



RESEARCH ARTICLE

Simulating nutrient release from parental carcasses increases the growth, biomass and genetic diversity of juvenile Atlantic salmon

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Abstract

1. The net transport of nutrients by migratory fish from oceans to inland spawning areas has decreased due to population declines and migration barriers. Restoration of nutrients to increasingly oligotrophic upland streams (that were historically salmon spawning areas) have shown short-term benefits for juvenile salmon, but the longer term consequences are little known.
2. Here we simulated the deposition of a small number of adult Atlantic salmon *Salmo salar* carcasses at the end of the spawning period in five Scottish upland streams ('high parental nutrient' treatment), while leaving five reference streams without carcasses ('low parental nutrient' treatment). All streams received exactly the same number of salmon eggs ($n = 3,000$) drawn in equal number from the same 30 wild-origin families, thereby controlling for initial egg density and genetic composition. We then monitored the resulting juvenile salmon and their macroinvertebrate prey, repeating the carcass addition treatment in the next spawning season.
3. Macroinvertebrate biomass and abundance were five times higher in the high parental nutrient streams, even 1 year after the carcass addition, and led to faster growth of juvenile salmon over the next 2 years (but with no change in population density). This faster growth led to more fish exceeding the size threshold that would trigger emigration to sea at 2 rather than 3 years of age. There was also higher genetic diversity among surviving salmon in high parental nutrient streams; genotyping showed that these effects were not due to immigration but to differential survival.

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McLennan and Auer contributed equally to this work.

4. *Synthesis and applications.* This 2-year field experiment shows that adding nutrients that simulate the presence of small numbers of adult salmon carcasses can have long-term effects on the growth rate of juvenile salmon, likely increasing the number that will migrate to sea early and also increasing their genetic diversity. However, the feasibility of adding nutrients to spawning streams as a management tool to boost salmon populations will depend on whether the benefits at this stage are maintained over the entire life cycle.

KEYWORDS

fisheries management, growth rate, marine derived nutrients, migration, oligotrophic, phosphorus, salmon, smolt

1 | INTRODUCTION

Anadromous species are born and reproduce in fresh water but achieve most of their growth in the ocean. This life cycle has consequences for freshwater ecosystems since migratory fishes can act as vectors for marine nutrients (Naiman, Bilby, Schindler, & Helfield, 2002), subsidized mostly via the production of gametes, waste products and the decomposition of adult carcasses arising from post-spawning mortality (Willson & Halupka, 1995). While emigrating juveniles also transport nutrients in the opposite direction, the relative scale of the nutrient flows is such that the majority of anadromous populations generate a net import of marine-derived nutrients to freshwater communities (Childress, Allan, & McIntyre, 2014; Flecker, McIntyre, Moore, Taylor, & Hall, 2010; Naiman et al., 2002; Walters, Barnes, & Post, 2009). The effect—generally in the form of increased productivity and/or biomass—is detectable in freshwater food webs, especially when ecosystems are otherwise oligotrophic (Claeson, Li, Compton, & Bisson, 2006; Guyette, Loftin, Zydlewski, & Cunjak, 2014; Nislow et al., 2010).

Recent declines in adult populations may result in the export of nutrients from fresh waters (by emigrating juveniles) being greater than the import by the breeding adults (Moore et al., 2011; Moore & Schindler, 2004; Scheuerell, Levin, Zabel, Williams, & Sanderson, 2005). This consequent steady decline in nutrient inputs ('oligotrophication') may significantly alter the architecture of the food webs that exist within these freshwater ecosystems (Doughty et al., 2016; Gerwing & Plate, 2019). This process is exacerbated by a rise in the number of artificial barriers to riverine migration, such as weirs or dams constructed for the purpose of hydropower generation or water storage. These have undoubtedly contributed to observed declines in anadromous fish populations (Lenders et al., 2016; Limburg & Waldman, 2009), which in turn have reduced the level of nutrient subsidies in ecosystems upriver of the barriers (Williams, Griffiths, Nislow, McKelvey, & Armstrong, 2009).

Restoring nutrient levels to some presumed previous level is one mitigation measure, but this needs to be carefully managed and evidence-based to avoid causing eutrophication (Stockner, Rydin, & Hyenstrand, 2000). Nutrients can be administered to freshwater

ecosystems via the addition of fertilizers (Griswold, Taki, & Stockner, 2003; Ward, McCubbing, & Slaney, 2003), fish carcasses (Bilby, Fransen, Bisson, & Walter, 1998; Williams et al., 2009), or fish carcass 'analogues' (Guyette, Loftin, & Zydlewski, 2013; Kohler et al., 2012), the latter usually being in the form of dried pellets made from marine fish (Pearsons, Roley, & Johnson, 2007). The addition of carcasses or their analogues has been found to be more effective than adding liquid fertilizers (Kiernan, Harvey, & Johnson, 2010; Wipfli et al., 2010), probably because the nutrient pulse lasts longer and also allows organisms to feed directly on the added biomass in addition to creating bottom-up effects (Bilby et al., 1998; Wipfli, Hudson, & Caouette, 1998). Carcass analogues have similar effects on freshwater productivity to real carcasses (Wipfli, Hudson, & Caouette, 2004), but have the advantages that they are lighter (being dried) and are more easily stored and transported (Pearsons et al., 2007).

