Dispersal and density-dependent growth of early juvenile Atlantic salmon (*Salmo salar*): Can density manipulations via stocking technique improve restoration?

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Abstract

Dispersal and density-dependent growth of early juvenile Atlantic salmon (*Salmo salar*): Can density manipulations via stocking technique improve restoration?

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Dispersal from nesting sites and habitat selection are essential for the fitness of young individuals and shapes the distribution, growth and persistence of populations. These processes are important to consider when releasing captive bred young individuals into the wild to restore extirpated or depleted populations. However, few studies have evaluated how manipulating densities during release affects the dispersal and growth of individuals with respect to crucial life history traits. I manipulated the density of young-of-the-year (YOY) Atlantic salmon to evaluate the effect of two stocking techniques on the life history characteristics of surviving fish. Salmon were either point-stocked (all fish released in a small area at the upstream end of a reach) or spread-stocked (fish were released evenly over the entire reach) in 14 reaches of the Boquet River, New York. I used snorkeling and electrofishing surveys to characterize the density, dispersal, growth and survival of salmon stocked via each technique. Density decreased and growth rate increased with distance downstream in point-stocking reaches, whereas density and growth were relatively constant within spread-stocking reaches. Overall, density, growth and survival did not differ between the two stocking techniques due to the greater-than-expected degree of dispersal observed in point-stocking reaches. YOY dispersed up to 1600m, with 41% moving over 200m downstream. Growth rate of individual fish was density-dependent, following the negative power curve observed in previous studies. My results provide insights into how the growth and survival of released individuals are altered via stocking techniques, ultimately shaping their distribution and persistence.

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Introduction

Habitat selection is an important process at the level of individuals and populations (Pulliam & Danielson 1991). Dispersal away from reproductive sites to find suitable habitat is essential for the fitness of young individuals in many populations of plants, birds, mammals and fishes (Bowler & Benton 2005; Matthysen 2005; Einum et al. 2011). While habitat at reproductive or nesting sites is often ideal, young animals often have to disperse to find unoccupied territories (Clarke et al. 1997). This initial phase of dispersal is particularly important for fishes, where population density can be extremely high around nest sites, causing young fishes to suffer from the negative effects of density-dependent growth or survival (Einum et al. 2011).

Salmonids are ideal model species for the study of dispersal and density-dependent effects due to the fecundity of adults, which deposit 1000s of eggs in small nesting sites (redds). The emerging young-of-the-year (YOY) are highly territorial (Grant & Kramer 1990; Steingrímsson & Grant 2008), limited in dispersal ability (Crisp 1995; Einum et al. 2008), and susceptible to density-dependent growth (Grant & Imre 2005). The first few weeks after emergence are a critical period in the growth and survival of YOY (Nislow et al. 2000), where 50% will likely starve in the wild, due to habitat limitation (Kennedy et al. 2008). Density-dependent survival and growth are described as a self-thinning process, where smaller individuals will die or be displaced downstream (Steingrímsson & Grant 1999) to less dense areas, resulting in less competition and an overall benefit to individual growth (Einum et al. 2011). However, with limited dispersal ability, most YOY remain close to redds (Einum et al. 2008, 2011) and hence suffer from lower growth and higher mortality. The combined effects of density-dependent growth, territoriality and limited dispersal ability during this critical life stage can severely limit population growth (Elliott 1994).

Like many species, salmonid populations have been declining in many regions of the world, resulting in numerous restoration and supplementation programs to boost population sizes (Jonsson & Jonsson 2009). These programs commonly involve rearing enormous numbers (millions to billions) of juveniles in hatcheries before release (stocking) (Naish et al. 2007; Gozlan et al. 2010) into stream habitats, chiefly as YOY or age 1+ juveniles. To reduce biodiversity loss, restoration and supplementation programs have become important for these socio-economically important fish populations, but the effectiveness of these practices remains understudied (Roni et al. 2002; Seddon et al. 2007; Lorenzen 2014).

Critical to the success of restoration programs is an understanding of the ecology, behaviour and basic habitat requirements of the target population and how these affect individual survival, density-dependence, and ultimately, population persistence and growth (Molony et al. 2003; Lorenzen 2005; Young et al. 2005). As part of these restoration programs, novel techniques are continuously being developed to address potential constraining effects on population growth (Cairns & Heckman 1996; Suding 2011; Lorenzen et al. 2014). Often the major factors threatening population persistence are the quality and amount of habitat available and the manner in which individuals are released (Wolf et al. 1998). Manipulating densities over an entire habitat during release can not only reduce the negative effects of density-dependence (McMenemy 1995), but also promote the effective use of the entire habitat available – something akin to the ideal free distribution (Fretwell 1972). Furthermore, it is important to account not only for the consequences of the density manipulation, but also the interaction of these manipulations with local habitat variability (Seddon et al. 2007; Lorenzen 2014).

Surprisingly little research has evaluated the ecological consequences associated with two of the most common techniques used during release: 'point' and 'spread' stocking (Cowx 1994). Point-stocking releases all fish in an uppermost site of a desired reach, whereas spread-stocking releases all fish evenly over the entire reach. Because of the limited dispersal abilities of young salmonids (Crisp 1995; Einum et al. 2008, 2011), point-stocking is thought to increase densities at the stocking location and the variance in density across the reach, both of which can lead to decreased growth and survival. By contrast, spreading fish over a large area may result in a more even distribution of fish, a lower effective density of fish (Grant et al. 1998), and less negative density-dependent effects (McMenemy 1995). However, point-stocking takes less time and effort and may decrease the time in transition from the hatchery to the river and subsequent mortality of fish prior to stocking. Because of the scope of many stocking operations, point-stocking is the typical method used. More generally, the few studies that have critically investigated the ecology and habitat of fish after release focused mainly on density manipulations using egg planting instead of YOY releases, and/or only considered density effects on YOY growth and dispersal without addressing other confounding factors such as habitat heterogeneity (Crisp 1995; McMenemy 1995; Einum et al. 2008, 2011).

In this study, I manipulated the density of YOY Atlantic salmon, *Salmo salar*, in a landlocked population by stocking known numbers of individuals into 14 separate reaches of the Boquet River, New York, using either a point or spread technique. I tested the general hypothesis that stocking techniques affect the density, growth and survival of hatchery reared YOY Atlantic salmon. I also evaluated how habitat availability and preference of YOY salmon affect their dispersal and growth.

Based on existing knowledge, I tested the following predictions: 1) spatial variation in density will be higher in point- than in spread-stocking reaches; 2) densities in point-stocking reaches will decrease with distance downstream, whereas densities in spread-stocking reaches will remain constant; 3) YOY mass will increase with distance downstream in point-stocking reaches, but not in spread-stocking reaches; 4) YOY mass will decrease as a negative power curve in relation to density.

Materials and methods

Study site

The Boquet River drains the Adirondack Mountains of NY, USA, and then flows 126km into Lake Champlain. The Boquet River is composed of mainly limestone/dolostone bedrock, surrounded by secondary hardwood growth (Wu & Kalma 2013), with stream gradients ranging from 0.52%, in the main stem, to 6.46% in adjacent tributaries. Topography ranges from fast, boulder-strewn riffles, to slower moving water with pebble substrates, to deep pools with sandy bottoms. The Boquet River and Lake Champlain once had a flourishing landlocked Atlantic salmon population that was extirpated in the mid 1800s due to habitat degradation and dams blocking access to spawning and rearing habitat (Marsden & Langdon 2012). Since the 1970s Atlantic salmon have been stocked into the Boquet River and Lake Champlain in an effort to rebuild the population, but reproduction by stocked fish is limited (Facey et al. 2012).

