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**Dispersal and density-dependent growth of Atlantic salmon
(*Salmo salar*) juveniles: clumped versus dispersed stocking**

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2 ***salar*) juveniles: clumped versus dispersed stocking**

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Abstract

Dispersal from nesting sites and habitat selection are essential for the fitness of young individuals and shape the distribution, growth and persistence of populations. These processes are important to consider when releasing young, hatchery-origin fishes into the wild to restore extirpated or depleted populations. By manipulating the density of released young-of-the-year (YOY) Atlantic salmon, we evaluated the effects of clumped- (releasing all the fish at one location) and dispersed-stocking (releasing the fish evenly over a complete reach) treatments on juvenile habitat use, dispersal, growth and survival. Across 14 river reaches, clump-stocked YOY density decreased and growth rate increased with distance downstream, whereas dispersed-stocked YOY densities and growth were relatively constant. Overall, density, spatial variance in density, growth and survival did not differ between these two stocking treatments, likely due to the greater-than-expected mobility of fish in clumped-stocking reaches: YOY dispersed up to 1600-m, with 41% moving over 200-m downstream. As predicted from previous work, growth rate of individual fish was density-dependent, following a negative power curve. Our results provide insights into how the growth and survival of released individuals are altered via stocking treatments, ultimately shaping their distribution and growth rate.

Keywords: Dispersal, Density-dependent, Stocking, Restoration, Young-of-the-year, Juvenile, Atlantic salmon, *Salmo salar*, salmonid.

47 **Introduction**

48 Habitat selection is an important process at the level of individuals and populations
49 (Pulliam and Danielson 1991). Young fishes often have to disperse from high-density
50 reproductive or nesting sites to find unoccupied territories or to reduce the negative
51 effects of density-dependent growth and survival (Elliott 1994; Einum et al. 2011).
52 Density-dependent effects in the juvenile life stages of many stream-dwelling fish species
53 (Imre et al. 2005; Lobon-Cervia 2007; Utz and Hartman 2009) occur within a few weeks
54 after emergence (Elliott 1994; Nislow et al. 2000), often due to habitat limitation
55 (Kennedy et al. 2008). Density-dependent survival and growth can be described as a self-
56 thinning process, where smaller individuals will die or be displaced downstream (Grant
57 and Kramer 1990; Elliott 1993; Steingrímsson and Grant 1999) to less dense areas,
58 resulting in lower competition and faster growth (Einum et al. 2011).

59 Fish populations have been declining in many regions of the world, resulting in
60 numerous restoration and supplementation programs to boost population sizes, especially
61 for salmonids (Jonsson and Jonsson 2009). These programs commonly involve rearing
62 large numbers of juveniles in hatcheries before release (stocking) (Naish et al. 2007;
63 Gozlan et al. 2010) into stream habitats, chiefly as young-of-the-year (YOY) or age 1+
64 juveniles. For extirpated populations, stocking can be the only means to re-establishing a
65 population. Critical to the success of restoration programs is an understanding of the
66 ecology, behaviour and basic habitat requirements of the target population and how these
67 affect individual survival, density-dependence, and ultimately, population persistence and
68 growth (Molony et al. 2003; Lorenzen 2005; Young et al. 2005). Major factors affecting
69 survival of hatchery-origin YOY after stocking into the wild are the quality and quantity

of habitat available and the manner in which individuals are released (Wolf et al. 1998). Releasing fish over an entire reach will reduce the negative effects of density-dependence (McMenemy 1995), and 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 of hatchery-origin YOY salmon: ‘point’ and ‘spread’ stocking (Cowx 1994; hereafter clumped versus dispersed). Clumped-stockings releases all fish at the upstream end of a reach, whereas dispersed stockings releases fish evenly over the entire reach. Because of the limited dispersal abilities of young salmonids (Crisp 1995; Einum et al. 2008, 2011), clumped-stockings is thought to increase densities at the stocking location and the variance in density across the reach, both of which can lead to decreased average growth and survival. Hence, density will decrease and growth rate will increase with increasing distances downstream of the clumped stocking site. By contrast, dispersing 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, clumped-stockings 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 (Cowx 1994). More generally, the few studies that have critically investigated the success of salmonids after release into the wild focused mainly on density manipulations using egg planting instead of fry releases,

and/or only considered intraspecific density effects (Crisp 1995; McMenemy 1995; Einum et al. 2008, 2011).

Atlantic salmon, *Salmo salar*, are an ideal model species for the study of dispersal and density-dependent effects due to the fecundity of adults, which deposit thousands of eggs in redds. Emerging young-of-the-year (YOY) are highly territorial (Steingrímsson and Grant 2008), limited in dispersal ability (Crisp 1995; Einum et al. 2008), and susceptible to density-dependent growth, typically following a negative power curve (Imre et al. 2005). 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 (Elliott 1994).