To date, most studies on the impact of nutrient restoration in freshwater streams find that the addition of carcasses or carcass analogues increases invertebrate abundance and biomass (Claeson et al., 2006; Nislow et al., 2010; Wipfli et al., 1998) and generally benefits fish growth and body condition (Guyette et al., 2013; Williams et al., 2009; Wipfli, Hudson, Caouette, & Chaloner, 2003). However, effects on fish density and biomass are unclear, in part due to the limitations of field studies in controlling for the immigration of non-experimental fish into restored areas, as shown by Bilby et al. (1998). There is also little knowledge of the longer term consequences of nutrient manipulations, since most studies have only lasted for a few months after supplementation (e.g. Wipfli et al., 2003; Williams et al., 2009). It is therefore unclear whether observed increases in growth rate are sustained in the long term and/or influence subsequent life histories. For example, the timing of emigration to sea in many anadromous fish species is size-dependent; therefore, it is possible that the age structure of migrant fish could be altered by nutritional subsidies from their parents (Nelson & Reynolds, 2015). Finally, to our knowledge no previous studies have considered how the addition of marine-derived nutrients may affect the longer term genetic diversity of freshwater fish populations, which is becoming increasingly recognized as an important aspect of conservation management (García de Leaniz et al., 2007; Kahilainen, Puurtinen, & Kotiaho, 2014).

Here we examine the effects of marine-derived nutrients on juvenile Atlantic salmon and their invertebrate prey. While Pacific salmon are semelparous and experience mass mortality after spawning, post-spawning mortality rates in Atlantic salmon are lower and vary on both a temporal and spatial scale (Fleming, 1998; Jonsson & Jonsson, 2003). Nevertheless, even relatively small influxes of marine nutrients have the potential to alter the highly oligotrophic upland streams in which these salmon typically breed (Jonsson & Jonsson, 2003; Nislow, Armstrong, & McKelvey, 2004), and there is evidence that this species used to spawn at much higher densities than is currently the case (Lenders et al., 2016). Using a study system that allows us to exclude the potential effects of immigrant fish on calculations of fish biomass and density, we recently demonstrated experimentally that marine-derived nutrients from salmon carcass analogues can have a positive effect on juvenile Atlantic salmon genetic diversity, growth and biomass over the first 3 months of life (Auer et al., 2018). Here we extend our work in this same study system to consider whether these effects persist across the freshwater stage. We also evaluate if such simulations of nutrient release may influence the age (and hence size) at which juveniles undertake the spring seaward migration, with potential implications for the subsequent marine phase of the Atlantic salmon's life history.

2 | MATERIALS AND METHODS

2.1 | Study sites and general experimental protocol

We selected 10 small headwater streams that were surrounded primarily by open moorland and drained into the Rivers Blackwater, Bran, and Meig of the River Conon catchment in northern Scotland (Figure 1, Table S1; Auer et al., 2018). Hydropower dams along each of the rivers prevent the passage of most returning adult salmon (Gowans, Armstrong, Priede, & McKelvey, 2003; Williams, 2007). Atlantic salmon (stocked as eggs or juveniles) and resident brown trout (*Salmo trutta*) are the dominant fish species in the system. Five of the study streams were randomly assigned to the 'high parental

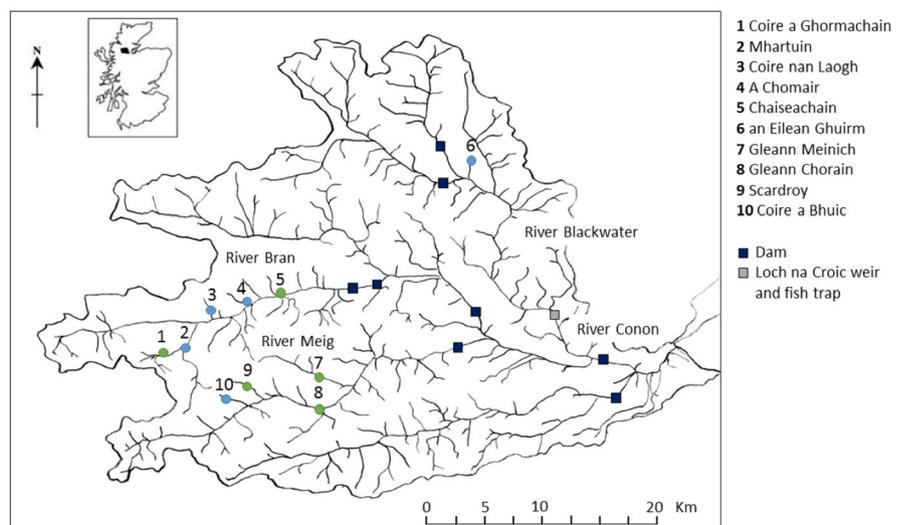
nutrient' treatment (addition of analogue carcasses), while the other five study streams were assigned to the 'low parental nutrient' treatment (without carcasses). We then planted out eggs from genotyped salmon families in each of the streams and subsequently monitored prey availability and fish growth, biomass, density, and genetic diversity of this focal cohort over the next 2 years (Figure S1). We also monitored these same fish variables in a second cohort of eggs planted out the second year to evaluate repeatability of parental nutrient effects during the first summer of growth (see Supplementary Information for details).

