Letter

Density-dependent growth of young-of-the-year Atlantic salmon (*Salmo salar*) revisited


Abstract – The length of individual young-of-the-year (YOY) Atlantic salmon (*Salmo salar*) in Catamaran Brook decreases with increasing population density following a negative power curve. Because most of this decrease in growth rate occurs at low densities (<1 fish m⁻²), Imre et al. (2005; Journal of Animal Ecology, 74: 508–516) suggested that exploitation competition for drifting prey rather than space limitation might be responsible for this pattern. Recently, Ward et al. (2007; Journal of Animal Ecology, 76: 135–138) showed that the negative power curve of growth rate versus density can be caused by other mechanisms and suggested that Imre et al.’s evidence for density-dependent growth would have been stronger if we had analysed final size versus initial density rather than final density. We examined (i) whether the negative power curve of size versus density was also apparent in an analysis of final size versus initial density and tested two predictions that emerge from Ward et al.’s model, (ii) the variance in body size increases with population density, and (iii) the maximum fish size at a site is density-independent. The final size of YOY salmon decreased with increasing initial density following a negative power curve. Our data did not provide strong support for the above predictions emerging from Ward et al.’s model. Our analyses of different years, sites and seasons were consistent with the hypothesis of density-dependent growth of YOY salmon.

Introduction

Imre et al. (2005) analysed a long-term data set of average fork length versus population density of young-of-the-year (YOY) Atlantic salmon *Salmo salar* L. at the end of the growing season (i.e., autumn size vs. autumn density) in Catamaran Brook, New Brunswick. Their data for Catamaran Brook (Imre et al. 2005) supported the hypothesis of a negative power curve between average growth rate and density. These results were surprising because density-dependent mortality and emigration occur most prominently at high densities, presumably due to space limitation caused by the territorial behaviour of juveniles (Grant & Kramer 1990; Elliott 1994). The contrasting patterns in population responses led us to suggest that density-dependent growth at low densities may occur by exploitation competition for stream drift rather than via space limitation (Imre et al. 2005).

Using a simple site-quality model based on Newman (1993), Ward et al. (2007) showed that the negative power curve of growth versus density can be caused by mechanisms other than pure exploitation competition (*sensu* Keddy 1989). Their model assumes that (i) fish growth is related to the intrinsic quality of a foraging site, (ii) fish are ideal (*sensu* Fretwell & Lucas 1970) and settle at the highest quality sites first, and (iii) subsequent individuals are prevented from settling in occupied sites via aggressive behaviour. In addition, their model implies that the intrinsic quality of a site is not affected by competitors – i.e., is density-independent (also see Newman 1993). Two strong predictions emerge from their model, in addition to density-dependent growth:

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the variance in growth rate will increase with population density, and the maximum observed growth rate of fish in a population will be density-independent (Newman 1993).

Recognising the need for caution when inferring cause and effect from analyses of observational data, we acknowledged that density-dependent growth may not be the only explanation for the negative power curve of autumn size versus autumn density observed at Catamaran Brook (Imre et al. 2005). Indeed, Ward et al. (2007) suggested, and we concur, that our case would have been stronger if we had analysed final size (in autumn) versus initial density of YOY salmon (measured in summer). We now have included population density and size data early in the growing season (i.e., July), which were not utilised for our previous analyses.

The purpose of this study is to re-examine the patterns of density-dependent growth in YOY Atlantic salmon in Catamaran Brook in light of the constructive comments and model proposed by Ward et al. (2007). First, we examine the generality of our previous analysis by testing whether the apparent density-dependent growth observed in the autumn size versus autumn density data is equally strong in analyses of autumn size versus summer density, and of summer size versus summer density. Second, we test two predictions of Ward et al.’s (2007) site-quality model: the variance in size or growth rate increases with density, and the maximum observed growth rate or size of fish at each site is density-independent. These new analyses provide a richer understanding of the patterns of density-dependent growth in Catamaran Brook and suggestions for future research.

Materials and methods

The study site, methods and data used for this study are identical to those described in Imre et al. (2005), except as noted below. Population censuses were conducted twice per year for 10 consecutive years (1991–2000). Imre et al. (2005) described and analysed data collected from late September to early December each year, hereafter called the autumn sample. In this study, we have included data collected during electrofishing surveys conducted from early July to mid-August each year, hereafter called the summer sample. The methods used for the summer census were identical to those used in the autumn census (Imre et al. 2005).

The average median sampling date and the average range of dates for the summer sample in 1991–2000 were July 15 (±SD = 1.5 days) and 18 (±2.6) days, respectively. In Catamaran Brook, YOY salmon emerge from the gravel at a median date of June 16, at a fork length of 2.63 cm and a mass of 0.19 g (Randall 1982). Because growth ceases for the season in early September (Randall 1982; Girard et al. 2004), the summer electrofishing samples captured YOY salmon after approximately 4 weeks of growth out of a 12-week growing season. On average (±SD), YOY salmon in the summer sample were 3.78 cm (±0.32 cm, N = 10 years) and 0.56 g (±0.14 g, N = 10), which represents approximately 39% (+9.7%, N = 10) of the seasonal increase in length and 23% (±7.9%, N = 10) of the seasonal increase in mass. The summer sampling is timed to allow YOY salmon to disperse from redds and to grow sufficiently for a reliable estimate of early population density via electrofishing (Cunjak et al. 1993).

