

## Patterns of density-dependent growth in juvenile stream-dwelling salmonids

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Literature data for 19 populations from 16 different studies of six species of stream-dwelling salmonids were analysed to test the hypothesis that density-dependent growth is stronger at low rather than at high population density. Fifteen of 19 populations showed evidence of a significant decrease in growth rate with increasing density. In 11 of these 15 populations, the pattern of density-dependent growth was better described by a negative power curve than by a linear regression (*i.e.* Akaike Information Criterion,  $AIC_{\text{linear}} - AIC_{\text{power}} > 2$ ), whereas only one population was better described by a linear regression than by a negative power curve; three populations were adequately described by both models ( $AIC < 2$ ). In 10 of the 11 populations that were best described by a negative power curve, most of the decrease in growth rate occurred at population densities  $< 1 \text{ fish m}^{-2}$ , when space limitation is unlikely. This analysis provides broad support for the hypothesis that density-dependent growth in stream salmonids occurs primarily at low population densities, probably due to exploitative competition.

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**Key words:** compensatory responses; exploitative competition; growth rate; population density; population regulation.

### INTRODUCTION

Whether or not fish populations exhibit compensatory responses to changes in population density is an important issue for fisheries managers. Stocking programmes want to maximize recruitment without wasting resources by risking density-dependent mortality or growth in either the stocked or the native fish populations. Similarly, restoration plans typically target the limiting habitat type for the limiting life stage (Dodson *et al.*, 1998). For example, the brown trout *Salmo trutta* L. population in Black Brows Beck are limited by density-dependent mortality during a critical period immediately after the fry emerge from the gravel, after which mortality is density-independent (Elliott, 1994). Nursery habitat appears to be limiting in Black Brow's Beck and should be the target for the habitat manager.

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Quantifying the abundance of fishes and habitat is a challenge for salmonid biologists. Population density is a suitable measure of abundance for studies of single cohorts, but is not ideal for populations composed of several age-classes or species (Grant *et al.*, 1998). Biomass is routinely used in these situations, but is not allometrically correct (Grant *et al.*, 1998). Hence, a variety of allometrically correct measures of total abundance include summing the metabolic requirements, food consumption (Post *et al.*, 1999), or space requirements (Grant & Kramer, 1990) of the cohorts in the population. Of these measures, per cent habitat saturation (PHS), the percentage of the streambed occupied by the territories of all salmonids in the stream (Grant & Kramer, 1990), may be the most useful for habitat managers, because it links total abundance to the amount of stream habitat. The remaining challenge is then to estimate the percentage of the total streambed that is actually usable for that population (Armstrong *et al.*, 2003; Girard *et al.*, 2004).

Density-dependent growth, mortality and emigration have been widely reported in stream-dwelling salmonid populations (Grant & Kramer, 1990; Elliott, 1994). Interference, the direct interactions between competitors (Keddy, 1989), is a probable explanation because of the conspicuous territorial behaviour in many of these populations and because the likelihood of these compensatory responses increases with increasing PHS (Grant & Kramer, 1990). Curiously, the brown trout in Black Brows Beck that exhibit such strong density-dependent loss rates, mediated by territoriality, also exhibit density-independent growth (Elliott, 1994). The recent demonstration by Jenkins *et al.* (1999) of density-dependent growth in brown trout, which was apparently strongest at population densities  $<1 \text{ fish m}^{-2}$ , suggests an empirical solution to the contrasting patterns of compensatory responses in Black Brow's Beck. Density-independent growth in Elliott's (1994) study may have resulted from a relatively narrow range about a high mean population density. Imre *et al.* (2005) provided strong support for the hypothesis of Jenkins *et al.* (1999) that density-dependent growth is strongest at low densities. In a 10-year data set, the seasonal growth of age 0+ year Atlantic salmon *Salmo salar* L. in Catamaran Brook was strongly density-dependent and the patterns of growth were better described by a negative power curve than by a linear regression. Furthermore, the densities at which growth was most strongly affected were too low to expect interference competition *via* territoriality.