2.2 | Experimental families and planting out eggs and carcass analogues

Over a 3-day period in December 2015, 54 full sibling families were created using in vitro fertilization of fish caught in a fish trap at a dam on the River Blackwater (Figure 1). Parental fish were those previously stocked in headwater streams above the dam that were returning from the sea to spawn. Of the 54 families, we selected a subset of 30 families that were chosen at random with respect to paternal age but controlled for maternal life history; only families from females that had spent a single winter at sea, confirmed by scalimetry, were selected since that was the dominant life history of captured adults. A small section of adipose fin was clipped from each parent and preserved in 100% ethanol for later DNA analysis (see Supplementary Information). Fertilized eggs were then reared overwinter in family-specific trays under identical water and temperature conditions at a nearby hatchery.

In late February–early March 2016, when eggs had reached the eyed stage of embryonic development, 100 eggs from each of the 30 families were collected from the hatchery, mixed together, and then planted out in a 300 m² experimental reach (75–100 m in length depending on stream wet width; Table S1) in each of the study streams (Table S1). Eggs were buried beneath the gravel in two Vibert boxes at the lower and upper limit of each experimental reach ($n = 100$ eggs per box) and the rest of the eggs were planted out in eight artificial

FIGURE 1 Map of River Conon catchment in Northern Scotland, including the location of study streams (green circle = high parental nutrients and blue circle = low parental nutrients), key hydroelectric dams and trap for collecting returning adult salmon on their spawning migration. Figure taken from Auer et al., 2018



15 months old, Table S1), and finally in March 2018 (when the fish were 22 months old, which we refer to as age 2; Table S1). A total of 1,272 fish were captured at age 0+ within the experimental reaches of the streams, 458 at age 1+ (plus 292 caught within 50 m of the experimental reaches) and 306 at age 2, this time within 100 m of the experimental reaches. Captured fish were anaesthetized, weighed (± 1.0 mg), measured for body length (± 0.01 mm), and a small fin clip was taken for later parental assignment (see Supplementary Information). By conducting triple-pass electro-fishing (see Supplementary Information), we were able to estimate the densities of age 0+ and age 1+ focal fish based on the removal method and analysed (using maximum-likelihood) by Microfish software (Dochtermann & Peacock, 2013; Van Deventer & Platts, 1989).

nests ($n = 350$ eggs per nest; McLennan et al., 2016) at equidistant points between the upper and lower Vibert boxes. In total, each experimental 300 m² reach received 3,000 eggs, equating to a density of 10 eggs/m² that falls within the range of observed spawning densities for Atlantic salmon (Fleming, 1996). The Vibert boxes were found to be empty of eggs when recovered in late May/early June 2016, indicating successful hatching in all streams. Similar methods were used to create the second cohort of eggs that were planted out in each of the study streams the following year (see Supplementary Information).

At the time of egg planting and again the following winter (Table S1), analogue carcasses, composed of dried hatchery salmon pellets (Coral 2000+40PAX B12, made of 60% marine-derived fish-based nutrients, Skretting, Invergordon UK) and similar to salmon carcasses in their nutritional content and decay rate (Pearsons et al., 2007), were distributed in high parental nutrient streams. Each experimental reach in the high parental nutrient streams received five mesh bags of pellets, each weighing 3 kg, and equivalent to 25 adult salmon carcasses, an amount similar to or less than that used in other nutrient supplementation experiments in Atlantic salmon streams (Guyette et al., 2013, 2014; Williams et al., 2009). The bags were evenly spaced along the length of each experimental reach and anchored to the substrate of the stream by stones to prevent removal by scavengers. HOBO temperature data loggers (Onset Computer Corporation, Bourne MA) were also placed in each stream at the time of egg deposition and programmed to record data every 4 hours (Figure S2).

2.3 | Macroinvertebrate prey abundance and biomass

Macroinvertebrates were sampled in each experimental reach during late May to early June 2016 and then again in late February–early March 2017, when the fish were in their first and about to enter their second year of life (age 0+ and 1+ respectively). The sampling in March 2017 took place immediately prior to the addition of the second set of carcass analogues. Invertebrates were collected using the electrobugging technique (Taylor, McIntosh, & Peckarsky, 2001), described in detail in the SI. Specimens were then later identified to the family level and their length and biomass was calculated. Only those macroinvertebrates equal to or smaller than 1 mm and 2.5 mm in width were included in estimates of prey abundance and biomass (for age 0+ and 1+ fish respectively), since these are the maximum prey sizes that gape-limited juvenile salmon can consume at their respective body sizes (Wankowski, 1979). These smaller macroinvertebrates were primarily from the Orders Ephemeroptera, Plecoptera, Trichoptera, Coleoptera, and Diptera, all of which are known to be in the diet of juvenile salmon in the Conon and other Scottish river catchments (Table S2; Maitland, 1965; Mills, 1964).