In this study, we manipulated the density of hatchery-origin YOY Atlantic salmon in a landlocked population from Lake Champlain, by stocking known numbers of individuals into 14 separate reaches of the Boquet River, New York, USA, using either a clumped or dispersed treatment. We tested the general hypothesis that stocking treatment affects the density, growth and survival of YOY Atlantic salmon, while also accounting for other fish species and water temperature. We tested the following specific predictions: 1) spatial variation in density will be higher in clumped- than in dispersed-stocking reaches; 2) densities in clumped reaches will decrease with distance downstream, whereas densities in dispersed reaches will remain constant; 3) YOY growth rate, as estimated by mass at the end of the summer, will increase with distance downstream in clumped reaches, but not in dispersed reaches; 4) YOY mass will decrease as a negative power curve in relation to density; 5) YOY survival will be higher in dispersed reaches.

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/dolomite bedrock, surrounded by secondary hardwood growth (Wu and Kalma 2013), with stream gradients ranging from 0.5%, in the main stem, to 6.5% in adjacent tributaries. Topography ranges from fast, boulder-strewn riffles, to slower moving water with pebble substrates, to deep pools with sandy bottoms. 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 in the Boquet River and other tributaries (Marsden and 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

Adult hatchery salmon used for stocking in Lake Champlain originated from Lake Sebago, Maine, USA. A total of 174,000 unfed Sebago strain Atlantic salmon YOY from the New York Department of Environmental Conservation (NYDEC) Adirondack Hatchery, New York, USA, 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 clumped- or dispersed-stocking treatment with numbers ranging from 7,500-19,500 YOY per reach; the number stocked per reach was based on numbers released in past years by the NYDEC (Table 1). In clumped reaches, all YOY were placed in a 50-m² area at the upstream end of the reach (density: mean±SD= 235.7±95.5 YOY•m⁻², range= 150-390 YOY•m⁻²; Table 1). Conversely, in dispersed reaches, fish were distributed as evenly as possible over a 1000-m long reach (density: mean±SD= 1.85±0.81 YOY•m⁻², range= 1.16-3.37 YOY•m⁻²; Table 1). The North Branch reach received a hybrid stocking treatment wherein 1/3 of the fish were clump-stocked in three evenly spaced 50-m² areas, at densities of 60 YOY•m⁻², over a 1000-m reach; this stocking treatment is routinely used by the NYDEC. 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 (hereafter called placement).

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 (captive brood), whereas the latter were stocked as juveniles into a holding pond and recaptured at maturation (feral brood). Eggs from 661 females were used to generate the YOY in our study, 461 and 200 of which were captive and feral brood, respectively (fertilized by 219 and 37 males, respectively, for the two groups). Fertilized eggs were kept at the Adirondack Fish Hatchery and placed in 21 incubators of which 13 and 8 were reared on well and lake water, respectively, and treated regularly with formalin and iodine. 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 2014).

Sampling sites and electrofishing surveys

Throughout the summer of 2014 two electrofishing surveys were conducted. A preliminary electrofishing survey was conducted in all 14 stocking reaches and detected no YOY salmon in five stocking reaches, which were omitted from future sampling and excluded from the analyses: Black River, Roaring Brook, North Branch and both reaches in the main stem. The remaining nine stocking reaches were electrofished again (August 7-21) to determine end of summer YOY densities and mass.

In each of the remaining nine stocking reaches, we electrofished 10 different sites. The first site was 50-m upstream from the stocking reach, the second was at the upstream end of the stocking reach and the remaining eight were 50, 100, 200, 400, 600, 800, 1000 and 1600-m downstream of the upstream end of the stocking reach. Each site included a 25-m length of the river ($\text{mean} \pm \text{SD} = 130 \pm 62.5 \text{ m}^2$; range = 49.5-339.5 m^2).

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 relative rather than absolute variation in fish abundances (Einum et al. 2008). All fish caught were placed in a bucket containing stream water. Once the entire site was sampled, YOY caught were measured for fork length (mm) and mass (0.1 grams) and returned to their appropriate site. Other fish species caught during the survey were identified, counted and classified by approximate size.

A survival index was estimated from the mean density in the 10 sites and the total area of the reach 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. Because we did not sample the entire reach or estimate population size, we could not estimate absolute survival of the stocked fish. Rather, we calculated an index of survival based on our estimates of relative densities of fishes in each site within a reach.

Statistical analysis

To analyze differences in the density, mass and survival index of YOY between the two stocking treatments within each stream, paired t-tests were used with reach as a datum in the analyses. A paired design was used to control for potential differences in the physical characteristics between tributaries; each clumped and dispersed reach was paired within the same tributary. As Sprucemills contained two clumped-stock stocking reaches, the dispersed-stock stocking reach was paired twice, making for a total of five paired observations from nine stocking reaches, however, the real means and standard errors are reported.