If the patterns of density-dependent growth observed by Jenkins *et al.* (1999) and Imre *et al.* (2005) are general, then stream salmonid populations may be regulated by two mechanisms. At high population abundance when space is limiting, density-dependent mortality and emigration probably occur *via* interference, as suggested by Grant & Kramer (1990). When population abundance is low, however, density-dependent growth probably occurs *via* exploitative competition, the depletion of food by competitors (Keddy, 1989). For a continually renewing resource like stream drift, increasing competitor density will have the greatest effect on the per capita foraging rate at low densities (Fretwell & Lucas, 1970). Hence, the two mechanisms of competition make contrasting predictions: as the average abundance of salmonids increases, the likelihood of observing density-dependent mortality and emigration increases, whereas the likelihood of observing density-dependent growth decreases.

The purpose of the present study was to test the generality of the Jenkins *et al.* (1999) hypothesis that density-dependent growth in stream-dwelling salmonids is more intense at low rather than at high population densities. Literature data were first used to test for the incidence of density-dependent growth. In those populations exhibiting density-dependent growth, the relative fit of a negative power curve *v.* a linear regression with negative slope were compared using the Akaike Information Criterion (AIC, Motulsky & Christopoulos, 2004).

## MATERIALS AND METHODS

The literature was searched for papers reporting the average growth rate of juvenile stream-dwelling salmonids in relation to population density (number  $m^{-2}$ ). The starting points for the search were the references in Grant & Kramer (1990), Jenkins *et al.* (1999), Imre *et al.* (2005), and the Web of Science. The reference section of each paper that provided data for the analysis was also searched for other data sets.

To be included in the analysis, a paper had to provide either tabulated data (Elliott, 1984 *a, b*) or scatterplots of data, from which growth rate and population density could be interpolated (Close & Anderson, 1992). Measures of growth rate included instantaneous growth rate per day (Crisp, 1993), per cent growth per day (Randall, 1982), or seasonal growth of age 0+ year fishes (*i.e.* body length or mass at the end of the growing season; Imre *et al.*, 2005). The growth rate of known individuals was not monitored in any of these studies, and so is reported as the average growth rate of the age 0+ year cohort. In the one exception (see below), the growth rate of the age 1+ year cohort was calculated as the average gain in mass over the summer (Hunt, 1974). Only one summary data set was included in the analysis from each of Jenkins *et al.* (1999) and Imre *et al.* (2005), because these studies are linked with the hypothesis.

To determine whether growth rate was density-dependent or not, growth rate was regressed on population density using ordinary least squares regression and a negative power curve, estimated by the non-linear-models module of Statistica 7.0 (StatSoft, 2004). The population was scored as exhibiting density-dependent growth if either model was significant (*i.e.*  $P < 0.05$ ), or in one study (Crisp, 1995), if the original authors reported a significant decrease in growth rate with increasing density. For those populations exhibiting density-dependent growth, the shape of the relationship was explored by calculating the AIC, for both models. The model with the smallest AIC value was considered to offer a markedly better description of the data if the difference in AIC values was  $>2$  (Motulsky & Christopoulos, 2004).

To compare the patterns of growth rate *v.* density for all 18 populations of age 0+ year fishes, all the data were plotted on the same double logarithmic axes. To facilitate this comparison, mass of the age 0+ year cohort at the end of the growing season was used as the common measure of average growth rate. Instantaneous growth rate in Crisp (1993) was translated to mass on 1 October by assuming that age 0+ year fishes emerge on 1 May at 0.19 g. Growth rate in Randall (1982) was translated to mass on 31 August by assuming that all fishes were 1 g on 1 July. Mass gain in Harvey & Nakamoto (1996) was translated to mass at the end of the experiment by assuming that the initial size of all fish was 3.59 g. Fork length ( $L_F$ ) in Gee *et al.* (1978) and Imre *et al.* (2005) were translated to mass using mass *v.*  $L_F$  relationships for those populations. For the three populations where no such relationship was available (Egglishaw & Shackley, 1985; Hartman & Scrivener, 1990; Whalen & LaBar, 1994),  $L_F$  (cm) was converted to mass ( $M$ , g) using the equation from Grant & Kramer (1990):  $\log_{10} M = 3.03 \log_{10} L_F - 1.93$ .

