

# Density-dependent growth of young-of-the-year Atlantic salmon *Salmo salar* in Catamaran Brook, New Brunswick

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## Summary

1. While density-dependent mortality and emigration have been widely reported in stream salmonid populations, density-dependent growth is less frequently detected. A recent study suggests that density-dependent growth in stream salmonids occurs at low densities, whereas density-dependent mortality and emigration occur at high densities.

2. To test the hypothesis that density-dependent growth occurs primarily at low rather than at high densities, we examined the relationship between average fork length and population density of young-of-the-year (YOY) Atlantic salmon at the end of the growing season using a 10-year data set collected on Catamaran Brook, New Brunswick. We tested whether (1) average body size decreases with increasing density; (2) the effect of density on average body size is greatest at low densities; (3) growth rate will decrease most rapidly at low effective densities [ $\Sigma(\text{fork length})^2$ ]; (4) density-dependent growth is weaker over space than over time; and (5) the strength of density-dependent growth increases with the size of the habitat unit (i.e. spatial scale) when compared within years, but not between years.

3. There was a strong negative relationship between the average body size and population density of YOY Atlantic salmon in the autumn, which was best described by a negative power curve. Similarly, a negative power curve provided the best fit to the relationship between average body size and effective density. Most of the variation in average body size was explained by YOY density, with year, location and the density of 1+ and 2+ salmon accounting for a minor proportion of the variation.

4. The strength of density-dependent growth did not differ significantly between comparisons over space vs. time. Consistent with the last prediction, the strength of density-dependent growth increased with increasing spatial scale in the within-year, but not in the between-year comparisons.

5. The effect of density on growth was strongest at low population densities, too low to expect interference competition. Stream salmonid populations may be regulated by two mechanisms: density-dependent growth via exploitative competition at low densities, perhaps mediated by predator-induced reductions in drift rate, and density-dependent mortality and emigration via interference competition at high densities.

*Key-words:* intraspecific competition, juvenile salmonids, population regulation, spatial scale, temporal scale.

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## Introduction

Density-dependent growth is a fundamental mechanism of population regulation, particularly in organisms with indeterminate growth (Sinclair 1989; Post, Parkinson & Johnston 1999). Slower growth of individuals at higher population densities typically increases age at

maturity, prolongs the period during which juveniles are susceptible to size-selective predators (Werner & Gilliam 1984; Post & Evans 1989) and leads to a smaller body mass at maturity and/or lower fecundity (Werner & Gilliam 1984; Wootton 1990). The primary cause of density-dependent growth is thought to be an increase in intraspecific competition at higher population densities (Sinclair 1989). Salmonid fishes are a particularly interesting model system for investigating density-dependent growth because different mechanisms of competition, either exploitation or interference (*sensu* Keddy 1989), are thought to act in different populations. In lentic populations, juvenile salmonids are typically non-aggressive, active foragers (Biro, Ridgway & Noakes 1997) who compete via exploitation. In contrast, juvenile salmonids in streams are typically territorial, sit-and-wait foragers who compete via interference (Keeley & Grant 1995).

While density-dependent mortality and emigration are widely described density-dependent population responses in stream-dwelling salmonids, density-dependent growth is less frequently reported (Grant & Kramer 1990). Most notably, the brown trout *Salmo trutta* L. population in Black Brows Beck shows no evidence of density-dependent growth, even though this population occurs at high densities and exhibits strong density-dependent mortality and emigration caused by territoriality (Elliott 1994). Jenkins *et al.*'s (1999) recent demonstration of density-dependent growth in *S. trutta* provides a potential explanation for the contrasting patterns of density-dependent growth and mortality observed by Elliott (1994). Surprisingly, density-dependent growth was strongest at low population densities (Jenkins *et al.* 1999), much lower than observed in Black Brows Beck (Elliott 1994). Hence, Elliott (1994) may have found no evidence of density-dependent growth because of a narrow range about a high mean population density.

Two mechanisms of population regulation may be at work in stream salmonid populations. At high population densities, space is limiting, so that density-dependent mortality and emigration may occur via interference competition (Grant & Kramer 1990; Elliott 1994). Density-dependent growth may occur at low densities via exploitative competition for stream drift, a continually renewing resource. For a continually renewing resource, increasing competitor density will have the greatest effect on the per capita foraging rate at low densities (Fretwell & Lucas 1970), perhaps explaining Jenkins *et al.*'s (1999) results.

Because of the allometry of consumption rate, the best metric of population density for testing the exploitation hypothesis is effective density ( $\Sigma[\text{length}]^2$ ; *sensu* Post *et al.* 1999). When growth rate is plotted against effective density, three outcomes are possible (see Fig. 1 in Post *et al.* 1999): (1) competition for space predicts growth rate will initially be high until space is limiting, after which growth rate will decrease with increasing effective density; (2) exploitation competition predicts a linear decrease in growth rate with

increasing effective density; (3) if the renewal rate of food decreases with increasing density, then growth rate will decrease most rapidly at low effective densities.