Because YOY density, temperature, and trout density were taken on a per site basis, growth rate was analyzed using the average mass of all YOY salmon found within a site as a datum in the analyses. Mixed multiple regression models (MRMs) were used for the three dependent variables (density, mass and survival index) to determine the strength of relationships including other confounding effects. The units of observation for density were based on all 87 sites within the nine stocking reaches with recaptured YOY; three stocking reaches did not have a -50-m site due to culverts or dams. The units of

observation for YOY mass were based on 77 sites within the nine stocking reaches with recaptured YOY; in 10 sites no YOY were found; the unit of observation for YOY survival index was based on the nine stocking reaches. Fixed effects, described below, were based on *a priori* predictions and effects known to influence YOY density, mass and survival; random variables, were reach nested within tributary (ex.: Derby clumped reach nested within Derby) to ensure relationships were not influenced by differences in tributary and reach characteristics. However, in dispersed reach MRMs, reach could not be nested within tributary as both accounted for identical observations (Tributary Derby= Reach A, Tributary Branch= Reach B, Tributary Sprucemills= Reach C, Tributary Southfork= Reach D), and therefore, only tributary was used as a random variable. Survival MRM could not use reach as a random variable due to each reach representing a single survival observation and therefore tributary was the only random variable used.

Fixed effects for mass and density models, included stocking treatment, distance, placement, trout density, and the interaction terms stocking treatment $\times$ distance and stocking treatment $\times$ placement. Additionally, YOY density and temperature effects were included in the model selection for YOY mass, because both are known to affect growth rate (e.g. Elliott 1994). Because survival index was based on only nine river reaches, to avoid over-fitting the model, MRMs for survival index only included stocking treatment, placement, trout density and the number of YOY stocked as fixed effects.

Stocking treatment was included in all our models as it was the main factor being tested in our study. Distance was included to determine whether YOY that dispersed farther downstream were found at lower densities and exhibited an increase in growth; this was expected mainly for YOY that were clump-stocked. The stocking treatment $\times$

distance interaction term was included as we expected YOY densities and mass to differ with distance downstream between each stocking treatment.

To control for confounding effects that are known to influence YOY density, mass and survival, placement of stocking reach (upstream or downstream) and trout density were included as fixed effects in all MRMs, whereas water temperature was only included in YOY mass models. Namely, placement and its interaction with stocking treatment were included to account for stream widths increasing downstream and their relative effects on YOY density and mass; in dispersed-stocking sites, stocking density decreased with placement downstream as the stream widened. Brook trout density (all age classes, see below) was included to consider the effects of interspecific competition on YOY densities, mass and survival (Fausch 1998). Temperature was included in the MRMs for YOY mass, as YOY have different growth rates at varying temperatures (see Elliott and Hurley 1997).

To determine the main fixed effects influencing the dependent variables, model selection was performed. Full models were fitted using all fixed effects and both two-way interactions using the R software package “glmulti” (Calcagno and Mazancourt 2010), which uses software package “lme4” (Bates et al. 2015) during model comparisons. An exhaustive search of all possible models was performed and the best-fit model was selected based on the lowest critical AIC (Akaike information criterion) value (Akaike 1987). The best-fit models were then analyzed using the software package “lme4”.

All fitted MRMs were performed using t-tests with Satterthwaite approximation for degrees of freedom. To determine overall effects of stocking treatment and placement on density, mass and the survival index, 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

A total 575 YOY were sampled during electrofishing surveys. Analyses of final density, YOY mass and the survival index used data from the remaining nine stocking reaches in four tributaries (Southfork, Derby, Branch and Sprucemills). Other than Atlantic salmon, the three most abundant fish species sampled were brook trout (age class: YOY=216, age 1+=272, >age 1+=35), black-nosed dace (*Rhinichthys atratulus*: 160) and sculpins (genus *Cottus*: 35)

YOY Density

Prediction #1: Spatial variance

Contrary to the prediction, there were no detectable differences in spatial variation in density ($\text{YOY} \cdot \text{m}^{-2}$) between the two stocking treatments. Mean densities did not differ significantly (paired t-test: $t_4 = 0.523$, $p = 0.629$) between dispersed- (mean $\pm$ SE= 0.051 ± 0.025) and clumped-stockings (mean $\pm$ SE= 0.07 ± 0.019) reaches, but the power to detect differences was low (power=0.06). The coefficient of variation (CV) of density also did not differ significantly (paired t-test: $t_4 = 2.080$, $p = 0.106$) between dispersed- (CV $\pm$ SE= 0.7 ± 0.1) and clumped-stockings (CV $\pm$ SE= 0.904 ± 0.115) reaches, 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 we would have required 11-paired samples to detect a significant difference.

276

277 *Prediction #2: Density vs distance*

278 When all stocking reaches were included in the analysis, the expected interaction
279 between distance $\times$ stocking treatment was highly significant (Table 2A). Hence, we also
280 performed MRMs for clumped- and dispersed-stocking data separately.

281 For clumped-stocking reaches, density was significantly affected by distance from
282 the stocking site; as predicted, density decreased with distance (Table 2B). Linear
283 regressions began at the site where density was highest and included all other sites
284 downstream: density decreased significantly with distance in 4 out of 5 clumped-stocking
285 reaches (Figure 2, Table 3A). Mean density for clumped-stocking reaches was highest at
286 50-m downstream (0.140 fish/m^2) and had not reached 0 by 1600-m ($0.004 \text{ YOY} \cdot \text{m}^{-2}$)
287 (Figure 3A). In clumped-stocking reaches, the mean dispersal distance was 229m with
288 41%, 17%, and 4.2% dispersing farther than 200, 600 and 1000-m downstream,
289 respectively.