Data analysis

The coefficient of variation (CV = SD/mean) is the typical measure for quantifying variation in body size. In our data, however, the CV of fork length decreased strongly with mean body length (r = −0.47, P < 0.00001, N = 157). Because CV was confounded with the mean in our data set, we did not use it as our primary measure of size variability. While the SD typically increases with the mean, the SD of fork length decreased slightly with increasing mean fork length in our data (r = −0.17, P = 0.025, N = 157). Because the SD of fork length was less biased than the CV of fork length, we used the SD of autumn fork length to quantify size variation in relation to population density; however, for transparency, we also reported the patterns of the CV of fork length in relation to density.

To investigate whether the maximum observed growth rate of individuals was affected by population density, we examined the relationship between maximum autumn fork length and initial summer density using regression analysis. Similar analyses were also conducted for the smallest fish at each site. To explore whether a straight line or a negative power curve was a better descriptor of the mean, maximum and minimum autumn fork length versus summer density relationship (Imre et al. 2005), respectively, we computed the Akaike Information Criterion (AIC, Motulsky & Christopoulos 2004) for each model using all data pooled together. The model with the smallest AIC value was considered to offer a markedly better fit to the data if the difference AIC = AIC_{power} – AIC_{linear} was >2. Regressions with fewer than five sites or 5 years were not included in the analyses. All analyses were performed both across sites within years and across years within sites.

We investigated whether there was evidence for density-dependent growth in the summer using regression analysis between summer average YOY fork length and summer YOY density. Juvenile salmon
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The average autumn fork length of YOY salmon decreased with increasing summer density in all 10 years – i.e., an analysis of within years across sites (Sign test, \( P < 0.002; \) data not shown). This relationship was significant in seven of the 10 years, with summer density explaining 10–79% of the variation in average autumn fork length. Data analyses within sites across years revealed a similar negative relationship evident in all 18 sites (Sign test, \( P < 0.0001; \) data not shown); YOY average autumn fork length showed a significant decline with increasing summer density in 16 out of 18 sites (\( R^2 = 0.13–0.99 \)). Overall, with all data pooled, YOY salmon summer density accounted for 56% of the variation in YOY autumn fork length (Fig. 1a), similar to the relationship between autumn density and autumn fork length shown previously (Imre et al. 2005). In addition, there was evidence of density-dependent growth in the summer data set; summer fork length decreased with increasing summer YOY density (partial \( R = -0.39, P < 0.0001 \)) and increased with sampling date (partial \( R = 0.49, P < 0.0001 \)). Summer YOY density and sampling date explained 32% of the variance in summer fork length (\( R^2 = 0.32, P < 0.0001, N = 179 \)). A negative power curve provided a markedly better fit than a straight line to the average autumn fork length – YOY summer density data pooled from all sites (\( \text{AIC}_{\text{power}} - \text{AIC}_{\text{linear}} = -10.9; \) Fig. 1a). In summary, our analyses were consistent with the hypothesis of density-dependent growth of YOY salmon.

To test the prediction that size variation increases with increasing population density, we examined the relationship between SD of autumn fork length and YOY summer density using regression analysis. The SD of autumn fork length increased with increasing summer density in 5 out of 10 years (Sign Test, \( P = 0.33 \)) and was significant (all positive) in only four sites (data not shown). When data from all sites were pooled, there was no significant relationship between the SD of autumn fork length and YOY summer density (Fig. 1b, \( R^2 = 0.01, P = 0.162, N = 143 \)). There was a significant, but weakly positive relationship between the CV of autumn fork length and YOY summer density (\( R^2 = 0.09, P < 0.001, N = 143 \)).

Maximum fork length decreased with increasing summer density in all 10 years (Sign test, \( P < 0.002 \); the relationship was significant in 5 out of 10 years (data not shown). Similarly, maximum autumn fork length declined with increasing summer density in 15 out of 17 sites (Sign test, \( P = 0.0024 \), but the relationship was significant at only one site (data not shown). When all sites were analysed together, YOY summer density explained 17% of the variation in maximum observed autumn fork length (Fig. 2). The AIC calculations based on all data pooled revealed that a straight line was a markedly better fit to the data than
Within years across sites, minimum autumn fork length decreased with increasing YOY summer density in 8 out of 10 years (Sign Test, $P = 0.11$; $R^2 = 5–66\%$), with the relationship being significant in 6 out of 10 years (data not shown). Within sites across years, there was a negative relationship between minimum autumn fork length and YOY summer density at all 17 sites (Sign Test, $P < 0.0001$; $R^2 = 14–96\%$), with the relationship being significant in 12 out of 17 sites. Overall, with all data pooled together, YOY summer density accounted for 45\% of the variation in minimum autumn fork length (Fig. 2). A negative power curve provided a markedly better fit than a line to the minimum autumn fork length – YOY summer density data pooled from all sites ($AIC_{power} - AIC_{linear} = 19.3$; Fig. 2).