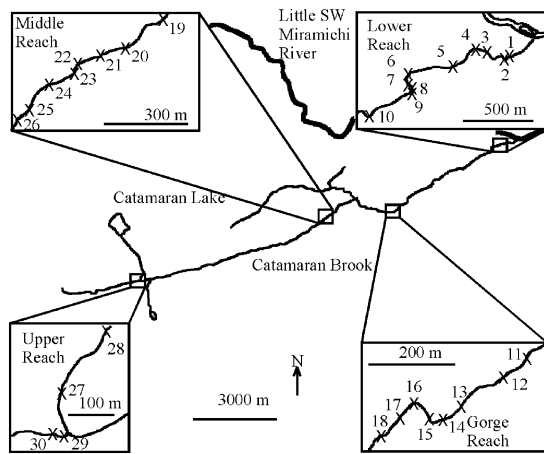
The ideal free distribution (*sensu* Fretwell & Lucas 1970) predicts that spatial scale will affect the intensity of density-dependent growth. At a small spatial scale, the movement of fish will equalize growth rates between patches differing in density and intrinsic quality (i.e. an ideal free distribution). Hence, at a given spatial scale, density-dependent growth will be weaker across space (i.e. patches within a year) than across time (i.e. within patches over years), because individuals can switch between patches in space but not between patches in time. However, as spatial scale increases, individuals will not be able to sample more distant patches, so that the intensity of density-dependent growth will increase when compared across space but not across time.

The purpose of our study was to investigate patterns of growth in young-of-the-year (YOY) Atlantic salmon, *Salmo salar* L., in Catamaran Brook, New Brunswick, to test the hypothesis that density-dependent growth occurs primarily at low rather than at high population densities. The Catamaran Brook data set is excellent for this analysis because 30 sites have been electrofished in the autumn for 10 consecutive years, allowing us to test for density-dependent growth in both space and time. Furthermore, the spatial and temporal variation in density is augmented by the presence of beaver (*Castor canadensis* Kuhl) dams in some years, above which densities are low or zero and below which densities are high. Specifically, we tested the following predictions: (1) the average body size of YOY *S. salar* decreases with increasing density; (2) the effect of density on average body size is greatest at low densities, resulting in a negative power curve; (3) growth rate will decrease most rapidly at low effective densities (Post *et al.* 1999); (4) density-dependent growth is weaker over space than over time; and (5) the strength of density-dependent growth increases with the size of the habitat unit (i.e. spatial scale) when comparing within years across habitat units, but not within habitat units across years.

## Materials and methods

### STUDY SITE AND SPECIES

The data used for this paper were collected during a multidisciplinary study in Catamaran Brook (46°52'7" N, 66°06'0" W), a third-order tributary of the Little South-west Miramichi River located in New Brunswick (Cunjak, Caissie & El-Jabi 1990). Atlantic salmon is the most common fish species in this relatively undisturbed stream, with YOY salmon being the most numerous of all age classes in any given year. The stream, its physical and chemical characteristics and its biota have been described in detail by Cunjak *et al.* (1990, 1993).



**Fig. 1.** Map of Catamaran Brook, showing the location of sampling sites and stream reaches (modified from Cunjak *et al.* 1993).

#### STUDY DESIGN

For our study, we used all four stream reaches (Upper, Middle, Gorge and Lower Reach) sampled during the multidisciplinary study, to cover a wide range of environmental conditions. The Upper Reach was located near the headwaters of Catamaran Brook, whereas the Lower Reach encompassed the lower 2 km of the brook (Cunjak *et al.* 1993) (Fig. 1). Replicates of four habitat types, flats, riffles, runs and pools, were selected within each reach (Fig. 1) for a total of 30 sites. None of the sites were located in the vicinity of beaver dams. Flats and pools are defined as slow-flowing ( $< 15 \text{ cm s}^{-1}$ ) habitats that are either shallow ( $< 46 \text{ cm}$ ) or deep ( $> 46 \text{ cm}$ ), respectively. Runs and riffles are fast-flowing ( $> 15 \text{ cm s}^{-1}$ ) habitats, with runs ( $> 23 \text{ cm}$ ) being deeper than riffles ( $< 23 \text{ cm}$ ) (Cunjak *et al.* 1993; Gibson *et al.* 1993). The characteristics of the habitat types and stream reaches are described in Cunjak *et al.* (1993).

#### DATA COLLECTION

Data were collected from late September to early December for 10 consecutive years (1991–2000). Stream sections (mean length =  $15.2 \text{ m}$ , range:  $9.3\text{--}32.6 \text{ m}$ ; mean area =  $110.1 \text{ m}^2$ , range:  $45\text{--}262 \text{ m}^2$ ) were blocked with barrier nets and electrofished three to five times to estimate population size using the removal method (Zippin 1958). Captured fish were identified to species and their fork length (to the nearest mm) and mass (to the nearest  $0.01 \text{ g}$ ) were measured. All fish were released back into the sections from which they were captured. For YOY Atlantic salmon the mass was measured for a subsample at each electrofishing site. Separate mass vs. fork length regressions were calculated for each site to estimate the individual mass of the unweighed YOY *S. salar*. The age of individual *S. salar* (three age groups:  $0+$ ,  $1+$ ,  $\geq 2+$ ) was estimated from length–frequency distributions based on all samples per season.