290 As predicted, distance had no effect on density in dispersed-stocking reaches
291 (Table 2B, Figure 2). Individual regressions also showed no significant change in density
292 with increasing distance downstream (Table 3B).

293

294 *Mixed multiple regression models*

295 When including reaches from both stocking treatments, the best-fit model showed that
296 distance and the stocking treatment $\times$ distance interaction term significantly affected
297 YOY density (Table 2A). Stocking treatment, placement, trout density and the stocking
298 treatment $\times$ placement interaction term had no influence on YOY density.

When MRMs were conducted on clumped-stocking reaches, distance was the only fixed effect to significantly effect YOY density (Table 2B). Placement and trout density were both excluded from the best-fit model and had no effect on YOY density.

When MRMs were conducted on dispersed-stocking YOY density, only placement was included as a fixed effect in the best-fit model (Table 2C). Densities in upstream reaches (mean $\pm$ SE= 0.09 $\pm$ 0.016 YOY $\cdot$ m⁻²) were higher than downstream reaches (mean $\pm$ SE= 0.012 $\pm$ 0.016 YOY $\cdot$ m⁻²), however, this relationship was not significant (Table 2C). As expected, distance had no effect on dispersed-stocking reach densities, and along with trout density, was not included within the best-fit model.

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

YOY mass

Prediction #3: YOY mass vs distance

As predicted, in clumped-stocking reaches, YOY mass (grams) increased with distance downstream (Table 4B, Figure 4). 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 the lower reach of Sprucemills (Table 5A). Contrary to the prediction, in dispersed-stocking reaches, the MRM showed that YOY

mass increased 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 (GLM: $t_{24}=1.766$, $p=0.09$). Furthermore, linear regressions including all sites for YOY mass in relation to distance also showed no significant change in dispersed-stocking reaches (Table 5B), suggesting an overall non-significant relationship.

To analyze differences in size variation of YOY, the CV of average YOY mass between clumped ($CV \pm SE = 0.3 \pm 0.071$) and dispersed reaches ($CV \pm SE = 0.219 \pm 0.04$) were compared (paired t-test: $t_4 = 0.972$, $p = 0.386$) and did not significantly differ. However, the power to detect differences was low (power=0.14).

Prediction #4: YOY mass vs Density

Overall, YOY mass decreased with increasing density (Table 4A) and was better fitted by a negative power curve than a linear model ($AIC_c > 10$). To analyze differences in the strength of density dependence between stocking treatments, we $\log_{10}$ transformed both density and YOY mass. The slopes differed significantly (analysis of covariance: interaction between stocking treatment x density ($F_{1, 74} = 7.455$, $p = 0.008$)); however, contrary to our prediction, the slope was steeper in dispersed-stocking (slope $\pm SE = -1.177 \pm 0.186$) than in clumped-stocking (slope $\pm SE = -0.429 \pm 0.184$) reaches (Figure 5).

Mixed multiple regression models

Overall, the MRM for both clumped- and dispersed-stocking reaches, showed the best-fit model included density, distance and placement as significant predictors of YOY mass.

The average mass of YOY stocked in upstream reaches of a tributary (mean $\pm$ SE= 3.185 $\pm$ 0.246g) was significantly smaller than in downstream reaches (mean $\pm$ SE= 5.31 $\pm$ 0.232g). Stocking treatment had no significant effect on YOY mass with dispersed-stocking reaches (mean $\pm$ SE= 4.476 $\pm$ 0.327g) being only slightly higher than clumped-stocking reaches (mean $\pm$ SE= 4.288 $\pm$ 0.315g); a paired t-test also found no significant difference (paired t-test: $t_4 = 0.154$, $p = 0.885$), however, the power to detect differences was low (power=0.03). Both interaction terms, trout density and temperature, were not included in the best-fit model. Because of our *a-priori* predictions we also investigated the data separately for clumped- and dispersed-stocking reaches.

When MRMs were conducted on clumped-stocking reaches, the best-fit model included density, distance and placement (Table 4B). However, distance and density were the only factors significantly affecting YOY mass. Although YOY were larger in downstream (mean $\pm$ SE= 4.958 $\pm$ 0.39g) than upstream reaches (mean $\pm$ SE= 3.166 $\pm$ 0.427g), this relationship was not significant. Trout density and temperature had no significant effect.

When MRMs were conducted on dispersed-stocking reaches, the best-fit model only included placement and distance as fixed effects, with the latter being significant (Table 4C). YOY were larger in downstream reaches (mean $\pm$ SE= 6.191 $\pm$ 0.862g) of a tributary than upstream (mean $\pm$ SE= 2.975 $\pm$ 0.848g), however this relationship was not significant (Table 4C). Density, temperature and trout density had no significant effect on average YOY mass.