2.4 | Recapture of juvenile salmon

Surviving juveniles were captured by triple-pass electro-fishing in July 2016 (when fish were age 0+, approximately 3 months old, Table S1), in July 2017 (when fish were aged 1+, approximately

15 months old, Table S1), and finally in March 2018 (when the fish were 22 months old, which we refer to as age 2; Table S1). A total of 1,272 fish were captured at age 0+ within the experimental reaches of the streams, 458 at age 1+ (plus 292 caught within 50 m of the experimental reaches) and 306 at age 2, this time within 100 m of the experimental reaches. Captured fish were anaesthetized, weighed (± 1.0 mg), measured for body length (± 0.01 mm), and a small fin clip was taken for later parental assignment (see Supplementary Information). By conducting triple-pass electro-fishing (see Supplementary Information), we were able to estimate the densities of age 0+ and age 1+ focal fish based on the removal method and analysed (using maximum-likelihood) by Microfish software (Dochtermann & Peacock, 2013; Van Deventer & Platts, 1989).

2.5 | Statistical analyses

Effects of parental nutrient levels on juvenile salmon and their macroinvertebrate prey were tested using a series of linear mixed models. All models included treatment (low vs. high parental nutrients) and salmon age (age 0 and age 1+ for invertebrate analyses and age 0+ and 1+ for fish analyses) as categorical fixed effects and stream as a random effect in cases where the dependent variable was measured more than once. Residuals were not normally distributed for most dependent variables, so we used a hierarchical bootstrapping approach to generate mean effects and p -values (Adèr & Adèr, 2008). For analyses of macroinvertebrate abundance and biomass and fish fork length, body mass, density and biomass, the bootstrap procedure first sampled with replacement among values within each stream and age, then streams and age within each treatment. Models were rerun 20,000 times. Significance values were then calculated as a two-tailed p -value from the bootstrapped distribution of the treatment effect. Results from models that included or excluded fish of unknown parentage were qualitatively the same since there were few fish with unknown parentage, so only results from models that excluded fish of unknown parentage are reported. The same analyses, albeit without age as a fixed effect, were run for body size, density, and biomass of the second fish cohort.

Effects of parental nutrient levels on family level diversity were examined using a bootstrap procedure that sampled, with replacement, values for the numbers of families represented in the captures from each of the streams per treatment and fish age. The model was rerun 20,000 times, and p -values were calculated as above. The number of fish captured per stream was included as a covariate in the analysis of family diversity, but was not statistically significant ($p > 0.05$; presumably because similar numbers were collected in each stream); so was dropped from the model. We ran two models, one that included and one that excluded fish captured outside the experimental reach section (see above).

Finally, differences in fork length between treatments (low vs. high parental nutrients) at age 2 were tested using a linear mixed model that included stream and family ID as random effects. The residuals from this model were normally distributed; therefore, the bootstrapping approach was not considered necessary.

3 | RESULTS

Both macroinvertebrate abundance (treatment $p < 0.001$; season $p = 0.18$; season \times treatment $p = 0.336$) and biomass (treatment $p < 0.001$; season $p < 0.001$; season \times treatment $p = 0.462$) were higher in streams with high compared to low parental nutrient levels. These differences were consistent across both the spring and the following winter, when juvenile salmon were age 0 and 1+, respectively (Figure 2).

Differences in prey availability among stream types were associated with distinct differences in juvenile salmon body size at both age 0+ and age 1+. Specifically, fork length increased with age as expected (Figure 3; $p < 0.001$), but juvenile salmon in high nutrient streams were also consistently larger than their siblings in low nutrient streams (treatment: $p = 0.001$; age \times treatment: $p = 0.609$). Likewise, body mass increased with age (Figure 3; $p < 0.001$), but juvenile salmon in high nutrient streams were consistently larger than their siblings in low nutrient streams (treatment: $p < 0.001$; age \times treatment: $p = 0.681$). Fish density declined with age (Figure 4; $p < 0.001$) but was not affected by nutrient level (treatment: $p = 0.966$; age \times treatment: $p = 0.495$). Fish biomass had declined at age 1+ (Figure 4; $p = 0.012$) but was consistently greater in high compared to low nutrient streams (treatment:

$p = 0.034$; age \times treatment: $p = 0.364$). Results for body size, density, and biomass were qualitatively the same for the second cohort of fish at age 0+ (Figure S3). Both length ($p < 0.001$) and biomass ($p = 0.012$), but not density ($p = 0.200$) were higher in streams with high compared to low parental nutrient levels.

Significant treatment differences in fork length were also observed when focal fish were age 2 (Figure 5, $p = 0.008$). Importantly, 89.6% of the captured individuals in high nutrient streams had reached the minimum fork length of 100mm required for smolt transformation in this river catchment (Malcolm, Millar, & Millidine, 2015), and so had a high likelihood of migrating to sea as an age 2 smolt. In contrast, only 38.3% of the fish in the low nutrient streams had fork lengths above this threshold size (Figure 5).

Finally, parental nutrient levels also influenced the genetic diversity of surviving fish (Figure 6). Specifically, there was a trend for surviving fish to be drawn from a higher mean number of families in streams with high compared to low parental nutrient levels ($p = 0.111$) at both age 0+ and age 1+ (age: $p < 0.001$, age \times treatment: $p = 0.559$) when the analysis excluded age 1+ fish captured outside the bounds of the experimental reach. These differences in family level diversity among stream types were statistically significant when these extra-limital fish were included (treatment: $p = 0.016$; age: $p = 0.127$; age \times treatment: $p = 0.559$).