The wetted area of the electrofishing site at the time of the sample collection was used for calculating fish

density. We used the average fork length and mass of YOY *S. salar* at a site as an estimate of the seasonal growth of these fish. This approach is considered conservative in terms of detecting density-dependent growth, because the smallest individuals are expected to suffer disproportionately high mortality at higher population densities (Jenkins *et al.* 1999).

All the analyses were performed both with average fork length and average body mass of YOY *S. salar*. However, only the results for the average fork length are reported because (1) the results for body mass showed almost identical trends to those for fork length; (2) body mass was measured for only a subsample of the YOY *S. salar* (mass was estimated from mass vs. fork length regressions for the rest); and (3) the average body mass was considered less reliable as a predictor of summer growth. YOY *S. salar* show little, if any, growth in length after the end of August (Steingrímsson & Grant 1999; Girard 2002). However, fish could conceivably lose varying amounts of body mass, depending on the particular conditions between the date of cessation of growth and the date of sampling, which varied between late September and early December.

#### SPATIAL AND TEMPORAL SCALE

For the spatial analysis, sites sampled in a year were grouped into increasingly larger habitat units: sub-reach, reach and stream. Three to five neighbouring sites were grouped into a subreach (mean length =  $51.9 \text{ m}$ , range:  $24.1\text{--}83.8 \text{ m}$ ; mean area =  $375.1 \text{ m}^2$ , range:  $114.0\text{--}722.0 \text{ m}^2$ ), two subreaches formed a reach (mean length =  $105.4 \text{ m}$ , range:  $66.9\text{--}152.0 \text{ m}$ ; mean area =  $758.7 \text{ m}^2$ , range:  $243.0\text{--}1257.0 \text{ m}^2$ ), and all reaches were combined at the stream level analysis (mean length =  $246.5 \text{ m}$ , range:  $125.4\text{--}334.5 \text{ m}$ ; mean area =  $1783.6 \text{ m}^2$ , range:  $737.0\text{--}2348.0 \text{ m}^2$ ). The total area sampled varied among years, because not all sites were sampled every year and not all sampled sites had YOY *S. salar* as beaver dams precluded recruitment to stream sections in some years. For our analyses, we used only those sites where YOY *S. salar* were sampled. Data on *S. salar* density and average fork length were recalculated for all spatial scales above the site level. Mean fork length for a certain spatial scale was calculated by pooling all the fish from the sites grouped into that spatial scale. Similarly, the *S. salar* numbers and the area used for calculating the density at a spatial scale were obtained by pooling all the salmon (at a given life stage) and the area, respectively, of the sites integrated into that spatial scale. All response variables were analysed within years across habitat units at the site and subreach scale and within habitat units across years at four spatial scales: site, subreach, reach and stream.

#### DATA ANALYSIS

To determine whether YOY growth was density-dependent, we regressed average fork length vs. population

density using either ordinary least-squares regression or a negative power curve, estimated from a linear regression of  $\log_{10}$  fork length vs.  $\log_{10}$  density. To explore whether a straight line or a negative power curve was a better descriptor of the fork length–density relationship, we computed the Akaike information criterion (AIC, Motulsky & Christopoulos 2004) for each model. The model with the smallest AIC value was considered to offer a markedly better fit to the data if the difference  $AIC = (AIC_{\text{power}} - AIC_{\text{linear}})$  was  $\geq 2$ . Regressions with fewer than five habitat units or 5 years were not included in the analyses. To test among the three alternative outcomes predicted by Post *et al.* (1999), we used the same method, with effective density  $[\Sigma(\text{fork length})^2]$  as the independent variable.

Analyses of covariance (ANCOVA) were used to investigate the effect of YOY *S. salar* density (covariate), older *S. salar* density (covariate), year (independent variable) and sampling site (independent variable) on average fork length. In order to linearize the relationship between *S. salar* density and average fork length, the data for the ANCOVAs were  $\log_{10}$  transformed.

The critical level of significance was 0.05. The assumption of normality was assessed by checking the residuals in the case of regressions and by performing Kolmogorov–Smirnov tests (with Lilliefors probabilities) for the analyses of covariance. The homogeneity of variances assumption was tested with the Levene's test. STATISTICA 5.0 (StatSoft Inc. 1995) was used to perform all statistical tests.