366

367 ***Survival index***368 *Prediction #5: YOY survival index*

369 When MRMs were conducted on the survival index, stocking treatment, number of YOY
370 stocked, placement and trout densities were not included within the best fit model; the
371 null model was the best fit model. Due to small sample sizes (4, 5 in dispersed- and
372 clumped-stocking reaches, respectively) separate MRM analyses were not performed for
373 each clumped- and dispersed-stocking reaches. The survival index was 3.52% across all
374 reaches that retained fish, and did not differ significantly between stocking treatments
375 (paired t-test: $t_4 = 0.418$, $p = 0.698$; dispersed-stocking: $\text{mean} \pm \text{SE} = 3.6 \pm 1.3$; clumped-
376 stocking reaches: $\text{mean} \pm \text{SE} = 3.3 \pm 1.1$). However, the power to detect differences was low
377 (power=0.05).

378

379 **Discussion**

380 Our study illustrates how manipulating densities during the release of animals for
381 restoration purposes can alter the spatial distribution and growth rate of individuals in a
382 cohort. Using YOY Atlantic salmon as a model species, we found that clumped stocking
383 resulted in a decrease in density and an increase in mass with increasing distance from
384 the release point, whereas dispersed stocking maintained relatively even densities and
385 masses within the reach. However, overall YOY density, spatial variance in density, mass
386 and survival index did not differ between stocking treatments, most likely due to the
387 unexpected mobility of YOY in clumped-stocking reaches. Furthermore, density and
388 mass of released YOY were also influenced by distance from release points and

placement (upstream vs. downstream), depending on which stocking treatment was used. These results have important implications for restoration and supplementation programs involving large-scale releases of fishes.

Spatial variance, mass and dispersal

Densities in clumped-stock stocking reaches were solely correlated with distance, declining with distance downstream. Yet, this relationship was much more gradual than expected due to the mobility of YOY, which dispersed an average of 229m with a median of 100-m. 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 50-100-m downstream. Beall et al. (1994) found similar results where the highest densities were 90-150-m downstream. However, 41%, 25%, and 9% of fish dispersed farther than 200, 400 and 800-m, respectively, compared to only 29%, 9% and 0.4% in Beall et al. (1994) and even fewer in Crisp (1995) (Figure 6). Dispersal distance was also the best predictor of mass in clumped-stock stocking reaches: individuals that moved farther were larger at the end of the summer, presumably because of less intra-specific competition for food.

In dispersed-stock stocking reaches, there was relatively little change in YOY density and mass relative to distance. While dispersed-stock stocking reaches tended to have lower coefficients of variation in density than clumped-stock stocking reaches, there was still large variation in density. Even though YOY were stocked at low densities up to 1000-m 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 50-m upstream. In the lower Sprucemills

clumped-stocking reach, the highest density was 50-m 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). If smaller individuals did disperse further in our study, then they grew faster than those that remained in higher density areas close to the stocking origin.

Dispersal is thought to be largely influenced by increased competition at higher densities, but our results suggest that environmental factors may also play an important role. Dispersal can also be linked to water flow velocities (Ottaway and Clarke 1981); during early life stages, individuals are more susceptible to being displaced downstream by water flow (Heggenes and Traaen 1988) in high gradient streams. Although no significant relationships were found between mean dispersal distance and water flow velocity (GLM: $t_3 = -0.76$, $p = 0.503$) or gradients (GLM: $t_3 = -1.80$, $p = 0.171$) in clumped-stocking reaches, our stocking reaches had higher gradients (mean $\pm$ SD = 5.64 ± 4.61 ; range = 2.4-14.6%) compared to other studies (Crisp 1995; Einum et al. 2011). Furthermore, hatchery YOY had little experience in flowing water prior to release. These combined effects are a plausible explanation for the dispersal distances seen in our study; past studies have used reaches with lower gradients (Crisp 1995) and/or have used egg-planting where emerging YOY were more accustomed to lotic environments (Einum et al. 2011).

Although clump-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 our study, may explain why no difference in average YOY density, mass and size variation was observed between stocking treatments.

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 our streams ($<0.3 \text{ YOY} \cdot \text{m}^{-2}$), 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 (Culp and Scrimgeour 1993; Scrimgeour et al. 1994) thus increasing the effects of density-dependent growth.

Mixed multiple regression models

Trout density and temperature did not appear in any of the best-fit models for YOY density, mass and survival index. There may have been too little variation in temperature between sites (mean $\pm$ SD = $15.4 \pm 1.29^\circ\text{C}$; range = $12.85\text{--}18.35^\circ\text{C}$), to affect growth rates. Although trout densities varied substantially between sites (mean $\pm$ SD = $0.58 \pm 0.07/\text{m}^2$; range = $0\text{--}0.277/\text{m}^2$), niche partitioning may explain the lack of effect on YOY density, mass or survival index (Hearn and Kynard 1986).

Overall, YOY mass was higher in downstream reaches but densities did not significantly differ. Placement did not significantly affect YOY density or mass in clumped- or dispersed-stocking treatments. This was surprising, as we expected lower densities and higher YOY mass in downstream dispersed-stocking reaches. Perhaps, densities within dispersed-stocking reaches were already sufficiently low in both upstream and downstream reaches, that competition for space was negligible.