Stocking procedure

A total of 174,000 unfed Atlantic salmon fry were stocked into 14 stocking reaches in eight tributaries of the Boquet River (Figure 1), where there was no evidence of natural reproduction. In an effort to maximize survival, YOY were stocked into previously used stocking reaches that contained good rearing habitat as defined by Girard et al. (2004). All YOY were stocked on May 6th and 7th 2014 using either a point or spread-stocking technique with numbers ranging from 7,500-19,500 YOY per reach. In point-reaches, all YOY were placed in a 50m^2 area at the upstream end of the reach, whereas in spread-stocking fish were distributed as evenly as possible over a 1000m long reach. The North Branch reach received a hybrid stocking technique wherein 1/3 of the fish were point-stocked at three evenly spaced locations in a 1000m reach; this stocking technique is routinely used by the New York State Fish and Wildlife Service. When possible, each tributary received equal numbers of YOY in both stocking treatments in a paired design; each treatment was placed equally in the upstream or downstream reach of a tributary (Placement).

Adult hatchery salmon used for stocking in Lake Champlain originated from Lake Sebago, Maine, USA. The YOY used in this study were generated from eggs and sperm collected from 3-year-old hatchery or hatchery-origin mature males and females in the fall of 2013; the former were maintained in the hatchery for their entire lives, whereas the latter were stocked as juveniles into Lake Champlain and recaptured at maturation. Eggs from 661 females were used to generate the YOY in my study: 461 and 200 of which were hatchery and hatchery-origin, respectively (fertilized by 219 and 37 males, respectively, for the two groups). Fertilized eggs were placed in 21 incubators of which 13 were on well water and eight were on lake water, and treated regularly with formalin and iodine. Once eggs had reached the 'eyed stage' they were shocked and healthy eggs were returned to trays. Hatched YOY were placed in holding tanks and allowed to absorb their egg yolks. All unfed YOY were thoroughly mixed into one holding tank before being randomly divided into bags for stocking (Aldinger 2013).

Sampling sites and methods

Throughout the spring and summer of 2014, two snorkeling and two electrofishing surveys were conducted. Snorkeling sessions occurred between June 10-20 and July 25-August 5 to assess the habitat that was used and not-used by YOY. Electrofishing surveys were performed between July 7-17 and August 7-21 for measurements of mass and density.

For each stocking reach, I sampled eight different sites during the first snorkeling and electrofishing survey. The first site was 50m upstream from the stocking reach, the second was at the upstream end of the stocking reach and the remaining six were 50, 100, 200, 400, 800 and 1600m downstream of the upstream end of the stocking reach.

For the first snorkeling session, sites varied between 6.1 and 104m^2 (mean±SD= 37.5±21.5m^2), depending on the site's width and the amount of high quality YOY habitat available (see Girard et al. 2004) at each site. However a total area of 50m^2 was sampled at each site during the first electrofishing survey.

The first snorkeling and electrofishing surveys detected no YOY salmon at five stocking reaches, which were omitted from the 2nd snorkeling and electrofishing surveys: Black River, Roaring Brook, North Branch and both reaches in the Mainstem. Two additional sites were added at 600m and 1000m downstream in each of the remaining stocking reaches. I increased the size of the 10 sites to include a 25-m length of river for the second snorkeling and electrofishing surveys so a larger total area was sampled (mean±SD = 130±62.5m^2; range = 49.5-339.5m^2).

During the 2nd snorkeling survey habitat data (see below) were collected along transects across the river. Transect data were taken for all 10 modified 25-m sites of a stocking reach.

Thermochron temperature loggers (DS1921G, Maxim Integrated, California, USA) were placed at 20 different locations in the Boquet River in late May and were removed in early September. Each stocking reach received at least one temperature logger, which recorded water temperatures every 72 minutes throughout the entire summer. Every site was also measured for water temperature and pH using a handheld portable meter (PCSTestr35, Oakton instruments, Illinois, USA) during each snorkeling survey.

Habitat used and not-used

Habitat use data were collected by snorkeling upstream through each site between 1000 and 1900 hrs (Girard et al. 2004), times when YOY are actively feeding (Breau 2003). While snorkeling, YOY were observed for up to five minutes to determine a central feeding station (Steingrímsson & Grant 2008), which was marked with a numbered washer. Once the entire site was snorkeled, habitat data were collected for each feeding station.

Habitat variables measured were water depth, dominant substrate diameter, water velocity and canopy cover. Water depth was measured to the nearest cm with a standard metre stick. Water velocity was measured, using a water-flow probe (FP211, Global Water Instrumentation, Texas, USA), at the approximate location of the focal fish's snout when holding position over the feeding station (Moyle & Baltz 1985). Canopy cover was determined using a convex bicycle mirror placed over the central feeding station and the percentage of mirror covered by foliage was estimated. Substrate was quantified using the Wentworth scale (see Wentworth 1922), and classified as boulder, cobble, pebble, granule or sand. For the purpose of this study, any particle smaller than 2mm in diameter was classified as sand. The diameter of the most abundant substrate present around the foraging station was noted on a scale of 1-5 (1= sand, 5 = boulder).

For each foraging station that was measured, I randomly selected a location that was not-used by YOY salmon. These locations were selected at a randomly selected distance (between 0-2m, at 0.25m intervals) and direction (a number between 1 and 12, representing directions on a clock with 12 facing directly upstream). Habitat variables at these not-used locations were measured using the same methods as for the used locations.

Habitat transects

Habitat data were collected for all 10 sites in each of the 14 stocking reaches during the second snorkeling survey. Each site received five evenly spaced transects across the stream. Each transect consisted of five evenly spaced points beginning 10 cm from the river-bank. At each point, I measured the same habitat variables that were quantified for habitat use. In between each site, at 50-m intervals up to 1000m downstream, more transect data were collected for an average of 60 transects per stocking reach.

Electrofishing surveys

Electrofishing surveys were performed using a backpack electrofisher (LR-24, Smith-Root, Washington, USA). Each site received a single-pass electrofishing sampling, which is sufficient to estimate variation in fish abundances (Einum et al. 2008). All fish caught were netted and placed in a bucket containing stream water. Once the entire site was sampled, YOY caught were measured for fork length (mm) and mass (grams) using a portable scale and returned to their appropriate site. Other fish species caught during the survey were identified, counted and classified by approximate size.

The total number of YOY per reach was estimated from the mean density in the 10 sites and the total area sampled. Estimates of density between sites were calculated as the mean density of the two adjacent sites. These mean densities were then applied to the total wetted area of a stocking reach to estimate the total number of YOY.

Statistical analysis

To analyze differences in the spatial variance of YOY between the two stocking techniques, paired t-tests were used. Since Sprucemills contained two point-stocking reaches, the spread-stocking reach was paired twice.

Two meta-analyses were performed on density and YOY mass for each stocking technique in relation to distance. Effect sizes were calculated using Pearson's correlation coefficients between density/mass and distance for individual reaches. For both meta-analyses spread-stocking reaches included all sites, whereas point-stocking reaches included the site with the highest density and all sites downstream. For YOY mass, a site was only included if it contained YOY.

Habitat quality was assessed by using habitat used/not-used data from the second snorkeling survey for three variables: water depth, water velocity and substrate. A multivariate logistic regression was used to distinguish between the habitats that were used versus not-used using the three measured variables along with their squared terms. Habitat quality was described by: probability of use= $1/(1+e^{-p})$, where the multivariate logistic regression model (p)=-5.589+0.104*water depth (cm)+0.107*water velocity (cm/sec)+2.765*substrate -0.00086*water depth^2 -0.00484*water velocity^2 - 0.4674*substrate^2). I then applied this equation to all transect data to estimate the mean habitat quality on a per site and reach basis.

As density, habitat quality, temperature and pH data were taken on a per site basis, YOY mass data were analyzed using the average mass of all YOY found within a site. Mixed models for the three dependent variables (density, mass and survival) were fitted using critical AIC (Akaike information criterion) values (Akaike 1987). Tributary was the only random variable in all models, except for survival, where it was used as an independent variable. Full models were fitted using all fixed effects and two-way interactions using the R software package "glmulti". First, I conducted an exhaustive search of all possible models containing up to 16 terms. Second, I searched with a genetic algorithm (see Calcagno & Mazancourt 2010) for models containing more than 16 terms, due to the large amount of candidate models (>2,000,000). The model with the lowest critical AIC score (>2) was chosen. If the difference between multiple models were within 2 AIC scores then the model with the least number of terms was chosen.