To estimate an overall relationship between mass and density for age 0+ year fishes, the average slope was calculated for the 18 populations, 17 of which were straight lines on double logarithmic axes (see below). For the single non-linear population (Gee *et al.*, 1978), the slope of the non-significant least squares regression of  $\log_{10}$  mass and  $\log_{10}$  density was used. Because each individual regression went through the mean density, mean mass for that population (*i.e.* mean  $x$  and mean  $y$ ), the overall slope was fitted

through the overall mean: average of the 18 mean densities, and average of the 18 mean masses (Sokal & Rohlf, 1995).

To determine whether the incidence of density-dependent growth was related to salmonid abundance across studies, a logistic regression was used. Whether or not a population exhibited density-dependent growth (yes = 1 and no = 0) was regressed against the median per cent habitat saturation (PHS, Grant & Kramer, 1990) for the cohorts of interest in each population. PHS was calculated from:  $PHS = 100 D_i T_i^{-1.19}$ , where  $D_i$  is the actual density (no  $m^{-2}$ ) of the cohort,  $T_i$  is the predicted territory size ( $m^2$ ) for the average fish in the cohort, and 1.19 is a correction factor (Grant & Kramer, 1990). Territory size ( $A$ ,  $m^2$ ) was calculated as (Grant & Kramer, 1990):  $\log_{10} A = 2.61 \log_{10} L - 2.83$  or,  $\log_{10} A = 0.86 \log_{10} M - 1.17$ . In this analysis each of the 19 populations in Table I (see below) was used, in addition to four populations described in Crisp (1995). These last four studies could not be used in the AIC analysis because the raw data were not available.

## RESULTS

Data from 16 different papers (Table I), representing six different species were used to evaluate the patterns of density-dependent growth in stream-dwelling salmonids. These data allowed the pattern of density-dependent growth for 19 different populations, 13 and six of which were from North America and the U.K., respectively, to be compared.

Fifteen of 19 populations showed evidence of density-dependent growth (Table I); in all 15 cases growth rate decreased significantly with increasing density (Fig. 1). Of the four populations showing density-independent growth, Elliott's (1984a, b) study of brown trout is perhaps the most notable [Fig. 1(f)]. In the three other cases [Fig. 1(a), (e), (l)], the population with density-independent growth represented one of two populations reported in the paper; in all three cases the other population showed density-dependent growth [*i.e.* Fig. 1(b), (d), (m)]. The real incidence of density-dependent growth in salmonid populations may be lower than the 75% noted in this analysis because of the reluctance of authors to publish non-significant results (the file drawer effect, Palmer, 2000). A regression of one measure of effect size, the  $r^2$ -value, v. sample size was not significant ( $n = 19$ ,  $P \gg 0.05$ ), however, indicating no strong evidence of a reporting bias (Palmer, 2000).

Of the 15 populations exhibiting density-dependent growth, 11 were markedly better described (*i.e.* absolute value of  $AIC > 2$ ) by a negative power curve than by a linear regression with a negative slope, whereas the opposite was true in only one case (sign test,  $P < 0.01$ ). In three cases, both models adequately described the significant decrease in growth rate with increasing density. Hence, this comparative analysis provides strong support for the Jenkins *et al.* (1999) hypothesis that changes in growth rate with increasing density within populations occur most strongly at low as opposed to high densities.

When all 18 age 0+ year populations were plotted on the same axes, considerable variation in both growth rate and population density were evident (Fig. 2). Three of four populations with density-independent growth exhibited a narrow range in population density; populations e, f, and g (Fig. 2) ranked 14th, 19th, and 18th out of 19 populations, respectively, in range of population density. In contrast, the steelhead trout *Oncorhynchus mykiss* (Walbaum) in the Stewart River (population a) had the third highest range in population density and yet

TABLE I. Literature data providing patterns of growth rate of stream-dwelling salmonids in relation to population density. The letters indicating the source of the data refer to the panels in Fig. 1