**Discussion**

The hypothesis of density-dependent growth described in our previous analysis of autumn fork length versus autumn density (Imre et al. 2005) was supported by our analysis of autumn fork length versus summer density, and of summer fork length versus summer density. Moreover, the negative power curve of size versus density was also observed in the current analysis. Hence, the occurrence of density-dependent growth and the shape of the size versus density curve seem to be robust over years, sites, and seasons of analysis. Because of the observational nature of our data, we acknowledge that explanations other than density-dependent growth are possible for the very robust patterns of size-at-age versus density observed in Catamaran Brook.

Contrary to the prediction of the site-quality model, there was no compelling evidence of a marked increase in the variance in body size with increasing population density. When all the data were pooled, summer population density explained only 1\% of the variation in the SD of body length and 9\% of the variation in the CV of body length, compared to 56\% of the variation in mean autumn body length. These modest increases in the variability were even less striking given that both the SD and CV of body length decreased significantly with body length and hence were strongly biased in favour of Ward et al.’s prediction.

An increase in some measure of size or growth rate variation with increasing density occurs in some stream salmonid populations (Newman 1993; Jenkins et al. 1999; Keeley 2001 – confined populations; Einum et al. 2006). Caution is needed, however, when inferring competitive mechanisms from patterns in data (see Ward et al. 2007) because an increase in size or growth variation with deteriorating environmental conditions, including an increase in population density, is a common observation across a variety of taxa that probably differ in mode of competition (Łomnicki 1988). Furthermore, no significant relationship between size or growth variation and density has been observed in other salmonid populations (Fraser 1969; Gee et al. 1978; Harvey & Nakamoto 1996; Keeley 2001 – unconfined populations). In contrast, Elliott’s (1994) study exhibited a decrease in size variation with increasing density.

Also contrary to the prediction of the site-quality model, the size of the largest fish at each site decreased with increasing density. This result is particularly powerful because the null hypothesis of density-independent growth predicts an increase in maximum size (and minimum size) with density due to an increase in extreme values with an increasing sample size (Sokal & Rohlf 1995). This sample-size effect probably explains why density accounted for less variation in the maximum size of fish at a site compared to the mean and minimum size of fish at each site. The literature also provides mixed results regarding the effect of density on maximum size or growth rate at a site. The data of Newman (1993) and Jenkins et al. (1999) provide the strongest support for the prediction; even in Jenkins et al.’s (1999) data, however, the maximum size of YOY brown trout decreased in only two of three analyses, one of which was significant (see their Fig. 7). In other studies, maximum body size either decreased with increasing density (Keeley 2001), or decreased, but not significantly (Harvey & Nakamoto 1996). Furthermore, the sample-size effect discussed above will tend to weaken any relationship of maximum size versus density compared to the mean or minimum size.
Hence, authors need to be cautious when concluding that the growth rate of larger individuals is less affected by competitors than smaller individuals, or use measures that are unaffected by sample size, such as the 90th and 10th percentile of the size distribution. Using some percentile of the frequency distribution of body sizes will not correspond to the same foraging site quality across different densities. For example, the 90th percentile will be the best site, the 10th best site and the 40th best site when there are 10, 100 and 400 fish in a site, respectively. Hence, using percentiles solves the sample-size issue but does not allow for testing the site-quality model. However, we agree with Ward et al. (2007) and earlier authors (Lomnicki 1988; Newman 1993; Jenkins et al. 1999), who called for studies of both the mean and variance in size distributions within populations.

In summary, a reanalysis of data for Catamaran Brook continued to support the hypothesis of density-dependent growth and did not provide strong support for the site-quality model. We hypothesise that the site-quality model may be more applicable to older salmon parr or trout in streams, where several age-classes compete for the same habitat and the size variation among competitors is high. Salmonid societies seem to shift from territorial mosaics early after emergence, when YOY densities are high and variation in body size and overlap between age-classes are low (e.g., Elliott 1994), to dominance hierarchies of larger, overlapping home ranges as fish get older and larger (Jenkins 1969; Höjesjö et al. 2007). Larger salmonids typically abandon shallow, fast-flowing habitats, which produce much of the stream drift (Mundie 1974), and take up residence in deeper, slower-flowing pools (Nakano 1995; Bremslet & Berg 1997; but see Gibson et al. 2008). In this scenario, the largest fish will occupy the best site in a pool, which will typically be upstream, deep and central (Nakano 1995). The quality of the best foraging sites may indeed be density-independent, because the closest upstream competitor will be separated by at least the length of one riffle-pool sequence. Future research should compare the frequency distributions of the intrinsic quality of foraging sites in populations that seem to support the site-quality model (Newman 1993; Einum et al. 2006) to those that do not (e.g., this study).

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References