## Results

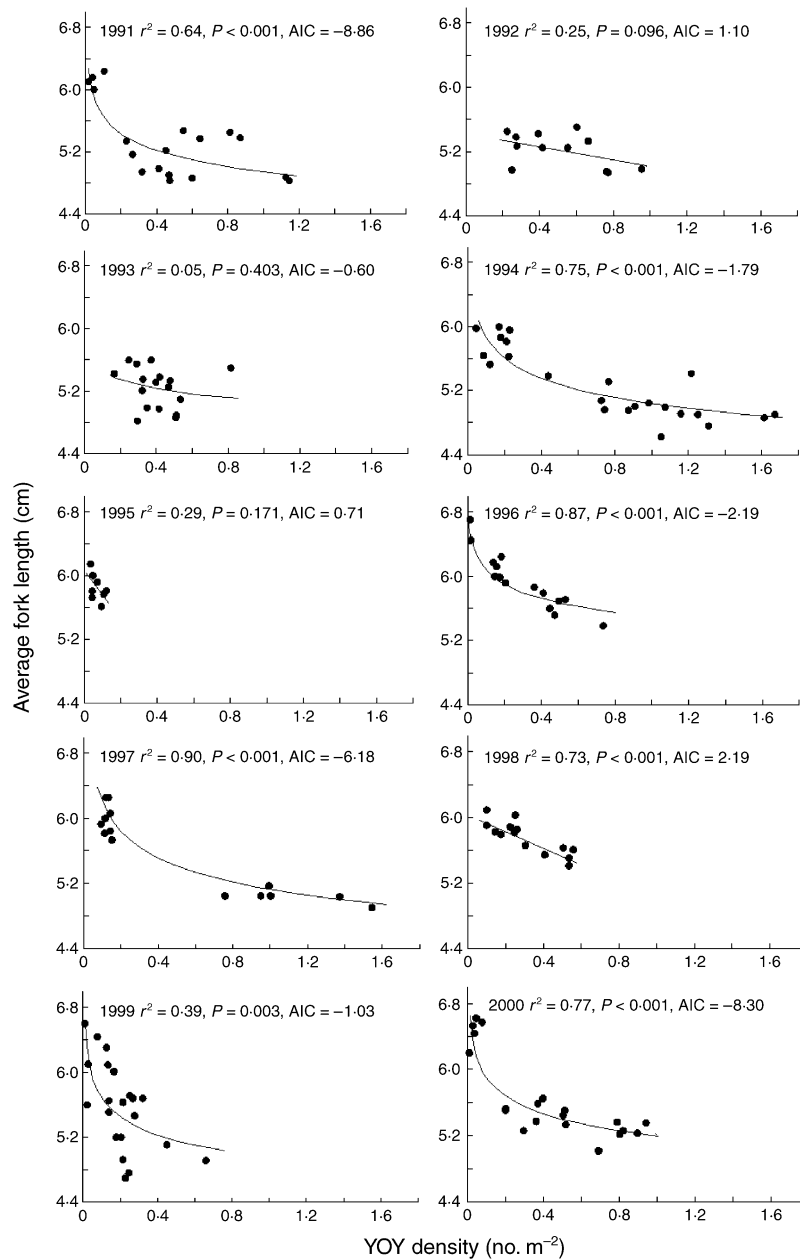
Within years across sites, the average fork length of YOY *S. salar* decreased with increasing YOY *S. salar* density in all 10 years. This relationship was significant in 7 of the 10 years; density explained 39–90% of the variation in average fork length (Fig. 2). The lack of a significant relationship in 3 of the 10 years was caused most probably by a small sample size and a narrow range in population density in 1995, and a narrow range in density in 1992 and 1993. Similarly, a negative relationship was evident in all 20 sites when data were analysed within sites across years (Fig. 3), with YOY fork length showing a significant decline with increasing density in 13 of 20 sites. Overall, YOY *S. salar* density accounted for 4–98% of the variation in YOY fork length. There were noticeable differences between reaches in the strength of the fork length–population density relationship: six of eight, one of six and six of six sites exhibited significant relationships in the Lower, Gorge and Middle Reaches, respectively. In summary, our analyses at the site level, whether in space or time, were consistent with the first prediction of density-dependent growth of YOY salmon.

At the subreach level, both the within-year-across-subreaches and the within-subreach-across-years analyses provided similar results to the site-level analyses. The average fork length of YOY *S. salar* was negatively related to the density of YOY *S. salar* in all cases, the relationship being significant in 5 of 6 years ( $r^2 = 0.40$ – $0.98$ , Table 1a),

**Table 1.** Regressions of average fork length (cm) vs. density ( $\text{no. m}^{-2}$ ) of young-of-the-year Atlantic salmon in Catamaran Brook, New Brunswick, analysed (a) within years across subreaches, (b) within subreaches across years, (c) within reaches across years and (d) within stream across years. Linear means that the Akaike information criterion (AIC) was smaller than the AIC for the negative power curve and vice-versa for the negative power curve. One model was considered to offer a markedly better fit to the data than the other if the difference in AIC values,  $AIC = (AIC_{\text{power}} - AIC_{\text{linear}})$  was  $\geq 2$