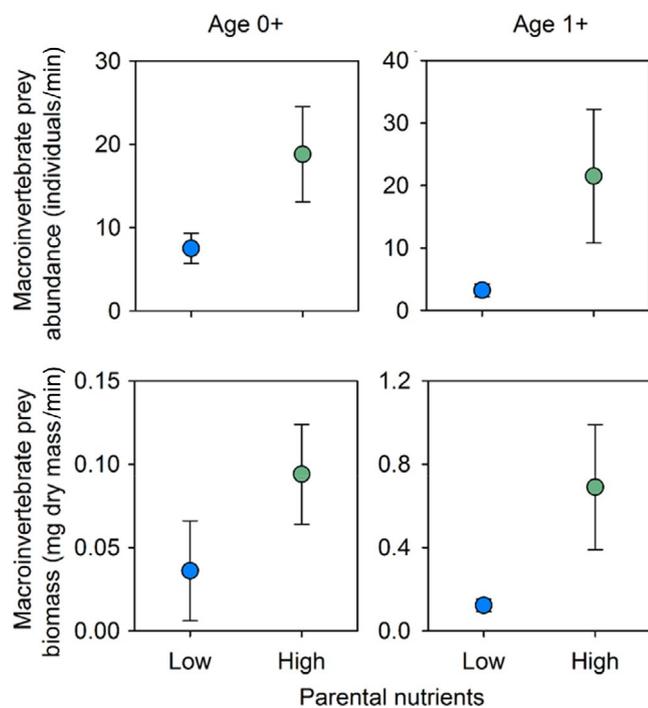


FIGURE 2 Mean ($\pm 1SE$) macroinvertebrate prey abundance and biomass when fish were age 0+ (May–June 2016) and age 1+ (March 2017) in streams with low (blue, $n = 5$) and high (green, $n = 5$) parental nutrient levels. Only invertebrates equal to or less than 1 mm in width during Spring 2016 and equal to or less than 2.5 mm in width in Winter 2017 were included since they represent the maximum prey size for age 0 and wintering age 1+ juveniles, respectively. Estimates are given as the mean catch per unit effort for 1-min samples taken at three locations at each of 50, 25 and 0 m above the downstream limit of each experimental reach. Data for May–June 2016 are from Auer et al., 2018

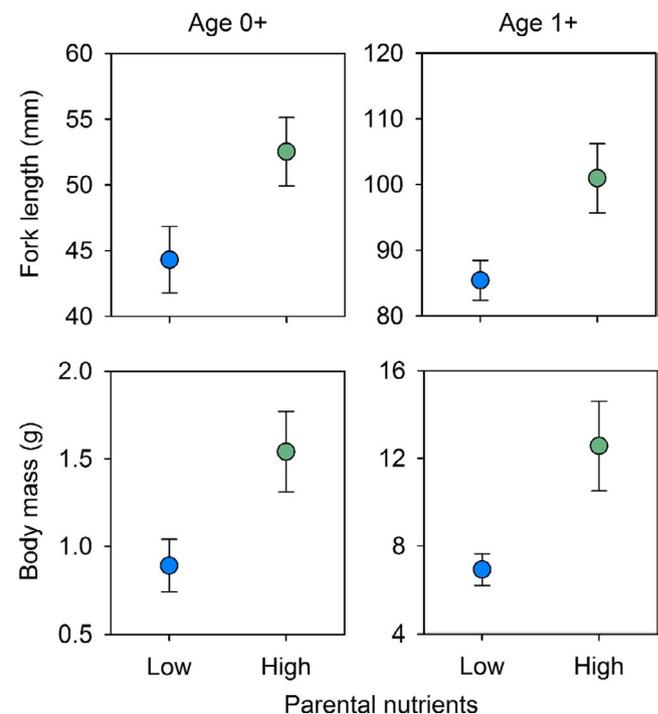


FIGURE 3 Mean ($\pm 1SE$) fork length and body mass of juvenile Atlantic salmon (*Salmo salar*) in streams with low (blue, $n = 5$) and high (green, $n = 5$) parental nutrient levels recaptured at age 0+ (July 2016) and age 1+ (July 2017). Data for age 0+ fish are from Auer et al., 2018

4 | DISCUSSION

4.1 | Sustained effects on prey availability and salmon growth rate

Previous studies have shown that the addition of marine-derived nutrients via carcasses or carcass analogues increases invertebrate

abundance and biomass (Claeson et al., 2006; Nislow et al., 2010; Wipfli et al., 1998). Marine-derived nutrients from salmon carcasses may become incorporated at multiple trophic levels within a stream (Nislow et al., 2010; Samways, Soto, & Cunjak, 2018). Therefore, a short-term increase in invertebrate abundance and biomass is perhaps unsurprising, given that many invertebrates feed directly on the carcass analogues and/or benefit from bottom-up effects of a nutrient pulse (Nislow et al., 2010). We show here that these effects can be both persistent and substantial: a year after the carcass addition (just prior to the second deposit of analogue carcasses) both the abundance and biomass of macroinvertebrate prey types for juvenile salmon were around five times higher than in streams receiving no carcasses. Since salmon carcasses are naturally deposited at yearly intervals, our results indicate that these natural annual nutrient pulses may sustain macroinvertebrate prey numbers at higher levels throughout the year. Scottish upland streams are often naturally nutrient poor (Elliott, Coe, Helfield, & Naiman, 1998; Nislow et al., 2004) and this has been further exacerbated by anthropogenic influence (Williams et al., 2009). Therefore, it is perhaps not surprising that even a relatively modest addition of simulated carcasses could significantly boost the productivity of the food webs that exist within these otherwise nutrient limited habitats.

