $\pm$ 38.6	156 $\pm$ 59.3	91.8 $\pm$ 9.80	154 $\pm$ 19.5	190 $\pm$ 25.5	190 $\pm$ 24.6
20	185 $\pm$ 54.2	94.3 $\pm$ 9.65	163 $\pm$ 22.2	241 $\pm$ 34.5	279 $\pm$ 41.2	165 $\pm$ 63.6	94.1 $\pm$ 9.72	164 $\pm$ 20.9	202 $\pm$ 27.7	198 $\pm$ 25.3

## A.4 Supplementary Material: Chapter 6

### A.4.1 Study sites

The six sites are shown in Figure 6.1 and described in Table A.12 - note that the upstream and downstream sites within each stream are defined as ‘upper’ and ‘lower’ respectively. Species present at sampling site locations were Atlantic salmon (*Salmo salar*) that were stocked but of wild parentage, alongside resident brown trout (*Salmo trutta*) and minnow (*Phoxinus phoxinus*).

### A.4.2 Details of egg planting

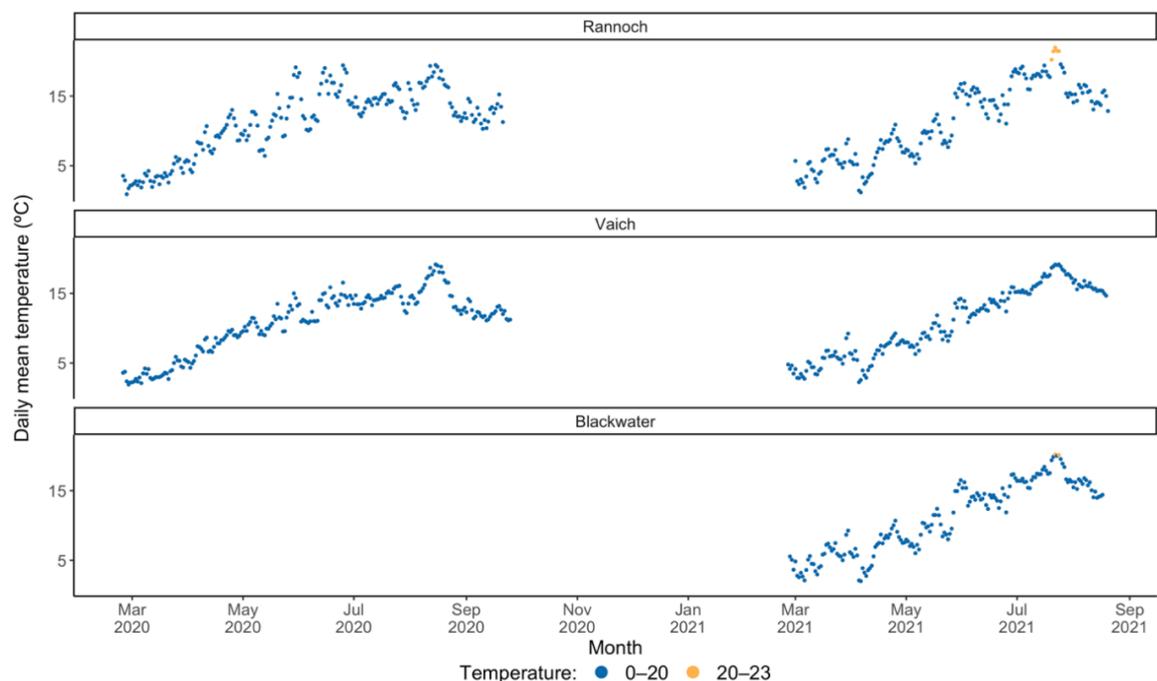
Within each site, eggs were planted into three artificial redds which were positioned at the top, middle and bottom of each site between 26-27/2/2020 and 25/2 - 1/3/2022. In each year the eggs were sourced from 25 unique families of one sea winter Atlantic salmon (families differed between years) returning to the River Blackwater and caught in a trap further downstream as part of routine fishery management operations (details in Auer *et al.*, 2018). Eggs were planted directly into the substrate, hence ova mortality data were not collected. The same personnel planted eggs in all sites in both years.

**Table A.12** | Site characteristics of study streams in Northern Scotland. Water depth ( $\pm$  SD) was measured at 10 randomly selected positions within each surveyed area. Substrate and flow scores were visually calculated for each site as proportions of area surveyed (SFCC, 2007) and then amalgamated to give a score; this theoretically ranged from 1 (100% sand substratum or still water respectively) to 6 (100% bedrock or torrent); higher values thus represent a site with a substratum made up of larger particle sizes or faster flowing water respectively. For further details of scoring method see McLennan *et al.* (2021). Elevation data were sourced from Yamazaki *et al.* (2017). See section A.4.4 below and Table A.15 for details of the PCA habitat scoring method.