Source of data	Species/age class	Condition	Metric of growth	n	Model	$AIC_{\text{power}} - AIC_{\text{linear}}$	$r^2$	P	Median PHS
a	<i>O.m.</i>	S, O, F	Mass	13	NS	NA	0.04	0.241	13.9
b	<i>O.m.</i>	S, O, F	Mass	23	Power	-6.37	0.46	<0.001	8.5
c	<i>S.t.</i>	S, O, F	Growth rate	78	Power	-4.09	0.36	<0.001	6.7
d	<i>S.s.</i>	W, O, F	Mass	19	Both	-0.84	0.29	0.019	21.3
e	<i>S.t.</i>	W, O, F	Length	19	NS	NA	0.13	0.122	19.2
f	<i>S.t.</i>	W, O, F	Mass	16	NS	NA	0.08	0.304	32.3
g	<i>O.k., O.m.</i>	S, E, L	Mass	4	Power	-8.05	0.99	0.018	59.2
h	<i>S.s.</i>	W, O, F	Length	16	Linear	2.60	0.26	0.046	16.6
i	<i>O.c., O.m.</i>	W, O, F	Length	16	Power	-3.77	0.60	<0.001	2.9
j	<i>O.k., O.m.</i>	W, O, F	Mass gain	12	Power	-2.40	0.59	0.006	30.5
k	<i>O.m.</i>	S, E, F	Mass	32	Power	-4.71	0.40	<0.001	4.4
l	<i>S.f.</i>	W, O, F	Mass	11	NS	NA	0.02	0.650	14.5
m	<i>S.f.</i>	W, O, F	Mass gain	11	Power	-2.40	0.51	0.027	31.0
n	<i>S.s.</i>	W, O, F	Length	162	Power	-42.83	0.60	<0.001	4.5
o	<i>S.t.</i>	W, E, F + L	Mass	27	Both	1.17	0.46	<0.001	17.8
p	<i>S.t.</i>	S, E, F	Mass	8	Power	-8.39	0.95	<0.001	77.6
q	<i>S.s.</i>	S, O, F	Mass	12	Power	-5.01	0.67	0.001	3.1
r	<i>S.s.</i>	W, O, F	Growth rate	6	Power	-2.75	0.93	0.002	18.3
s	<i>S.s.</i>	S, E, F	Length	18	Both	1.25	0.57	<0.001	2.6

a, Close & Anderson (1992; Fig. 3, top panel); b, Close & Anderson (1992; Fig. 3, bottom panel); c, Crisp (1993; Fig. 3, bottom panel); d, Egglishaw & Shackley (1985; Table I); e, Egglishaw & Shackley (1985; Table I); f, Elliott (1984a, b; a: Table III; b: Appendix); g, Fraser (1969; Table II and Appendix I); h, Gee *et al.* (1978; Tables II and III); i, Hartman & Scrivener (1990; Fig. 70); j, Harvey & Nakamoto (1996; Table I); k, Hume & Parkinson (1987; Fig. 6a); l, Hunt (1974; Appendix and Table I); m, Hunt (1974; Appendix and Table I); n, Imre *et al.* (2005; Fig. 4a); o, Jenkins *et al.* (1999; Fig. 8); p, LeCren (1965, 1973; Figs 2 and 164); q, Nislow *et al.* (2004; Fig. 3c); r, Randall (1982; Fig. 4); s, Whalen & LaBar (1994; Table III).

*O.c.*, *Oncorhynchus clarki* (Richardson); *O.k.*, *Oncorhynchus kisutch* (Walbaum); *O.m.*, *Oncorhynchus mykiss* (Walbaum); *S.s.*, *Salmo salar* L; *S.t.*, *Salmo trutta* L; *S.f.*, *Salvelinus fontinalis* (Mitchill); all fish were age 0+ years, except for those in m, which were age 1+ years.

W, wild fish; S, stocked fish; E, experimental study; O, observational study; L, laboratory study; F, field study.

Mass, mass at the end of the summer; mass gain, average gain in mass; Length, fork ( $L_F$ ) or total length ( $L_T$ ) at the end of the summer; growth rate, instantaneous growth rate. Power, the Akaike Information Criterion (AIC) was markedly smaller for a negative power curve than for a linear regression ( $AIC_{\text{linear}} - AIC_{\text{power}} > 2$ ) and that the negative power curve was significant ( $P < 0.05$ ), and *vice versa* for linear. Both means that the negative power curve and the linear regression were both significant, but neither provided a markedly better fit than the other according to the AIC. NS; not significant. PHS, per cent habitat saturation (Grant and Kramer 1990).