Survival index

Overall, the index of survival was relatively low (3.52%) compared to the 19% and 27% for clumped- and dispersed-stocking treatments, respectively, observed by Crisp (1995). However, actual survival estimates would likely be higher if we had used multiple-pass electrofishing (Einum et al. 2008) and sampled the entire stocking reach. We found that the survival index was unaffected by stocking treatment 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 dispersed treatment. Once again, our results are likely due to the mobility of the clump-stocked YOY reducing the density-dependent effects, however, our power to detect differences was low (power=0.05).

Restoration implications

We found no difference in YOY mass and survival index between stocking treatments that were expected to generate very different outcomes in post-release performance. Clump-stocked fish were able to disperse over large distances thus reducing the effects of

density-dependent growth/survival and the inherent benefit of dispersed-stocking fish at lower densities.

In the absence of detailed knowledge of reproductive and juvenile habitats, we suggest that an ideal method for stocking juvenile salmonids would be a combination of both clumped- and dispersed-stocking treatments. Stocking 2000-3000 fish at locations 400-m apart throughout a river will allow for a relatively even distribution of densities throughout the reach, with dispersal seeding the habitat in between each clumped-stocking. Furthermore, the stocking of 2000-3000 YOY at one location mimics the dispersal and competition that occurs in nature.

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637 Table 1. Tributary, stocking treatment, placement, number of YOY stocked, initial density (no•m⁻²) and reach characteristics in all 14
638 stocking reaches. Placement “NA” refers to a section of river where only one stocking sites was used. Dominant substrate and water
639 depths (cm) are based on measurements taken for the entire width of the river throughout the entire reach.

Tributary	Stocking treatment*	Placement	Number stocked	Initial density [†]	Dominant substrate‡	Water depth Mean±SD
Sprucemills	Dispersed	Upstream	10,500	2.04	Boulder	18.33±13.19
Sprucemills	Clumped	Downstream	10,500	210	Cobble	16.86±10.48
Sprucemills	Clumped	Downstream	7,500	150	Cobble	11.98±8.29
Derby	Dispersed	Downstream	7,500	1.58	Boulder	13±9.99
Derby	Clumped	Upstream	7,500	150	Boulder	20±12.69
Southfork	Dispersed	Downstream	15,000	1.28	Boulder	25.52±19.27
Southfork	Clumped	Upstream	15,000	300	Cobble	13.29±9.81
Branch	Dispersed	Upstream	15,000	3.37	Cobble	15.53±11.47
Branch	Clumped	Downstream	15,000	300	Cobble	20.01±12.6
Mainstem	Dispersed	Downstream	19,500	1.16	Cobble	19.63±13.26

Mainstem	Clumped	Upstream	19,500	390	Boulder	19.79±14.8
North branch	Hybrid	NA	9,000	60	Cobble	29.35±23.60
Roaring brook	Dispersed	NA	15,000	1.67	Boulder	18.18±11.66
Black river	Clumped	NA	7,500	150	Cobble	20.04±11.57

640 *Clumped means that the fry were released in a 50m² area at the upstream end of a 1000 m reach, whereas dispersed means
 641 the fry were evenly dispersed over the reach. Hybrid means fry were clump-stocked at three evenly spaced 50m² areas over
 642 the reach.

643 †Initial densities were calculated per 50m² stocking area for clumped and for the complete 1000m reach x the average stream
 644 width for dispersed. Initial densities for the hybrid stocking treatment are for each of the 50m² areas.

645 ‡Cobble = diameters between 6.4-25.6cm, whereas boulder = diameters above 25.6cm.

646 Table 2. Results of mixed multiple regression models for the dependent variable density using (A) all stocking reaches and separate
647 analyses for (B) clumped- and (C) dispersed-stocking reaches. Units for variables are density (No.YOY•m⁻²), distance (m), stocking
648 treatment (dispersed or clumped) and placement (upstream or downstream). The results shown are from the best-fit models determined
649 by AICc model selection. R² values are presented as both marginal (mR²) and conditional (cR²) values.

Term	Estimate (•10 ³)	SE (•10 ³)	df*	t	P
A) All reaches (n= 9, mR ² = 0.117, cR ² = 0.552)					
Intercept	104.1	21.23	7.28	4.9	0.002
Distance	-0.072	0.013	76	-5.532	<0.0001
Stocking treatment	-50.45	30.92	5.7	-1.632	0.157
Distance × Stocking treatment	0.068	0.02	76.01	3.408	0.001
B) Clumped-stocking reaches (n=5, mR ² = 0.247, cR ² = 0.508)					
Intercept	98.91	21.38	4.03	4.627	0.01
Distance	-0.072	0.015	43.02	-4.902	<0.0001

C) Dispersed-stocking reaches ($n=4$, $mR^2=0.249$, $cR^2=0.479$)

Intercept	0.0112	0.015	1.998	0.758	0.528
Placement	0.079	0.022	1.998	3.62	0.069

*df adjusted to Satterthwaite approximation for degrees of freedom

Draft

650 Table 3. Linear regression coefficients for density relative to distance across all (A) clumped- and (B) dispersed-stocking reaches.