This sustained increase in prey availability may explain why we also found that the salmon in these nutrient-supplemented streams were significantly larger at the end of the experiment, when they were 2 years old. While there is evidence of correlations between prey availability and the growth rate of age 0+ salmon in the field (Kennedy, Nislow, & Folt, 2008), less is known about the older freshwater life stages, when other sources of growth limitation (e.g. enhanced risk averse behaviour; see Nislow, Armstrong, & Grant, 2011) may act to decouple individual growth from the availability of prey. Here we have shown a similar growth response to a nutrient pulse and associated enhanced prey availability among the different freshwater age classes of salmon. Previous studies that report a positive effect of parental nutrients on fish biomass have been limited in determining the underlying mechanisms of such an effect (e.g. Williams et al., 2009). In this

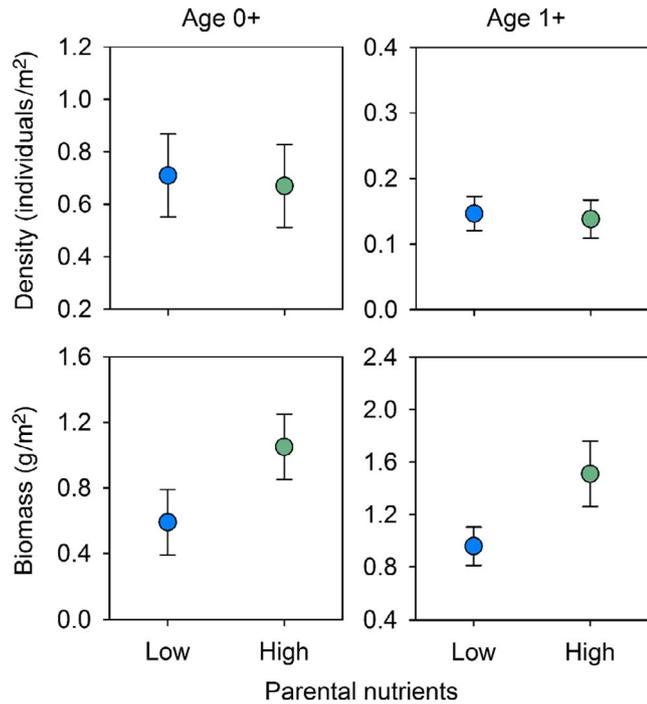


FIGURE 4 Mean ($\pm 1SE$) density and biomass of juvenile Atlantic salmon (*Salmo salar*) captured at age 0+ (July 2016) and again at age 1+ (July 2017) in streams with either low (blue, $n = 5$) and high (green, $n = 5$) parental nutrient levels. Fish density for each age class was estimated from depletion curves of the number of fish captured during triple-pass electrofishing. Fish biomass was calculated as the product of the average fish body mass and the estimated density for each stream. Data for age 0+ fish are from Auer et al., 2018

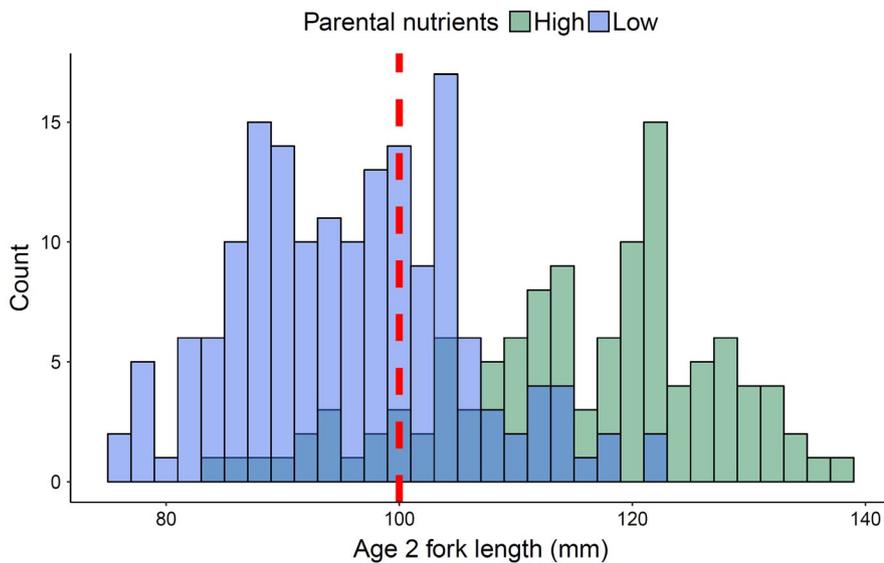


FIGURE 5 Distribution of fork length in streams with low (blue, $n = 5$) and high (green, $n = 5$) parental nutrient levels. Blue represents low parental nutrients, green represents high parental nutrients and purple represents overlaid data. The red dotted line corresponds to the minimum smolting size for this river system