All fitted linear mixed models were performed using t-tests with Satterthwaite approximation for degrees of freedom. To determine overall effects of stocking techniques and placement on density, mass and survival, least squared means were used. To analyze overall and per stocking reach trends of density and mass in relation to distance, linear regressions were performed.

Results

Over the entire summer 472, 263, 300 and 575 YOY were sampled during the first snorkeling, first electrofishing, second snorkeling and second electrofishing survey, respectively. Five of the stocking reaches had no fish during the first two surveys and were, therefore, excluded from all analyses except for survival. Analyses of final density and YOY mass used data from the second electrofishing survey, whereas those for habitat used/not-used included data from the second snorkeling survey, across the remaining nine stocking reaches in four tributaries (Southfork, Derby, Branch and Sprucemills).

YOY Density

Prediction #1: Spatial variance

Unexpectedly, there were no detectable differences in spatial variation in density (YOY/m^2) between the two stocking techniques. Mean densities did not differ significantly between spread- and point-stocking reaches (Table 1) but the power to detect differences was low (power=0.06). The coefficient of variation also did not differ significantly between spread- and point-stocking reaches (Table 1) but was in the predicted direction. However, the power to detect a difference was relatively low (power=0.36). Based on the observed variation in density I would have required 11-paired samples to detect a significant difference.

Prediction #2: Density vs distance

When all stocking reaches were included in the analysis, the expected interaction between distance and stocking technique was highly significant (Table 2A). Hence, I also performed mixed model analyses for point and spread stocking data separately.

For point-stocking reaches, density was only significantly affected by distance from the stocking site; as predicted, density decreased with distance (Table 2B). For point-stocking reaches, linear regressions and the meta-analysis began at the site where density was highest and included all other sites downstream. As predicted, density decreased significantly with distance in 4 out of 5 point-stocking reaches and in the overall meta-analysis (Figure 2 and Table 3A). Mean density for point-stocking reaches was highest at 50 metres downstream (0.140 fish/m^2) and had not reached 0 by 1600m

(0.004 fish/m^2) (Figure 3). In point-stocking reaches, the mean dispersal distance was 229m with 41%, 17%, and 4.2% dispersing farther than 200m, 600m and 1000m downstream, respectively.

As predicted, distance had no effect on density in spread-stocking reaches and remained relatively constant (Table 2B, Figure 2). Individual regressions and the meta-analysis also showed no significant change in density with increasing distance downstream (Table 3B).

Mixed model results

The density in spread-stocking reaches was primarily affected by placement in a tributary (Table 2C), with densities in upstream reaches (mean±SE= 0.07±0.012 fish/m^2) being significantly higher than downstream reaches (mean±SE= 0.012±0.009 fish/m^2). To determine whether this placement effect was caused by tributaries getting wider downstream, I compared the width of every site relative to placement. Tributary widths differed significantly (t_{85}=-4.388, p<0.0001); downstream reaches (mean±SE= 7.191±0.699m) were wider than upstream reaches (mean±SE= 4.685±0.710m). However, in spread-stocked reaches, the number of YOY also differed significantly (t_{36}=5.801, p<0.0001); downstream reaches (mean±SE= 1.67±1.46) had fewer YOY than upstream reaches (mean±SE= 8.71±1.46) over an entire stocking reach. In point-stocked reaches the number of YOY did not significantly differ (t_{47}=-1.646, p=0.106) between downstream (mean±SE= 8.26±2.751) and upstream (mean±SE= 5.6±2.822) reaches.

Spread-stocking reaches were also significantly affected by the interaction of placement and temperature; density decreased at a faster rate with increasing temperatures in upstream reaches (slope±SE= -0.052±0.022) than in downstream reaches (slope±SE= -0.001±0.014). An analysis of covariance showed a significant difference between slopes ($F_{1,34}$=13.73, p<0.001).

Upstream dispersal

Due to culverts or waterfalls, dispersal upstream was only possible in six of the nine stocking reaches; 8.9% of all YOY that were sampled in those six reaches dispersed

50m upstream. Surprisingly, 42% of upstream dispersers were found in spread-stocking reaches.

YOY mass

Prediction #3: YOY mass vs distance

As predicted, in point-stocking reaches, YOY mass (grams) increased with distance downstream (Table 4B and Figure 4). The meta-analysis and individual regressions were performed from the sites where density was highest and included all sites downstream; significant positive relationships were found in all reaches except Sprucemills lower reach (Table 5A). Contrary to the prediction, in spread-stocking reaches, mixed model analysis showed YOY mass to increase with distance (Table 4C). However this increase was highly influenced by the fast growth of the few fish that dispersed to the 1600-m site. Excluding the 1600-m site resulted in no significant change in YOY mass (t_{24}=1.766, p= 0.09). Furthermore, the overall linear regression and meta-analysis, including all sites, of YOY mass in relation to distance also showed no significant change in spread-stocking reaches (Table 5B), suggesting an overall non-significant relationship.

Prediction #4: Density vs YOY mass

Overall, YOY mass decreased with increasing densities (Table 4A) and was better fitted by a negative power curve than a linear model (AICc>10). To analyze differences in the strength of density dependence between stocking techniques, I $\log_{10}$ transformed both density and YOY mass. The slopes differed significantly (Analysis of covariance, interaction between stocking technique x density ($F_{1,74}$=7.455, p=0.008); however, contrary to my predictions the slope was steeper in spread-stocking (slope±SE=-1.177±0.186) than in point-stocking (slope±SE= -0.429±0.184) reaches (Figure 5).

Mixed model results

Overall, mass of YOY stocked in upstream reaches of a tributary (mean±SE= 3.269±0.227) were significantly smaller than YOY stocked downstream (mean±SE= 5.568±0.223). Stocking technique had no significant effect on YOY mass in spread (mean±SE= 4.476±0.327) or point (mean±SE= 4.288±0.315) reaches. Because of my apriori predictions I also investigated the data separately for point- and spread-stocking reaches.

In point-stocking reaches, mass was significantly affected by density, distance, placement and the interaction term of distance X temperature (Table 4B). In addition to the density and distance effects, YOY were larger in downstream reaches (mean±SE= 5.301±0.259g) than in upstream reaches (mean±SE= 2.747±0.426g). The significant interaction term of distance x temperature occurred because mass decreased at a faster rate in relation to temperature farther downstream.

In spread-stocking reaches, mass was significantly affected by density, distance, placement and the interaction term of placement X density. In addition to the effect of density and distance, YOY were larger in downstream reaches of a tributary than upstream (Table 4C). The significant interaction term occurred because mass decreased with increasing densities faster in downstream (slope±SE= -110.011±41.776g) than upstream (slope±SE= -1.688±5.352g) reaches.

Survival

Overall survival was unaffected by stocking technique, number of YOY stocked, placement and tributary. Survival was 3.52% across all reaches that retained fish. Survival for spread-stocking reaches was slightly higher (mean±SE= 0.036±0.113) than point-stocking reaches (mean±SE= 0.033±0.011) (Figure 6) but not significantly. Individual stocking technique analyses showed survival to only be significantly affected by placement in spread-stocking reaches ($F_{1, 4}$=40.13, p=0.003); survival in upstream reaches was higher (mean±SE= 0.058±0.008) than downstream (mean±SE= 0.007±0.004) (Figure 6).

Discussion

The present study illustrates how manipulating densities during the release of animals for restoration purposes can alter the spatial distribution and growth trends of a cohort. Using YOY Atlantic salmon as a model species, I found that point-stocking resulted in a decrease in density and an increase in mass with increasing distance from the release point, whereas spread-stocking maintained relatively even densities and masses within the reach. However, overall YOY density, spatial variance in density, mass and survival did not differ between stocking techniques, most likely due to the dispersal ability of YOY in point-stocking reaches. Furthermore, density, mass and survival of released YOY were also influenced by distance from release points, placement (upstream vs. downstream) or temperature, depending on which stocking technique was used. These results have important implications for restoration and supplementation programs involving large-scale releases of fishes, mammals and amphibians.