Year or subreach	Range in density ( $\text{no. m}^{-2}$ )	<i>n</i>	Model	$AIC_{\text{power}} - AIC_{\text{linear}}$	Intercept	Slope or exponent	$r^2$	<i>P</i>
(a) Within-years-across-subreaches								
1991	0.04–0.86	6	Power	–2.50	4.944	–0.072	0.83	0.014
1993	0.35–0.45	5	Linear*	0.03	6.819	–4.068	0.40	0.252
1994	0.11–1.32	6	Power	–7.12	4.974	–0.081	0.97	< 0.001
1996	0.01–0.53	6	Power	–2.93	5.487	–0.045	0.95	< 0.001
1999	0.07–0.40	6	Power	–2.31	4.303	–0.145	0.79	0.024
2000	0.03–0.71	6	Power	–11.95	5.110	–0.072	0.98	< 0.001
(b) Within-subreaches-across-years								
Gorge 1	0.05–1.01	7	Linear*	0.07	5.775	–0.727	0.46	0.095
Gorge 2	0.09–1.24	8	Power*	–0.53	5.065	–0.033	0.18	0.318
Lower 1	0.13–1.06	9	Power	–4.73	4.776	–0.115	0.88	< 0.001
Lower 2	0.07–1.32	9	Power	–3.42	5.021	–0.073	0.72	0.004
Middle 1	0.04–0.45	7	Power	–4.10	5.079	–0.069	0.94	< 0.001
Middle 2	0.03–0.70	7	Power	–9.51	5.204	–0.060	0.94	< 0.001
(c) Within-reaches-across-years								
Gorge	0.07–1.08	8	Power*	–1.05	5.08	–0.041	0.28	0.152
Lower	0.13–1.20	10	Power	–2.78	4.906	–0.086	0.80	< 0.001
Middle	0.04–0.58	7	Power	–16.34	5.095	–0.072	0.98	< 0.001
(d) Within-stream-across-years								
Stream	0.07–0.79	10	Linear	2.71	5.856	–1.235	0.75	0.001

\*The fit provided by the two models is not markedly different; the model with the lower AIC value is indicated.