Site	Mean water depth (cm) $\pm$ SD	No. sections	Area surveyed (m <sup>2</sup> )	Degree hours > 23°C	Substrate score	Flow score	Elevation (m)	PC1 habitat score	Number of salmon fry caught
<i>Upper Rannoch</i>									
2020	11.6 $\pm$ 2.76	7	191.38	23.7	3.5	4	253	-1.28	63
2021	12.1 $\pm$ 2.18	7	196.42	195	3.5	4	253	-1.25	2
<i>Lower Rannoch</i>									
2020	19.1 $\pm$ 5.30	8	154.08	39.3	3.5	3.8	235	-0.262	44
2021	21.5 $\pm$ 7.52	9	186.12	156	3.5	3.8	235	-0.227	7
<i>Upper Vaich</i>									
2020	18.6 $\pm$ 3.52	6	144	0	3.5	4.95	230	-0.934	129
2021	26.3 $\pm$ 5.03	6	172.62	0	3.5	4.95	230	-0.409	51
<i>Lower Vaich</i>									
2020	27.4 $\pm$ 4.20	6	163.63	0.784	3.25	4.95	215	-0.589	153
2021	26.6 $\pm$ 8.04	6	142.8	12.4	3.25	4.95	215	-0.644	46
<i>Upper Blackwater</i>									
2021	27.7 $\pm$ 8.86	4	208.48	24	3.6	3.95	197	2.71	40
<i>Lower Blackwater</i>									
2021	30.3 $\pm$ 6.13	4	121.2	14.3	3.7	3.45	161	2.76	54

### A.4.3 Temperature data

Data from each logger closely matched that from other loggers within the same streams, and the same temperature patterns were observed both within and between streams (Fig. A.4). Loggers were placed in Vibert boxes and weighted with rocks in order to avoid removal during periods of high discharge; there were no aberrant values or fluctuations that would have indicated air exposure. It is not known whether the lost loggers were washed out or buried by substratum.



**Figure A.4** | Daily mean temperatures recorded at each stream in each year (means of the values from the upper and lower sampling site). Yellow symbols indicate temperatures in the range 20–23°C, indicating days where the mean temperature was close to that stressful to Atlantic salmon (see Fig. 6.2 in the main text for equivalent plots of daily maximum temperatures).

Temperatures were recorded hourly in 2020 but two-hourly in 2021 in order to increase battery life. To assess the effect of doubling the 2021 temperature data in order to generate temperature estimates every hour, tests were carried out using the hourly 2020 data. Every second value was first removed from the 2020 data to produce ‘degraded’ two hourly data (as in 2021). Degree hours were then recalculated and then doubled, and compared to the original temperature values for 2020. The two methods gave extremely similar values for degree hours

exceeding 23°C (Table A.13). The degraded data were reanalysed using the same model structure as in the original data; again the results were similar to those obtained using the original data, with no difference in the significance of predictor variables (Table A.14, compared to Table 6.1 in main text), indicating that the two hourly temperature data from 2021 were sufficient for estimating the degree hours above 23°C.

**Table A.13** | Differences in degree hours > 23°C from sampling locations in 2020 when temperature data are degraded into two-hourly data and then doubled.

Location (2020)	Degree hours >23°C calculated from original data	Degree hours >23°C calculated by degrading temperatures then doubling
Upper Rannoch	23.7	24
Lower Rannoch	39.3	40
Upper Vaich	0	0
Lower Vaich	0.784	0.784

#### A.4.4 Habitat data

In order to test whether density and biomass were influenced by the microhabitat availability in each sampling site, a Principal Components Analysis (PCA) with the R package ‘stats’ (Table A.15) was used to reduce four habitat variables (mean depth, elevation, substratum and discharge scores) to a single habitat variable (Principal Component 1 of the PCA), with unique values for this Component 1 generated for each site (Table A.12). Higher positive values for this habitat variable corresponded to sites that were at lower elevations, had deeper and slower flowing water and smaller substrate particle sizes (although variation in these variables among sites was relatively minor - see Table A.12). The habitat variable was included in the initial model structures but had no significant effect (Table A.16), so was not retained in the final model structures.

**Table A.14** | Model coefficients for a) log density and b) log biomass using degree hours > 23°C calculated by degrading temperatures and then doubling data from 2020.

Predictors	Estimate	SE	<i>z value</i>	<i>P</i>
<i>a) Density model</i>				
<b>Fixed effects</b>				
Intercept	-0.099	0.252	-0.395	0.692
Degree hours > 23°C	-0.008	0.001	-5.026	< 0.001
Year (2021)	-0.850	0.187	-5.024	< 0.001
Stream (Rannoch)	-1.397	0.316	-2.690	< 0.01
Stream (Vaich)	-0.020	0.241	-0.084	0.932
<b>Random effects</b>	$\sigma^2$			
Site	0.0000000004908			
Section:site	0.0890113865018			
<i>b) Biomass model</i>				
<b>Fixed effects</b>				
Intercept	-0.056	0.278	-0.203	0.839
Degree hours > 23°C	-0.009	0.001	-4.729	< 0.001
Year (2021)	-0.861	0.207	-4.151	< 0.001
Stream (Rannoch)	-0.914	0.354	-2.581	< 0.01
Stream (Vaich)	0.529	0.269	1.963	< 0.05
<b>Random effects</b>	$\sigma^2$			
Site	0.00923			
Section:site	0.07146			

**Table A.15** | Principal Component 1 loadings for each of the four habitat variables.

Habitat variable	PC1 loading score
Mean depth	0.4543400
Elevation	-0.5820716
Substrate score	0.5177464
Flow score	-0.4320954

**Table A.16** | Model coefficients for log density (a) and log biomass (b) for linear mixed effect models equivalent to those in the main text except also containing habitat variable PC1 as a fixed effect.