Spatial variance, mass and dispersal

Densities in point-stocking reaches were solely correlated with distance, declining with distances downstream. Yet, this relationship was much more gradual than expected due to the mobility of YOY. YOY dispersed an average of 229m with a median of 100m. In contrast to most previous studies (Crisp 1995; Einum et al. 2011), the highest densities were never found at the origin of a stocking reach but were typically 50-100m downstream. Beall et al. (1994) found similar results where the highest densities were 90-150m downstream. However, 41%, 25%, and 9% of fish dispersed farther than 200, 400 and 800m, respectively, compared to only 29%, 9% and 0.4% in Beall et al. (1994) and even fewer in Crisp (1995) (Figure 7). Dispersal distance was also the best predictor of mass in point-stocking reaches: individuals that moved farther were larger, presumably because of less intra-specific competition for food.

In spread-stocking reaches, there was relatively little change in YOY density and mass relative to distance. While spread-stocking reaches tended to have lower coefficients of variation in density than point-stocking reaches, there was still large variation in density. Even though YOY were stocked at low densities up to 1000m downstream, dispersal still occurred to the 1600-m site.

In stocking-reaches where upstream dispersal was not impeded by culverts, waterfalls or dams, 8.9% of YOY were found 50m upstream. In the lower Sprucemills point-stocking reach, the highest density was 50m upstream, likely due to shallow, slow flowing water at this stocking reach compared to other reaches.

Dispersal is often referred to as a size-dependent strategy in YOY salmon. Because of their reduced competitiveness, smaller individuals tend to disperse downstream, take advantage of low densities and grow faster than larger individuals (Einum et al. 2012). However, they also suffer higher rates of predation risk than larger individuals that disperse less. These trends appear to hold true in the present study. If smaller individuals did disperse further in my study, then they grew faster than those that remained in higher density areas close to the stocking origin.

Dispersal is often thought to be largely influenced by increased competition at higher densities, but my results suggest that environmental factors may also play an important role. Dispersal can also be linked to water flow velocities (Oatway & Clarke 1981); during early life stages, individuals are more susceptible to being displaced downstream by water flow (Heggenes & Traaen 1988) in high gradient streams. Although no significant relationships were found between mean dispersal distance and water flow velocity (t_3=-0.76, p=0.503) or gradients (t_3=-1.8, p=0.171) in point-stocking reaches, stocking reaches had gradients ranging from 2.375%-14.563% (mean±SD= 5.638±4.61) and were relatively high compared to other studies. Furthermore, fry originated from a landlocked population and held in holding tanks with little experience in flowing water prior to release. These combined effects are a plausible explanation for the dispersal distances seen in my study; past studies have used reaches with lower gradients and/or have used egg-planting where emerging YOY were more accustomed to flow velocities which were from anadromous populations (Crisp 1995; Einum et al. 2011).

Although point-stocked YOY densities and mass followed the expected trends in relation to distance, neither was as pronounced as anticipated. The great mobility of YOY in my study, may explain why no difference in YOY density and mass was observed between stocking techniques.

Density-dependent growth

The effect of density on YOY mass corresponded to past findings and was best represented by a negative power curve (Imre et al. 2005). While YOY densities were relatively low in my streams (<0.3/m^2), strong density-dependent growth was still detected. These results were consistent with the hypothesis that exploitation is the dominant form of competition (Jenkins et al. 1999; Imre et al. 2005; Einum et al. 2006 but see Ward et al. 2007). Imre et al. (2005) suggested two mechanisms for the negative power curve: per capita foraging rate will decrease with increasing numbers of neighboring individuals following a (1/n) curve (Kramer et al. 1997); and, drifting invertebrate prey increasingly hide with increased predation risk thus increasing the effects of density-dependent growth.

Surprisingly, density-dependent growth was stronger in spread- than point-stocking reaches. This could be partly due to habitat selection during dispersal. Since YOY were spread-stocked at lower densities the pressure to disperse may not have been as strong as when point-stocked, resulting in less dispersal over smaller distances. Habitat selection would then be limited to a smaller habitat range thus finding optimal habitat less likely. Point-stocked YOY would have experienced a larger range of habitat qualities during dispersal thus increasing the likelihood of finding/settling into optimal habitat. This hypothesis is based on the assumption that spread-stocked YOY dispersed shorter distances than point-stocked fish. Furthermore, in point-reaches, the extended dispersal of YOY inevitably led to a more even distribution of YOY and ultimately less density-dependent growth than we were expecting based on Crisp (1995) who observed density-dependent growth relationships with slopes up to -0.588 compared to only -0.429 here.

Habitat quality and stocking reach placement

YOY salmon were larger in downstream reaches in both stocking treatments although densities were only significantly lower in downstream spread-stocking reaches. While the faster growth in downstream reaches was partly due to lower densities, it may have also been related to warmer temperatures; point-stocked YOY found in downstream reaches were still significantly larger, most likely due to an increased growth rate from warmer temperatures (°C) (Dwyer & Piper 1987) in downstream reaches (mean±SE=

16.345±0.054) when compared to upstream (mean±SE= 14.365±0.056). When placed downstream, spread-stocked YOY benefited more from the combined effects of lower densities and warmer temperatures whereas point-stocked YOY only benefited from the latter.

Surprisingly, habitat quality had no effect on the density and mass of YOY in a site. This may be due to the habitat quality not varying much at the site level. Only those rivers that were assessed in the past as providing good rearing habitat were used for stocking. The significant interaction of distance and temperature in point-stocking reaches could be explained by faster growth rates from higher temperatures being stronger in lower density areas further downstream whereas further upstream growth rates were more limited by higher densities.

Survival

Overall, survival estimates were relatively low (3.52%) when compared to Crisp (1995) where survival estimates, in September, were up to 19% and 27% for point- and spread-stocking techniques, respectively. However, our actual survival estimates would likely be higher if we had used multiple-pass electrofishing (Einum et al. 2008). I found that survival was unaffected by stocking technique and stocking densities whereas Beall et al. (1994) and Crisp (1995) found that survival was increased by stocking at lower densities and/or via a spread technique. These results are in part due to point-stocked YOY effectively reducing density-dependent survival by distributing themselves over large areas, regardless of stocking density. Reduced survival rates were only seen when YOY were spread-stocked in downstream reaches of a river, and could perhaps be due to increased predation risk at lower densities downstream.

Conservation implications

I found no difference in YOY mass and survival between stocking techniques that were expected to generate very different outcomes in post-release performance. Point-stocked YOY were able to disperse over large distances thus reducing the amount of density-dependent growth/survival and the inherent benefit of spread-stocking YOY at lower densities. The overall limiting factor on YOY mass was the amount of habitat available in a stocking reach; YOY grew larger in downstream reaches of a river where more habitat or warmer water was available. However, spread-stocking in reaches downstream had lower survival rates.

In the absence of detailed knowledge of reproductive and juvenile habitats, I suggest that an ideal method for stocking YOY salmon would be a combination of both point- and spread-stocking techniques. Point-stocking 2000-3000 YOY at locations 400m apart throughout a river will allow for a relatively even distribution of YOY throughout the reach by dispersal filling in the area in between each point-stock, while also using the entire habitat available. Furthermore, point-stocking 2000-3000 YOY together mimics the dispersal and competition that occurs at natural redds and perhaps avoids the retention of less fit subordinates that could arise from reduced competition at lower densities from spread-stocking.

There are several unique aspects of my study system, including the stocking of landlocked salmon into a multitude of locations with relatively little obstacles to impede YOY dispersal. Nevertheless, my results can be used to understand how density, dispersal and growth interact to affect the life history characteristics of the survivors in other streams. However, more research is needed to assess how stocking techniques can improve overall growth and retention when faced with limited dispersal potential, limited habitat availability, different stocking intensities and perhaps be followed through multiple life stages to determine the ultimate effects on population growth and persistence.