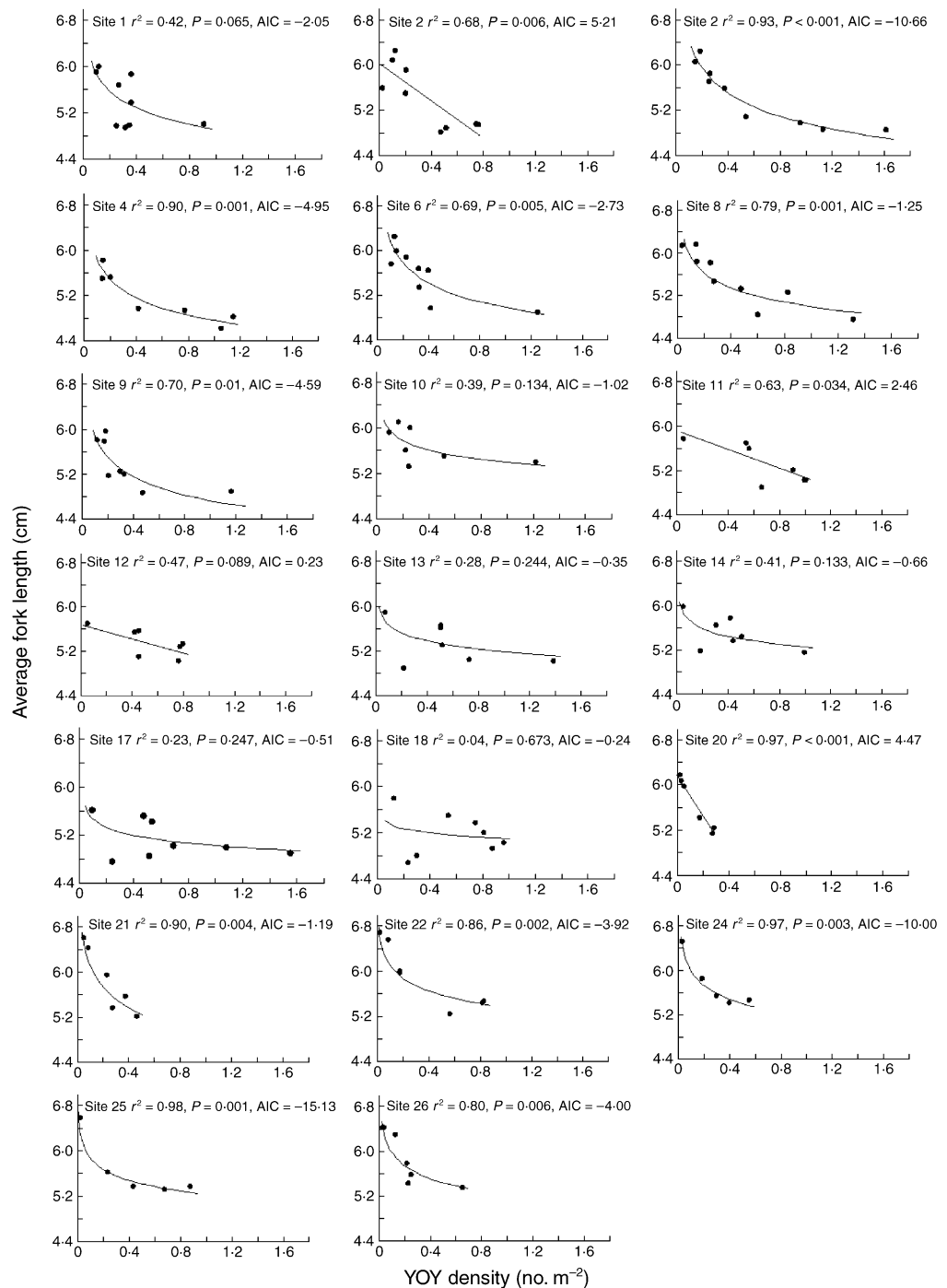


**Fig. 2.** Average fork length relative to density of YOY Atlantic salmon across sites within years during the 1991–2000 autumn sampling in Catamaran Brook, New Brunswick. Linear fit means that the Akaike information criterion was smaller than the AIC for the negative power curve and vice-versa for the negative power curve. One model was considered to offer a markedly better fit to the data than the other if the difference in the AIC values  $AIC = (AIC_{power} - AIC_{linear})$  was  $\geq 2$ .

and four of six subreaches ( $r^2 = 0.18$ – $0.94$ , Table 1b), respectively. Consistent with the site-level analysis, the fork length–population density relationship was not significant in 1993 and in the two subreaches of the Gorge Reach. The data at the reach and stream level within years could not be analysed due to the small sample size. The results of the within-reach-across-years (Table 1c) and within-stream-across-years (Table 1d) analyses, respectively, were consistent with the findings at the smaller spatial scales. Average fork length of YOY *S. salar* declined significantly with increasing YOY *S. salar* density in the Lower and Middle Reach ( $r^2 = 0.80$ – $0.98$ ), but not in the Gorge Reach ( $r^2 = 0.28$ ). At the

stream level, YOY *S. salar* density explained 75% of the variation in the average fork length of the YOY *S. salar*. In summary, our analyses at spatial scales larger than the site were also consistent with the first prediction.

The ANCOVA analyses within years across sites (Table 2a) and within sites across years (Table 2b) revealed that most of the variation in the average fork length of YOY *S. salar* was related to YOY *S. salar* density. Average fork length of YOY *S. salar* also differed significantly between years (Table 2a) and between sites (Table 2b). The density of older *S. salar* had a negative, relatively weak effect on the growth of YOY salmon in the within-site analysis.



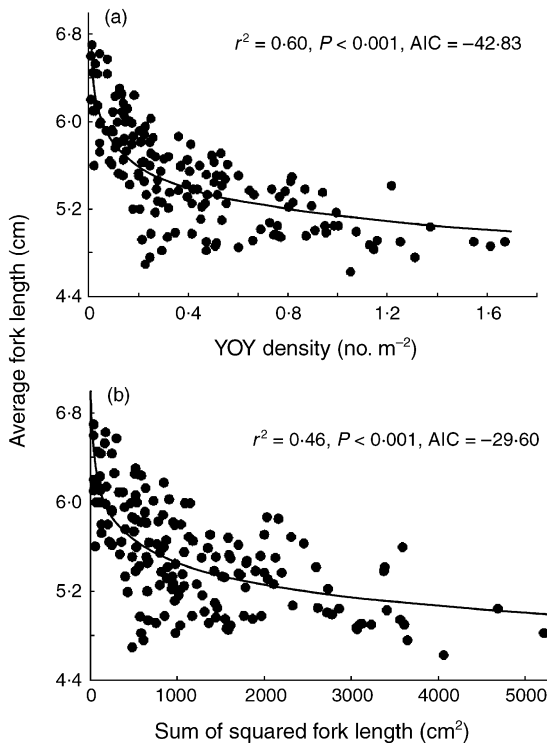
**Fig. 3.** Average fork length relative to density of YOY Atlantic salmon in sites across years during the 1991–2000 autumn sampling in Catamaran Brook, New Brunswick. Linear fit means that the Akaike Information criterion was smaller than the AIC for the negative power curve and vice-versa for the negative power curve. One model was considered to offer a markedly better fit to the data than the other if the difference in the AIC values  $AIC = (AIC_{\text{power}} - AIC_{\text{linear}})$  was  $\geq 2$ .

To test the second prediction, that the effect of population density on growth rate is strongest at low densities, we compared the shape of the 46 regressions done at all spatial scales, for both the within-year-across-habitat-units and the within-habitat-unit-across-years analyses. In 17 of 46 cases we were not able to distinguish between the fit provided by linear regressions and negative power curves ( $AIC_{\text{power}} - AIC_{\text{linear}} < 2$ ). In most of these cases (14 of 17), however, the relationship between average fork length and density of YOY

Atlantic salmon was not significant. In 24 of the remaining 29 cases ( $AIC_{\text{power}} - AIC_{\text{linear}} \geq 2$ ) negative power curves provided a markedly better fit to the average fork length–density data than linear regressions (sign test,  $P < 0.01$ ), while in five of 29 cases the opposite was true. When all sites, regardless of reach or year, were analysed together, YOY salmon density alone explained 60% of the variation in the fork length of YOY salmon (Fig. 4a). Furthermore, the negative power curve model provided a much better fit than the