River‡	n* (sites)	Site of highest density† (m)	Slope±SE (•10 ⁴)	r ²	P
A) Clumped-stocking reaches					
All reaches (A)	40	50	-0.823±0.176	0.365	<0.0001
Branch (C)	8	50	-0.254±0.092	0.559	0.033
Derby (E)	8	50	-0.518±0.300	0.331	0.135
Southfork (G)	7	100	-1.120±0.351	0.671	0.024
Sprucemills Upper (I)	8	50	-1.600±0.281	0.844	0.001
Sprucemills Lower (K)	10	-50	-0.757±0.326	0.403	0.049
B) Dispersed-stocking reaches					
All reaches (B)	38	NA	-0.036±0.180	0.001	0.843
Branch (D)	9	NA	-0.293±0.335	0.098	0.410
Derby (F)	9	NA	0.005±0.100	0.0004	0.958
Southfork (H)	10	NA	-0.012±0.038	0.013	0.758

Sprucemills (J)	10	NA	0.078±0.341	0.006	0.825
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651 *Sites for clumped-stocking reaches included the site of highest density and all sites downstream.

652 †For clumped-stocking reaches linear regression began at the site of highest density and included all sites downstream, whereas

653 dispersed-stocking reaches included all sites.

654 ‡Letters beside each river name correspond to panels in figure 2.

Draft

655 Table 4. Results of mixed multiple regression models for the dependent variable average YOY mass using (A) all stocking reaches,
656 and separate analyses for (B) clumped- and (C) dispersed-stocking reaches. Units for variables are YOY mass (grams), density
657 (No.YOY•m⁻²), distance (m) and placement (upstream or downstream). The results shown are from the best-fit model determined by
658 AICc model selection. R² values are presented as both marginal (mR²) and conditional (cR²) values.

Term	Estimate	SE	df*	t	P
A) All stocking reaches (n=9, mR ² = 0.545, cR ² = 0.694)					
(Intercept)	5.311	0.425	11.79	12.486	<0.001
Distance	0.001	2.8e-04	67.99	3.72	<0.001
Density	-5.993	2.401	72.13	-2.496	0.015
Placement	-2.199	0.551	6.96	-3.988	0.005
B) Clumped-stocking reaches (n=5, mR ² = 0.538, cR ² = 0.687)					
(Intercept)	4.925	0.531	7.47	9.28	<0.001
Distance	0.001	3.86e-04	37.08	2.991	0.005
Density	-5.516	2.673	38.59	-2.063	0.046

Placement	-1.767	0.655	3.15	-2.695	0.07
C) Dispersed-stocking reaches (n=4, $mR^2 = 0.515$, $cR^2 = 0.744$)					
(Intercept)	5.687	0.888	2.337	6.404	0.015
Distance	0.001	4.24e-04	29.027	2.376	0.024
Placement	-3.216	1.2095	2.012	-2.659	0.116

*df adjusted to Satterthwaite approximation for degrees of freedom

659 Table 5. Linear regression coefficients for average YOY mass (per site) relative to distance across all (A) clumped- and (B) dispersed-
660 stocking reaches.

River‡	n* (sites)	Site of highest density† (m)	Slope±SE (•10 ³)	r ²	P
A) Clumped-stockung reaches					
All reaches (A)	40	50	2.061±0.543	0.31	<0.001
Branch (C)	7	50	1.543±0.565	0.554	0.019
Derby (E)	7	50	4.054±0.664	0.926	0.009
Southfork (G)	6	100	3.765±0.256	0.986	<0.001
Sprucemills lower (I)	10	-50	0.099±0.340	0.01	0.779
Sprucemills upper (K)	7	50	3.645±0.599	0.881	0.002
B) Dispersed-stockung reaches					
All reaches (B)	38	NA	0.965±0.786	0.045	0.228
Branch (D)	9	NA	0.278±0.128	0.399	0.068
Derby (F)	9	NA	0.201±1.445	0.005	0.896

Southfork (H)	10	NA	1.641±1.246	0.199	0.229
Sprucemills (K)	10	NA	1.267±0.541	0.407	0.047

661 *Sites for clumped-stocking reaches included the site of highest density and all sites downstream.

662 †For clumped-stocking reaches linear regression began at the site of highest density and included all sites downstream, whereas
 663 dispersed-stocking reaches included all sites.

664 ‡Letters beside each river name correspond to panels in figure 4.

Draft

Figure 1. Location (Inset) and map of Boquet River, New York, USA, with all tributaries used for stocking YOY Atlantic salmon. Stars denote the location and stocking treatment of a reach.

Figure 2. Linear regressions for YOY density relative to distance downstream. Regression analyses for clumped-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 dispersed-stocking reaches are represented by a single line that includes all sites within a reach. Clumped-stocking reaches: A, C, E, G, I, K; Dispersed-stocking reaches: B, D, F, H, J.