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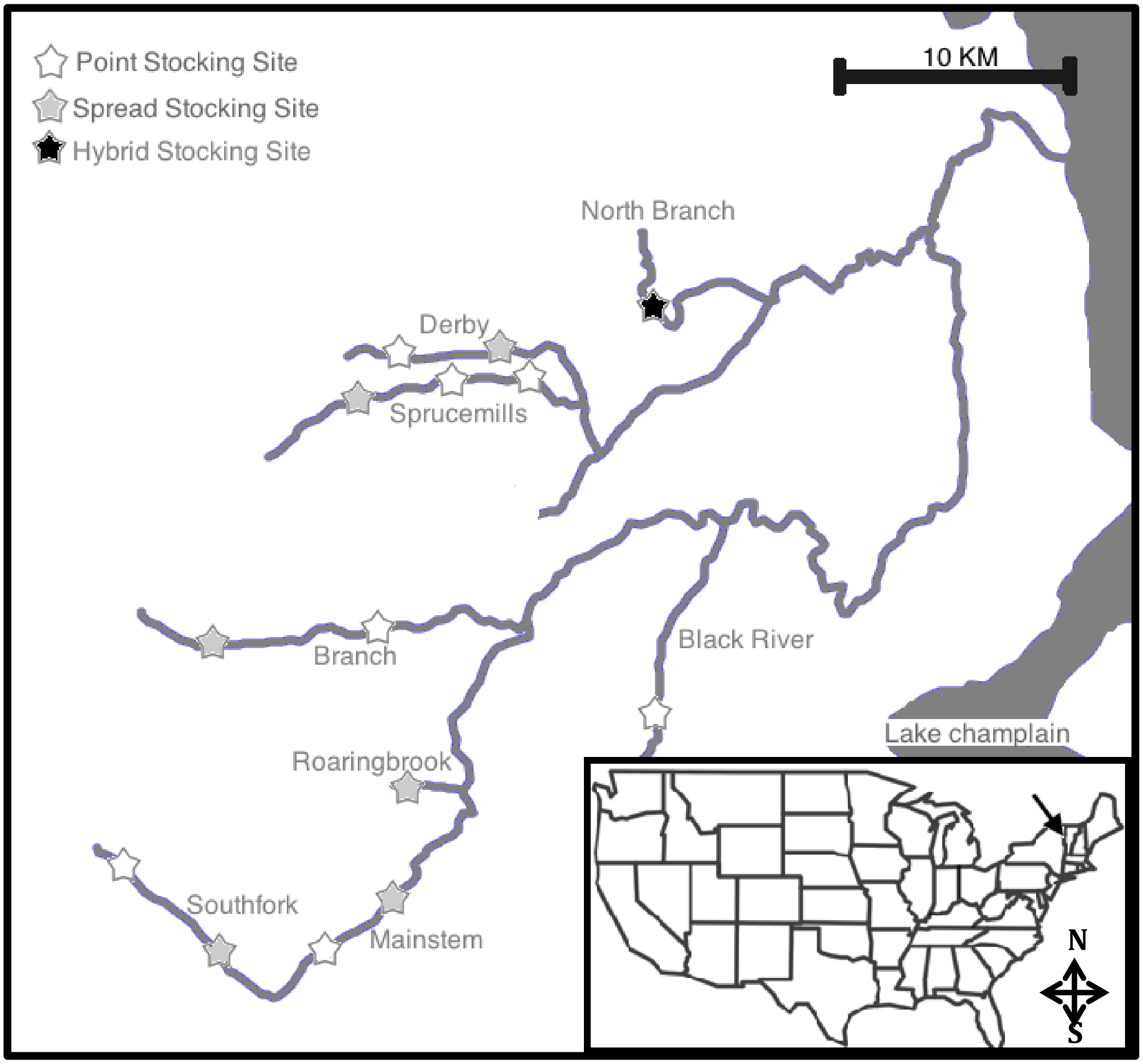

Figure 1. Location (Inset) and map of Boquet River, New York, USA (Lat: 44.368103, Long: -73.381205) with all tributaries used for stocking YOY Atlantic salmon. Stars denote the location and stocking technique used of a reach.

Table 1. Comparisons of the mean and coefficient of variation (CV) of YOY density between the two stocking techniques.

Variable	Stocking technique	Mean±SE	t	df	P
Mean	Point	0.070±0.019	0.523	4	0.629
	Spread	0.055±0.019			
CV	Point	0.904±0.115	2.080	4	0.106
	Spread	0.709±0.078			

Table 2. Results of mixed effects models for the dependent variable density using (A) all stocking reaches and separate analyses for (B) point- and (C) spread-stocking reaches.

Term	Estimate (*10^3)	SE (*10^3)	df	t	P
A) All reaches (n= 9)					
Intercept	253	97	74.59	2.608	0.011
Distance	-0.071	0.014	78.05	-5.097	<0.0001
Stocking technique	444	200	80.09	2.223	0.029
Temperature	-10	6.196	80.47	-1.625	0.108
Distance x Stocking technique	0.088	0.022	78.42	4.046	<0.001
Stocking technique x Temperature	-33	13	80.04	-2.504	0.014
B) Point stocking reaches (n=5)					
Intercept	97	21	4.03	4.661	0.009
Distance	-0.072	0.015	44.15	-4.789	<0.0001
C) Spread stocking reaches (n=4)					
Intercept	30	116	34	0.260	0.796
Placement	834	208	34	4.018	<0.001
Temperature	-1	7	34	-0.161	0.873
Placement x Temperature	-51	14	34	-3.706	<0.001

*df adjusted to Satterthwaite approximation for degrees of freedom

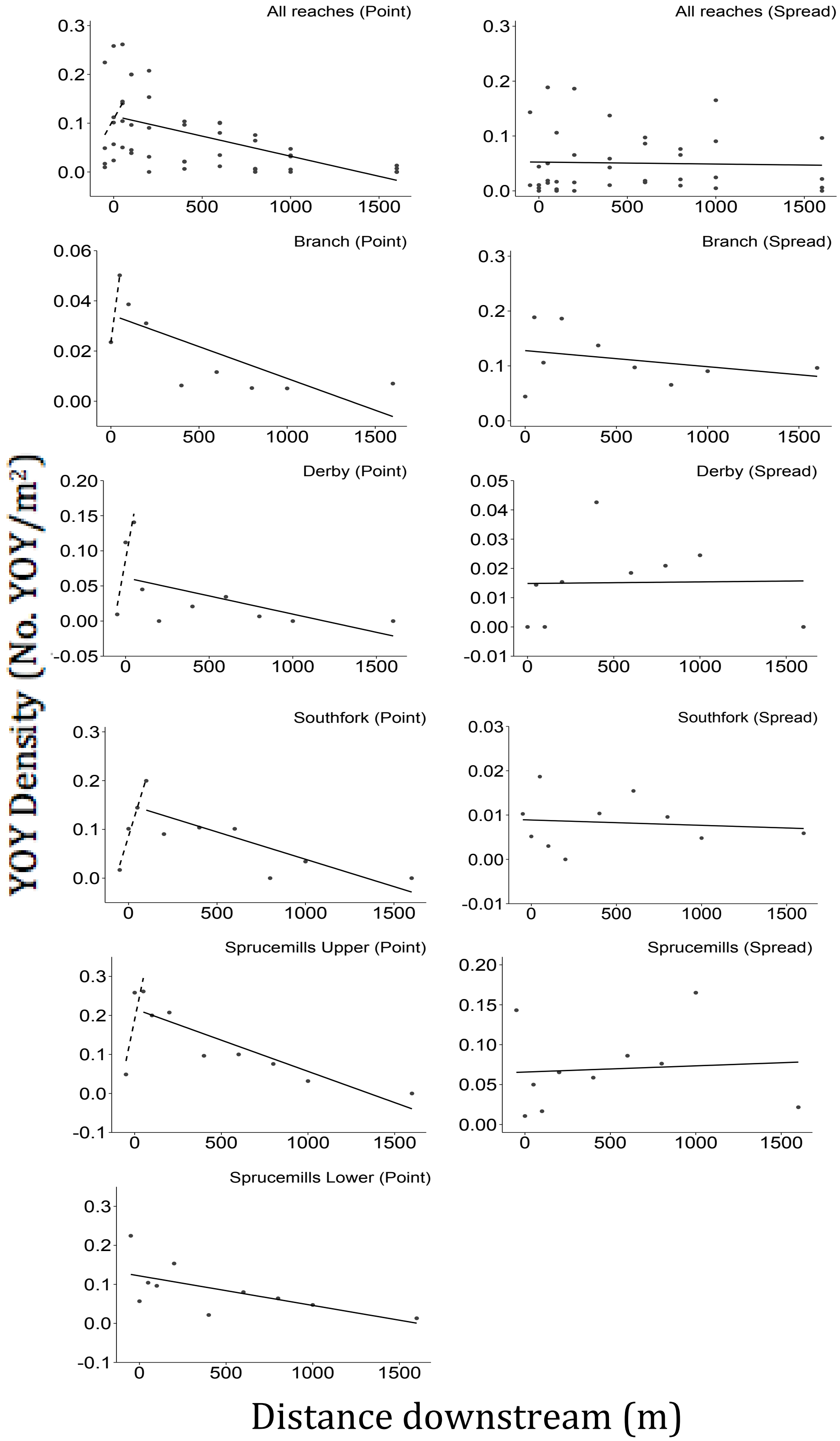
All reaches (Point)
All reaches (Spread)
Branch (Point)
Branch (Spread)
Derby (Point)
Derby (Spread)
Southfork (Point)
Southfork (Spread)
Sprucemills Upper (Point)
Sprucemills (Spread)
Sprucemills Lower (Point)
YOY Density (No. YOY/m²)
Distance downstream (m)