**Table 2.** Analysis of covariance of the effects of YOY Atlantic salmon  $\log_{10}$  density (no.  $m^{-2}$ ), older Atlantic salmon  $\log_{10}$  density (no.  $m^2$ ) and (a) year (within years across sites) and (b) site (within sites across years), on the  $\log_{10}$  average fork length (cm) of YOY Atlantic salmon at the end of the growing season sampled from Catamaran Brook, New Brunswick, 1991–2000

Source of variation	SS	F	d.f.	P
(a) Within years across sites (overall $r^2 = 0.71$ )				
Year	0.027	7.12	9, 148	< 0.0001
YOY Atlantic salmon density	0.085	205.60	1, 148	< 0.0001
Older Atlantic salmon density	0.001	2.26	1, 148	0.135
(b) Within sites across years (overall $r^2 = 0.69$ )				
Site	0.022	2.32	19, 124	0.003
YOY Atlantic salmon density	0.069	138.56	1, 124	< 0.0001
Older Atlantic salmon density	0.002	4.31	1, 124	0.040

**Fig. 4.** Average fork length relative to density (a) and sum of squared fork length (b) of YOY Atlantic salmon in all sites during the autumn sampling for 1991–2000 in Catamaran Brook, New Brunswick.

linear model ( $AIC_{\text{power}} - AIC_{\text{linear}} = -42.83$ ). Hence, these data are consistent with the second prediction.

To test among the three alternatives proposed by Post *et al.* (1999), we plotted the average fork length data in Fig. 4a vs. effective density (Fig. 4b). A negative power curve explained 46% of the variation in fork length and provided a markedly better fit than a linear relationship. Hence, these data are not consistent with either the space competition or the simple exploitation hypotheses.

To assess whether the strength of density-dependent growth was different over space than over time, the coefficients of determination from the within-year-across-habitat-units and the within-habitat-unit-across-years analyses were compared with *t*-tests. The strength of

density-dependent growth did not differ significantly between comparisons over space (within-year-across-habitat-units analysis) vs. over time (within-habitat-unit-across-years analysis) at the site (*t*-test,  $t = -0.75$ , d.f. = 28,  $P = 0.459$ ,  $n_1 = 10$ ,  $n_2 = 20$ ) or subreach (*t*-test,  $t = 0.54$ , d.f. = 9,  $P = 0.602$ ,  $n_1 = 5$ ,  $n_2 = 6$ ) scale.

To evaluate the effect of spatial scale on the strength of density-dependent growth in the within-year-across-habitat-units analyses, the coefficients of determination from the within-year-across-habitat-units analyses at the site and subreach level were correlated against the corresponding  $\log_{10}$  average surface area of the sites and subreaches. Similarly, to explore whether spatial scale affected the strength of density-dependent growth in the within-habitat-unit-across-years analyses, the coefficients of determination from the within-habitat-unit-across-years analyses for all four spatial scales (site, subreach, reach and stream) were correlated against the corresponding  $\log_{10}$  average surface area of the habitat units at each spatial level. As predicted, the strength of the density-dependent growth increased significantly with increasing habitat unit surface area in the within-year-across-habitat-units (site and subreach,  $r = 0.53$ ,  $P = 0.036$ ,  $n = 16$ ) analyses, but not in the within-habitat-unit-across-years (all four spatial scales,  $r = 0.11$ ,  $P = 0.546$ ,  $n = 30$ ) analyses.

## Discussion

Our study provided strong evidence of density-dependent growth in YOY *S. salar*. Young-of-the-year population density alone explained 60% of the variation in the average fork length of YOY *S. salar* in the combined 10-year data set. The patterns of growth observed in our study were equally strong within years over sites as within sites over time, perhaps because the sampling was well replicated in both dimensions. The effects of year and site were significant, but weak, on average, in comparison with the effect of YOY population density. In contrast, Jenkins *et al.* (1999) found substantial year effects, and consequently no density-dependent growth was detected when data were analysed within sections across years. The presence of older age classes had a weak, negative effect on growth of YOY, as noted in

previous studies (e.g. Egglshaw & Shackley 1980; Kennedy & Strange 1986; Crisp 1993).

Because of the observational nature of our data set we cannot rule out other explanations for density-dependent growth, such as water temperature. For example, the Middle Reach tends to have low densities of fast-growing YOY *S. salar*, consistent with density-dependent growth. However, the Middle Reach also has the lowest maximum summer water temperatures (Edwards 2001), conditions that promote optimal growth of *S. salar*. While we cannot rule out the potential effects of other factors, water temperature does not explain the equally strong pattern of density-dependent growth within sites over years.