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Figure 3. Mean±SE of density (A) and average mass (B) of YOY at all sampled sites, in relation to distance downstream and stocking treatment.

730 Figure 4. Linear regressions for average YOY mass (per site) relative to distance
731 downstream. Regression analyses for clumped-stocking reaches are represented by two
732 separate lines; for all sites upstream and including the site of the highest density (dashed)
733 and all sites downstream and including the site of highest density (solid). Linear
734 regressions for dispersed-stocking reaches are represented by a singular line that included
735 all sites within a reach. Clumped-stocking reaches: A, C, E, G, I, K; Dispersed-stocking
736 reaches: B, D, F, H, J.

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

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751 Figure 6. YOY abundance estimates versus distance downstream of clumped-stocking

752

locations in our study compared to Beall et al. (1994) and Crisp (1995).

Table S1. Top 10 mixed multiple regression models of YOY Density for all stocking reaches (A), clumped (B) and dispersed (C) reaches. Models were chosen based on lowest critical AIC scores (>2). Stock= stocking treatment, Trout= trout density.

Model	AICc	Weight
A)		
Stock + Distance + Stock:Distance	-256.7322	4.655471e-01
Placement + Stock + Distance + Stock:Distance	-255.3681	2.353648e-01
Stock + Distance + Trout + Stock:Distance	-254.5420	1.557269e-01
Placement + Stock + Distance + Trout + Stock:Distance	-253.1429	7.736600e-02
Distance	-249.8301	1.476323e-02
Placement + Stock + Distance + Stock:Placement	-248.9113	9.325635e-03
Placement + Stock + Distance + Stock:Placement + Stock:Distance	-248.9113	9.325635e-03
Placement + Distance	-248.3878	7.177908e-03
Stock + Distance	-247.9666	5.814600e-03
Distance + Trout	-247.8305	5.432169e-03
B)		
Distance	-132.1149	5.371020e-01
Distance + Trout	-130.5101	2.407616e-01
Placement + Distance	-129.6922	1.599435e-01
Placement + Distance + Trout	-127.7974	6.201896e-02
null model	-114.9505	1.006581e-04
Trout	-112.7334	3.322182e-05
Placement	-112.5936	3.097863e-05

Placement + Trout	-110.1317	9.046045e-06
C)		
Placement	-129.5816	0.491809037
Placement + Trout	-128.3538	0.266189204
Placement + Distance	-126.8721	0.126891720
Placement + Distance + Trout	-125.4130	0.061179763
null model	-124.1367	0.032318382
Trout	-121.7454	0.009776647
Distance	-121.6466	0.009305247
Distance + Trout	-119.0418	0.002530000

Table S2. Top 10 mixed multiple regression models of average YOY mass for all stocking reaches (A), clumped (B) and dispersed (C) reaches. Models were chosen based on lowest critical AIC scores (>2). Stock= stocking treatment, Trout= trout density, Temp= temperature, AvgWeight= Averag YOY mass.

Model	AICc	Weight
A)		
Placement + Distance + Density	251.6702	2.303741e-01
Stock + Placement + Distance + Density	253.7275	8.235739e-02
Placement + Distance + Density + Trout	254.0055	7.166740e-02
Placement + Distance + Density + Temp	254.1431	6.690283e-02
Stock + Placement + Distance + Density + Placement:Stock	255.0943	4.158061e-02
Stock + Placement + Distance + Density + Placement:Stock + Stock:Distance	255.0943	4.158061e-02
Placement + Distance	255.7687	2.967938e-02
Stock + Placement + Distance + Density + Trout + Temp + Placement:Stock + Stock:Distance	256.1821	2.413695e-02
Stock + Placement + Distance + Density + Trout + Temp + Placement:Stock	256.1821	2.413695e-02
Stock + Placement + Distance + Density + Trout + Temp	256.1821	2.413695e-02
B)		
Placement + Distance + Density	135.6083	2.542053e-01
Distance + Density + Temp	136.7330	1.448632e-01

Placement + Distance	137.3404	1.069214e-01
Distance + Temp	137.5985	9.397584e-02
Placement + Distance + Density + Temp	138.3699	6.390166e-02
Placement + Distance + Density + Trout	138.5098	5.958355e-02
Distance + Density	139.0323	4.588449e-02
Placement + Distance + Temp	139.6549	3.361130e-02
Distance + Density + Trout + Temp	139.7669	3.178116e-02
Placement + Distance + Trout	139.7874	3.145672e-02
C)		
Placement + Distance	128.5875	0.2821801586
Placement	130.8604	0.0905697671
Placement + Distance + Density	131.0998	0.0803495797
Placement + Temp	131.3709	0.0701637575
Placement + Distance + Trout 1	31.4608	0.0670805727
Distance	131.6485	0.0610729644
Placement + Distance + Temp	131.7513	0.0580108742
Placement + Density	132.7903	0.0345064155
Placement + Trout	133.1504	0.0288203044
Distance + Trout	133.6334	0.0226377214