Figure 2. Linear regressions for YOY density relative to distance downstream. Regression analyses for point-stocking reaches are represented by two separate lines; for all sites upstream and including the site of the highest density (dashed) and all sites downstream and including the site of highest density (solid). Linear regressions for spread-stocking reaches are represented by a single line that includes all sites within a reach.

Table 3. Meta analysis and linear regression coefficients for density relative to distance across all (A) point- and (B) spread-stocking reaches. The effect size for the meta-analysis was Pearson's correlation coefficient.

River	n	Site of highest density	Slope±SE (*10^4)	r^2	P
A) Point-stocking reaches					
All reaches	40	50	-0.823±0.176	0.365	<0.0001
Branch	8	50	-0.254±0.092	0.559	0.033
Derby	8	50	-0.518±0.300	0.331	0.135
Southfork	7	100	-1.120±0.351	0.671	0.024
Sprucemills Upper	8	50	-1.600±0.281	0.844	0.001
Sprucemills Lower	10	-50	-0.757±0.326	0.403	0.049
Meta analysis	5			0.866	0.007
B) Spread-stocking reaches					
All reaches	38	NA	-0.036±0.180	0.001	0.843
Branch	9	NA	-0.293±0.335	0.098	0.410
Derby	9	NA	0.005±0.100	0.0004	0.958
Sprucemills	10	NA	0.078±0.341	0.006	0.825
Southfork	10	NA	-0.012±0.038	0.013	0.758
Meta analysis	4	NA		0.051	0.715

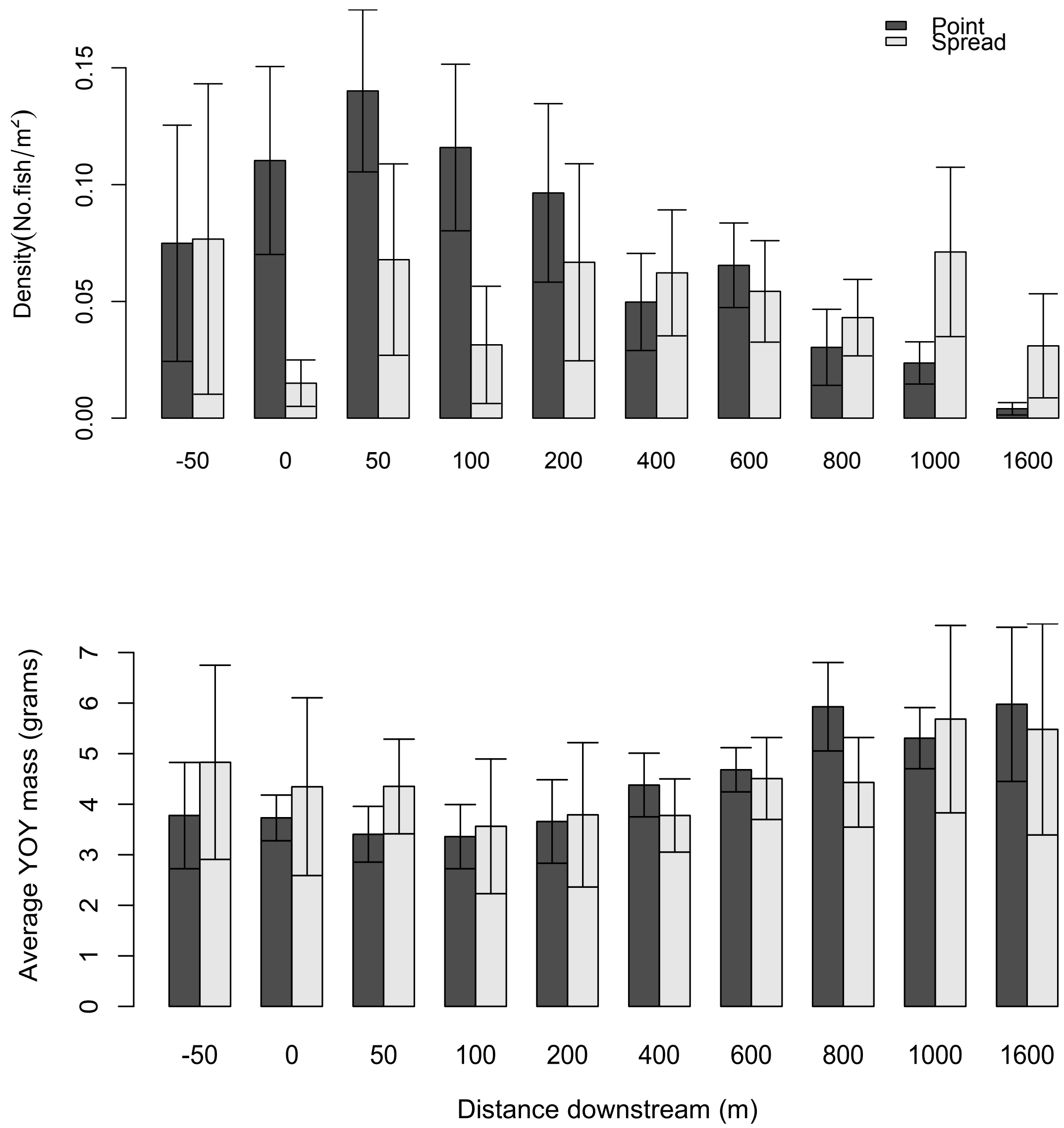

Figure 3. Mean±SE of density (top) and body mass (bottom) at all sampled sites, in relation to distance downstream and stocking technique.

Table 4. Results of mixed effects models for the dependent variable average YOY mass using (A) all stocking reaches, and separate analyses for (B) point- and (C) spread-stocking reaches.