Our data are consistent with Jenkins *et al.*'s (1999) hypothesis that body size follows a negative power curve in relation to density. Jenkins *et al.* (1999) suggested that density-dependent growth is stronger at low densities (typically  $< 1 \text{ fish m}^{-2}$ ) and becomes increasingly weaker at high trout densities, as observed in the Black Brows Beck (Elliott 1994). The decrease in average fork length in our combined data set was steepest at densities less than approximately  $0.3 \text{ salmon m}^{-2}$  (Fig. 4a). Several other studies also suggest a curvilinear relationship between average body size or growth rate and density (e.g. Hartman & Scrivener 1990; Crisp 1993; Newman 1993), implying that this may be a general phenomenon for stream-dwelling salmonids.

Post *et al.* (1999) developed simple predictions about the nature of density-dependent growth using effective density ( $\Sigma L^2$ ) as a metric of population density. Of the three possible outcomes (see Introduction), our data did not support the space-as-a-limiting-resource, and the simple-exploitative-competition scenarios. Our results were consistent with the negative power curve, which could be caused by a rapid decrease in prey renewal rates with increasing predator abundance at low effective densities (see Post *et al.* 1999). Compared to numeric density ( $r^2 = 60\%$ ), effective density ( $r^2 = 46\%$ ) explained less of the variation in average fork length.

The negative power curve between average body size and density in our study and in other studies of stream-dwelling salmonids (Crisp 1993; Newman 1993; Jenkins *et al.* 1999) suggests that juvenile stream-dwelling salmonids are regulated by two very different mechanisms: density-dependent growth at low population densities, and density-dependent mortality and emigration at high population densities (Elliott 1994; Cunjak & Therrien 1998). Based on the interference competition model, the occurrence of density-dependent growth at densities  $< 1 \text{ salmon m}^{-2}$  is surprising, because space limitation is thought to occur at much higher densities (Grant & Kramer 1990). For example, at a population density of  $0.3 \text{ salmon m}^{-2}$ , a  $5.5 \text{ cm } S. salar$  would have  $3.33 \text{ m}^2$  of available space, 7.4 times more than the average territory size ( $0.45 \text{ m}^2$ ) for an individual of that body size (Keeley & Grant 1995). At this population density, the territories of YOY *S. salar* would occupy only  $\sim 13.6\%$  of the available stream bottom (PHS,

Grant & Kramer 1990), about half the  $27.2\%$  value above which density-dependent population responses were considered to be likely (Grant & Kramer 1990).

Our findings suggest that density-dependent growth may occur via exploitative competition at much lower densities than for space-related interference competition. In the case of exploitative competition for a renewing food source, such as stream drift, the per capita foraging rate will decrease as  $1/n$  ( $n =$  number of competitors, Kramer, Rangeley & Chapman 1997), i.e. a negative power curve. In addition, the abundance of drift may be reduced (Jenkins *et al.* 1999), as stream invertebrates hide in interstitial crevices in response to the foraging activities of predators (e.g. Culp & Scrimgeour 1993; Scrimgeour, Culp & Cash 1994). These mechanisms are not mutually exclusive; we suspect that the latter mechanism exacerbates the intensity of exploitative competition, resulting in density-dependent growth at densities substantially lower than those at which space related competition is expected.

We have no satisfactory explanation for the lack of density-dependent growth in the Gorge Reach. In most years, a series of beaver dams between the Gorge & Middle Reaches (1991–1997) restricted or prevented spawning in the Middle and Upper Reaches. The concentration of spawning adults below the dams in the Gorge Reach may have resulted in high initial fish densities and density-dependent mortality and emigration. Strong density-dependent loss from these sites might have obscured any effects of density-dependent growth.

Contrary to our expectation, the strength of density-dependent growth did not differ significantly between comparisons over space (within-year-across-habitat-units analysis) vs. over time (within-habitat-unit-across-years analysis) at the site or subreach scale. As predicted, the strength of density-dependent growth increased with increasing spatial scale in the within-year but not in the between-year comparisons. In a within-year comparison, Jenkins *et al.* (1999) reported strong density-dependent growth at the section scale ( $230\text{--}670 \text{ m}^2$  and  $930\text{--}1260 \text{ m}^2$ ) but not at the smaller segment scale ( $12\text{--}90 \text{ m}^2$ ). The difference between the results of the two studies may be related to differences in the mobility of the two species. YOY *S. salar* are relatively sedentary, with the majority of the individuals typically moving only a few meters over the entire summer (Steingrímsson & Grant 2003), whereas 43% of the recaptured juvenile *S. trutta* moved  $20\text{--}550 \text{ m}$  in Jenkins *et al.*'s (1999) study. Due to the sedentary nature of YOY *S. salar*, small-scale heterogeneity in density and growth rate will persist over time (see Grant *et al.* 1998). Hence, YOY *S. salar* will only probably conform to ideal free distribution at a local scale (i.e.  $1\text{--}10 \text{ m}^2$ ; see Girard 2002), whereas the more mobile *S. trutta* may be able to achieve ideal free distribution at a larger spatial scale.

Stream-dwelling salmonids are an interesting model system for exploring compensatory population responses. Profitable areas for future research include the extent that density-dependent growth regulates



stream salmonid populations, the relationship between mobility of fish and the spatial scale at which density-dependent growth occurs and the densities at which interference and exploitative competition affect growth, mortality and emigration.

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