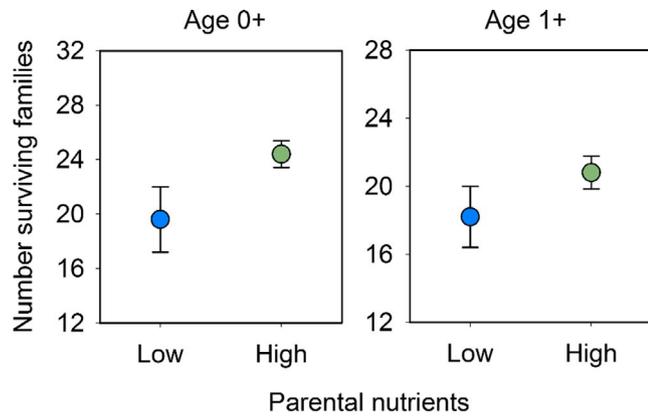


FIGURE 6 Genetic diversity of Atlantic salmon (*Salmo salar*) from streams with low (blue, $n = 5$) and high (green, $n = 5$) parental nutrient levels. Plotted are raw estimates for the mean ($\pm 1SE$) number of surviving families among fish captured at age 0+ (July 2016) and age 1+ (July 2017). Data include fish captured in the experimental reach as well as extra-limital areas 50 m up and downstream of the experimental reach. Data for age 0+ fish are from Auer et al., 2018

study, all matings occurred at the same time and all streams received the same genetic mix of eggs, so the only explanation for the larger juvenile size-at-age in high nutrient streams is a faster growth rate. Likewise, the greater biomass of juvenile salmon in the high parental nutrient streams was driven by differences in growth rate since we found no effect on their density. Other studies have found a positive effect on fish density from adding carcasses (e.g. Williams et al., 2009), but this could be caused by increased immigration (Bilby et al., 1998), which might imply no overall increase in population size. Our study reduced the noise in estimating the effects of nutrients on juvenile salmon by seeding all streams with the same number and genetic diversity of salmon eggs, and then genotyping the surviving offspring, so allowing us to show that levels of immigration were trivial. The upper density limit (i.e. carrying capacity) of juvenile salmon populations is linked to size of feeding territory that the fish defend (Grant & Kramer, 1990). However, stream salmonids (including Atlantic salmon) make only minor adjustments to territory size in response to changes in food supply (Grant, Weir, & Steingrímsson, 2017), which could explain the lack of difference in density between streams despite the difference in food abundance.

4.2 | Sustained effects on genetic diversity

We have demonstrated previously that higher parental nutrient levels lead to the survival of a higher number of salmon families through to 3 months of age (Auer et al., 2018). Here we show that this higher genetic diversity persists until at least 15 months of age: of the original families present in a stream at the egg stage (which was the same for all streams), more families had surviving representatives in the high compared to low parental nutrient streams. This indicates stronger selection against particular families when nutrient levels are low (Auer et al., 2018). For this experiment, eggs were artificially

planted in mixed family nests. While this may have possibly altered early life competition dynamics between the focal families, juveniles from different nests would have invariably become mixed (and so run into competition with each other), since average dispersal distances are likely to be much greater than average distances between the nests.

The importance of including genetic diversity in conservation management plans is becoming increasingly recognized (Garcia de Leaniz et al., 2007; Kahilainen et al., 2014). Though clearly a complex issue, genetic diversity is generally linked to the adaptive potential of a population (Kahilainen et al., 2014), which is of particular current importance given increasingly unstable environmental conditions and associated new selection pressures (Hoffmann & Sgrò, 2011). An additional reason for considering genetic diversity in conservation management plans is that low genetic diversity can be linked to inbreeding depression and population extinction (O'Grady et al., 2006). We still know very little about how Atlantic salmon populations are impacted by genetic loss, in part due to our limited knowledge of historic genetic diversity levels (Wang, Hard, & Utter, 2002). It has been suggested that salmon populations are already under inbreeding risk by evolutionary design, since they exhibit a high degree of natal homing, which in turn restricts the genetic make-up of spawning aggregates (Allendorf & Waples, 1996). There is evidence that Atlantic salmon have evolved inbreeding avoidance mechanisms and, in part, choose mates based on MHC dissimilarity (Landry, Garant, Duchesne, & Bernatchez, 2001). However, while mechanisms such as these can help to increase the genetic diversity of offspring, they rely on there being sufficient existing variation in MHC alleles, which may not be the case if low nutrient levels create selection pressures that reduce the genetic variation in already small populations. Restoring nutrient levels can thus have the benefit of improving genetic diversity and so increasing population resilience, even if it does not boost the size of the juvenile population size.