Term	Estimate	SE	df	t	P
A) All stocking reaches (n=9)					
(Intercept)	30.48	8.710	13.90	3.500	0.004
Density	-5.159	2.385	66.98	-2.163	0.034
Distance	8.311e-04	2.999e-04	70.91	2.771	0.007
Placement	-39.89	10.4	68.28	-3.836	<0.001
pH	-3.339	1.164	14.04	-2.868	0.012
Placement x pH	5.037	1.386	68.43	3.635	<0.001
B) Point-stocking reaches (n=5)					
(Intercept)	5.162	2.896	28.37	1.783	0.085
Placement	-2.554	0.538	5.79	-4.748	0.003
Distance	0.019	0.005	36.60	4.301	<0.001
Density	-5.262	2.205	12.82	-2.386	0.033
Temp	-0.003	0.175	31.65	-0.014	0.989
Distance x Temperature	-0.001	2.8e-04	36.77	-4.069	<0.001

C) Spread-stocking reaches (n=4)					
(Intercept)	7.442	0.921	5.148	8.081	<0.001
Placement	-4.799	1.213	4.336	-3.955	0.014
Distance	0.001	3.883e-04	27.31	2.505	0.019
Density	-110.0	36.97	27.13	-2.975	0.006
Placement x Density	108.3	37.33	27.23	2.902	0.007

*df adjusted to Satterthwaite approximation for degrees of freedom

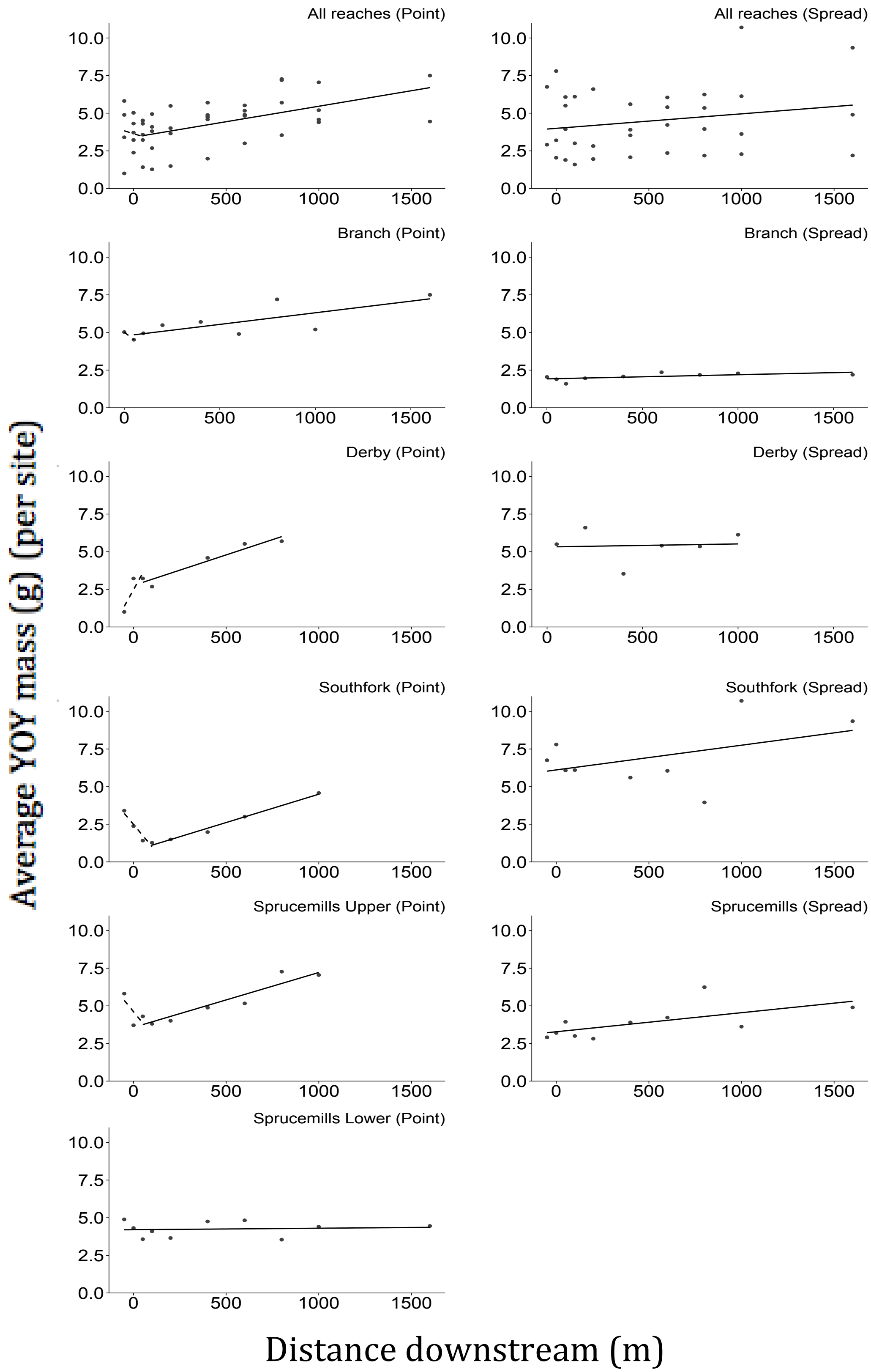
All reaches (Point)
All reaches (Spread)
Branch (Point)
Branch (Spread)
Derby (Point)
Derby (Spread)
Southfork (Point)
Southfork (Spread)
Sprucemills Upper (Point)
Sprucemills (Spread)
Sprucemills Lower (Point)
Average YOY mass (g) (per site)
Distance downstream (m)

Figure 4. Linear regressions for Average YOY mass (per site) relative to distance downstream. Regression analyses for point-stocking reaches are represented by two separate lines; for all sites upstream and including the site of the highest density (dashed) and all sites downstream and including the site of highest density (solid). Linear regressions for spread-stocking reaches are represented by a singular line that included all sites within a reach.

Table 5. Meta analysis and linear regression coefficients for average YOY mass (per site) relative to distance across all (A) point- and (B) spread-stocking reaches. The effect size for the meta-analysis was Pearson's correlation coefficient.

River	Site of highest density	N	Slope±SE (*10^3)	r^2	P
A) Point-stocking reaches					
All reaches	50	40	2.061±0.543	0.31	<0.001
Branch	50	7	1.543±0.565	0.554	0.019
Derby	50	7	4.054±0.664	0.926	0.009
Sprucemills lower	-50	10	0.099±0.340	0.01	0.779
Sprucemills upper	50	7	3.645±0.599	0.881	0.002
Southfork	100	6	3.765±0.256	0.986	<0.001
Meta-analysis		5		0.878	0.019
B) Spread-stocking reaches					
All reaches	NA	38	0.965±0.786	0.045	0.228
Branch	NA	9	0.278±0.128	0.399	0.068
Derby	NA	9	0.201±1.445	0.005	0.896
Sprucemills	NA	10	1.267±0.541	0.407	0.047
Southfork	NA	10	1.641±1.246	0.199	0.229
Meta-analysis	NA	4		0.664	0.186