Predictors	Estimate	SE	<i>z value</i>	<i>P</i>
<b><i>a) Density model</i></b>				
<b>Fixed effects</b>				
Intercept	0.330	0.733	0.451	0.652
Degree hours > 23°C	-0.009	0.001	-5.071	< <b>0.001</b>
Year (2021)	-0.887	0.199	-4.449	< <b>0.001</b>
Habitat PC1	-0.174	0.273	-0.638	0.524
Stream (Rannoch)	-1.397	0.936	-1.492	0.136
Stream (Vaich)	-0.588	0.930	-0.632	0.527
<b>Random effects</b>	<b><math>\sigma^2</math></b>			
Site	0.003			
Section:site	0.0906			
<b><i>b) Biomass model</i></b>				
<b>Fixed effects</b>				
Intercept	0.776	0.549	1.413	0.157
Degree hours > 23°C	-0.009	0.001	-5.004	< <b>0.001</b>
Year (2021)	-0.761	0.214	-3.543	< <b>0.001</b>
Habitat PC1	-0.336	0.195	-1.724	0.084
Stream (Rannoch)	-1.973	0.690	-2.860	< <b>0.01</b>
Stream (Vaich)	-0.568	0.682	-0.833	0.404
<b>Random effects</b>	<b><math>\sigma^2</math></b>			
Site	0.000000002286			
Section:site	0.066848787304			

#### A.4.5 Verification of constant

In order to verify the choice of constant (0.02) applied to fish capture data, I tested the effect of using an alternative constant of 0.01 or 0.001 in place of the original by running the models with the revised constants. This alteration did not significantly affect the strength of the effect of degree hours exceeding 23°C, but did cause slight changes to the significance level of the effects of stream ID and

year, as detailed in Tables A.17 and A.18. However, since the main conclusions of the analyses were unchanged, I judged the 0.02 choice of constant to be appropriate and robust.

**Table A.17** | Model coefficients for log density (a) and log biomass (b) for linear mixed effect models equivalent to those in the main text except that a constant of 0.01 was applied instead of 0.02.

Predictors	Estimate	SE	<i>z value</i>	<i>P</i>
<b><i>a) Density model</i></b>				
<b>Fixed effects</b>				
Intercept	1924.927	463.277	4.155	< 0.001
Degree hours > 23°C	-0.011	0.002	-5.529	< 0.001
Year (2021)	-0.952	0.229	-4.157	< 0.001
Stream (Rannoch)	-0.837	0.381	-2.193	< 0.05
Stream (Vaich)	-0.058	0.289	-0.203	0.839
<b>Random effects</b>				
	$\sigma^2$			
Site	0.00000001861			
Section:site	0.115732592735			
<b><i>b) Biomass model</i></b>				
<b>Fixed effects</b>				
Intercept	1740.218	419.735	4.146	< 0.001
Degree hours > 23°C	-0.009	0.001	-4.719	< 0.001
Year (2021)	-0.861	0.207	-4.148	< 0.001
Stream (Rannoch)	-0.919	0.354	-2.598	< 0.01
Stream (Vaich)	0.529	0.269	1.961	< 0.05
<b>Random effects</b>				
	$\sigma^2$			
Site	0.009425			
Section:site	0.071214			

**Table A.18** | Model coefficients for log density (a) and log biomass (b) for linear mixed effect models equivalent to those in the main text except that a constant of 0.001 was applied instead of 0.02.

Predictors	Estimate	SE	<i>z value</i>	<i>P</i>
<i>a) Density model</i>				
<b>Fixed effects</b>				
Intercept	0.080	0.540	0.149	0.881
Degree hours > 23°C	-0.021	0.003	-5.641	< 0.001
Year (2021)	-0.942	0.421	-2.236	< 0.05
Stream (Rannoch)	-0.713	0.676	-1.054	0.291
Stream (Vaich)	-0.201	0.495	-0.406	0.684
<b>Random effects</b>	$\sigma^2$			
Site	0.00000001617			
Section:site	0.205459616389			
<i>b) Biomass model</i>				
<b>Fixed effects</b>				
Intercept	-0.056	0.278	-0.204	0.838
Degree hours > 23°C	-0.009	0.001	-4.719	< 0.001
Year (2021)	-0.861	0.207	-4.148	< 0.001
Stream (Rannoch)	-0.919	0.354	-2.598	< 0.01
Stream (Vaich)	0.529	0.269	1.961	< 0.05
<b>Random effects</b>	$\sigma^2$			
Site	0.009423			
Section:site	0.071216			