4.3 | Possible effects on later life stages

The age at which juvenile Atlantic salmon transform into the smolt stage of the life cycle and migrate to sea is variable, but since the seaward migration only takes place in the spring this generates discrete year classes of smolts. Across the geographic range of the species, migrants range in age from 1 to 8 years, with most rivers containing 1–4 year classes (Metcalf & Thorpe, 1990); those in the River Conon catchment are generally either 2 or 3 years old (McLennan et al., 2017). The probability of an individual smolting is governed by whether it is on course to exceed a threshold body size by the time of the smolt migration; presumably because survival rates of the smolts are strongly dependent on body size at the time of the migration (Armstrong, McKelvey, Smith, Rycroft, & Fryer, 2018; Jokikokko, Kallio-Nyberg, Salonemi, & Jutila, 2006). Those individuals that are projected to fall short of the threshold will exhibit suppressed growth over winter and will delay smolting for at least a further year (Dodson, Aubin-Horth, Thériault, &

Páez, 2013; Metcalfe, 1998). These differences in growth strategy make it possible (with up to 90% accuracy) to differentiate those fish that will/will not migrate, several months prior to the migration (Pearlstein, Letcher, & Obedzinski, 2007). Therefore, although the last sampling was conducted in March, prior to smolts developing the characteristic silver body colouration, we can presume that the larger individuals would have smolted. Given the size distribution of migrating smolts in this river system (Malcolm et al., 2015), it is reasonable to assume that the majority of fish larger than 100 mm when captured in March would have smolted that spring. Therefore, it is likely that the nutrient manipulation greatly boosted the proportion of fish that would have become 2- rather than 3-year-old smolts, since almost 90% of individuals in the high nutrient streams were ≥ 100 mm in March, compared to less than 40% in the low nutrient streams.

If the simplifying assumption is made that all fish ≥ 100 mm in March smolted at age 2, and that 80% of the remaining fish smolted at age 3 (the remainder having died or were males that failed to smolt after becoming sexually mature), then the addition of nutrients reduced the mean age of smolts from 2.56 to 2.09. In an analysis covering the geographic range of the Atlantic salmon, Metcalfe and Thorpe (1990) showed that the mean age of smolts in a river was closely related to growth conditions (measured in 'degree-hours' during which foraging could occur, being the annual sum of monthly mean temperatures above a baseline of 5.5°C (the threshold for growth) multiplied by daylight hours each month). Using the same approach as used in Metcalfe and Thorpe (1990), we calculate that at the latitude of the Conon river system the nutrient addition was the equivalent of an average increase in annual mean water temperature of 1.4°C.

How this acceleration of the freshwater phase of the life cycle might influence overall population dynamics is not clear, since there are a number of potential interacting factors. Individuals that migrate to sea after only 2 years in fresh water have an increased likelihood of surviving the freshwater phase of their life cycle, since age-3 smolts are subjected to freshwater mortality for an additional year. All else being equal, an increased smolt yield due to a greater proportion of age-2 smolts could cause a substantial decrease in generation time, with an associated increase in the population growth rate. However, age-2 smolts are also typically smaller than those migrating a year later from the same river (Jonsson, Jonsson, & Hansen, 1998), and so may experience higher mortality during migration (Armstrong et al., 2018; Jokikokko et al., 2006), which could then counteract the positive effect of increased smolt production on population size. Aspects of growth, size and age during the freshwater stage of the Atlantic salmon life cycle are often correlated with subsequent marine growth dynamics and the numbers of years spent at sea (Hutchings & Jones, 1998). These interactions are complex; however, if there were a negative relationship between smolt age and the duration of the marine phase (i.e. younger smolts spending an extra year or more at sea), the overall generation time would not be reduced and there would be no effect on population growth rate. This considered,

an increased proportion of age-2 smolts could still result in a net population gain via reduced inter-cohort competition within the stream (Einum, Robertsen, Nislow, McKelvey, & Armstrong, 2011). Older fish are likely to be competitively superior to those of younger age classes but have differing microhabitat requirements, so the impact of a reduction in the size of older cohorts is not straightforward (Nislow et al., 2011). However, it is possible that reduced competition from older cohorts could increase the carrying capacity of younger cohorts (Nordwall, Näslund, & Degerman, 2001), which might also increase the number of smolts being produced.

Though clearly complex, the results of our study suggest that restoring nutrients to the spawning grounds of Atlantic salmon could have significant implications for both population dynamics and fisheries management. Further work is needed to evaluate whether the gains from both increasing genetic diversity and reducing the time spent by fish in fresh water are actually sufficient to offset the higher mortality that individuals may then experience as a result of potentially being smaller at the time of migration. However, the groundwork is now partially laid for encouraging a greater consideration of how the nutrient decline of fresh waters may affect the species that live within these ecosystems, and how such effects may be better managed and mitigated.

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AUTHORS' CONTRIBUTIONS

D.M., S.K.A., S.M., K.H.N., J.D.A. and N.B.M. conceived the ideas and designed the methodology; D.M., S.K.A., G.J.A., T.C.R., S.M., K.H.N., R.D.B., D.C.S., E.C., J.S. and N.B.M. collected the data; D.M., S.K.A. and R.D.B. analysed the data; D.M., S.K.A. and N.B.M. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository <https://doi.org/10.5061/dryad.c6v3838> (McLennan et al., 2019).

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SUPPORTING INFORMATION

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