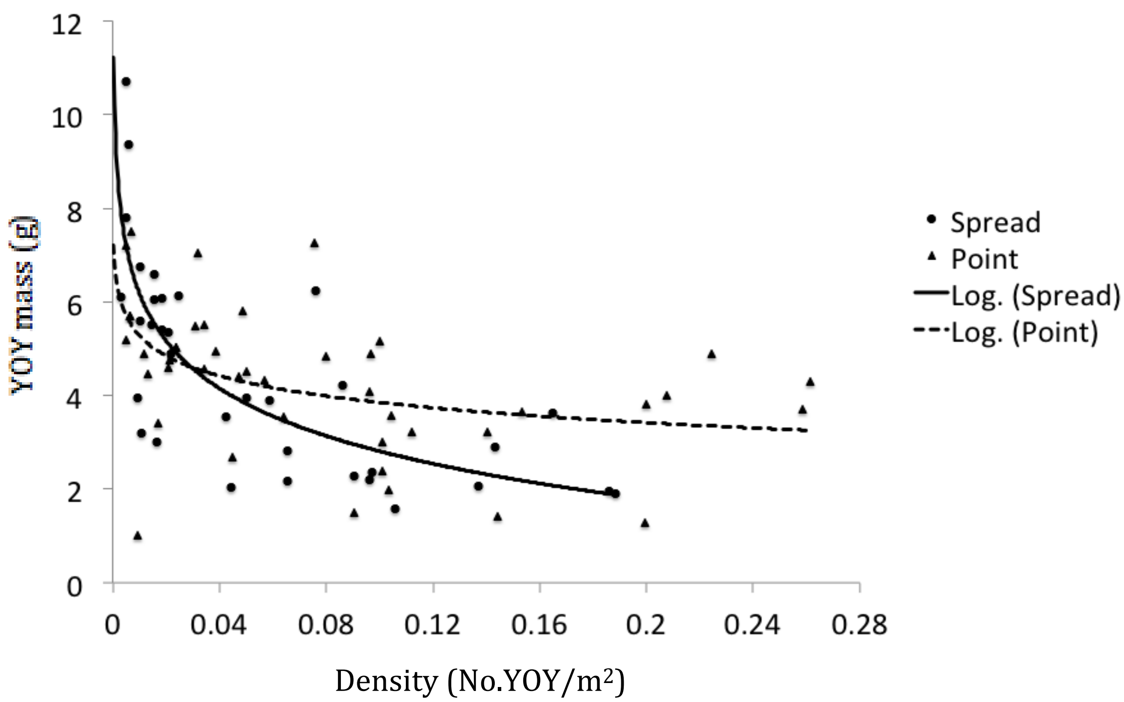

Figure 5. Average YOY mass (per site) and density relationship relative to stocking techniques. The power curves were estimated from linear regressions for $\log_{10}$ transformed density versus $\log_{10}$ transformed mass.

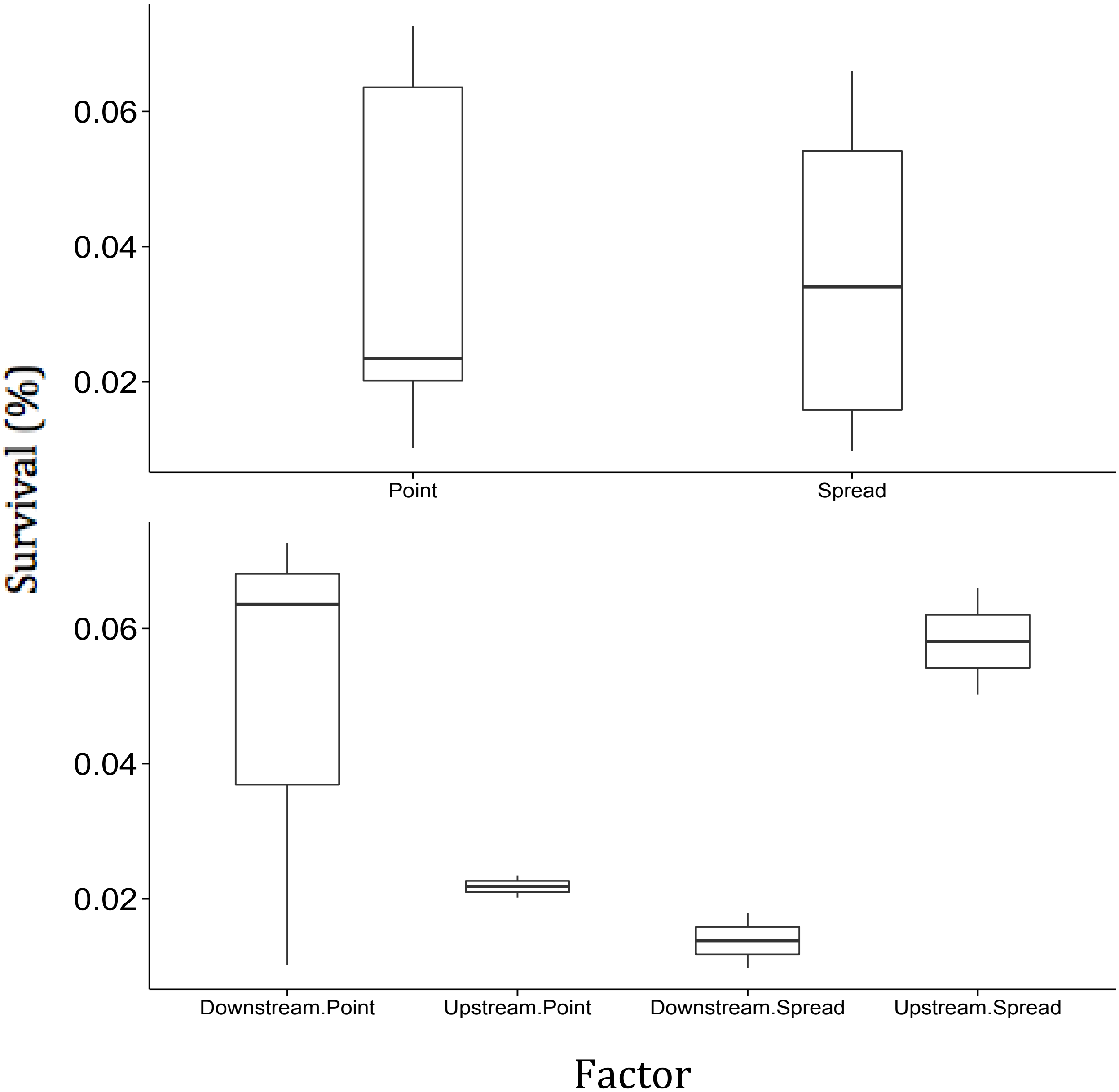

Figure 6. Boxplots for YOY survival between stocking techniques and the interaction of stocking techniques and placement.

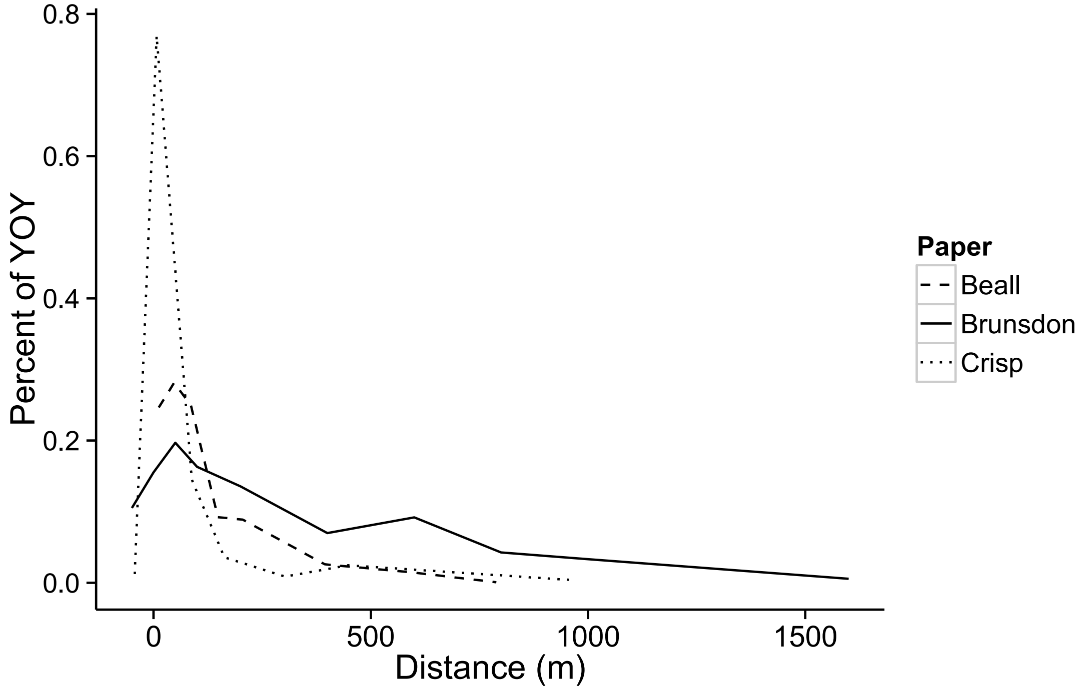

Figure 7. YOY abundance estimates versus distance downstream of point-stocking locations in my study compared to Beall et al. (1994) and Crisp (1995).