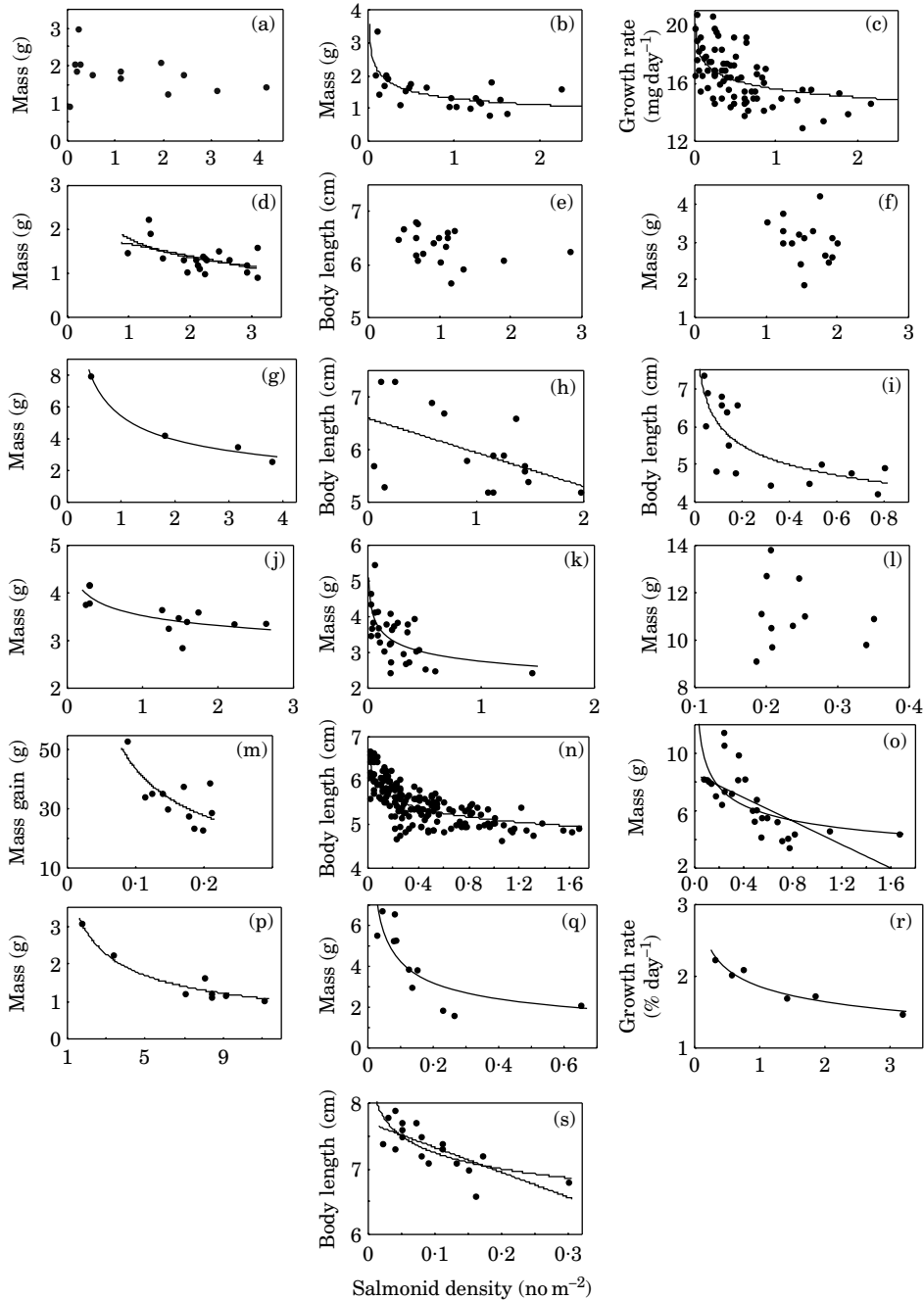


FIG. 1. Average growth rate (mass or length of age 0+ year fishes at the end of the summer, mass gain, or instantaneous growth rate) of juvenile salmonid fishes in streams in relation to population density. No line means that growth rate was not significantly ( $P > 0.05$ ) related to population density. A curved line means that the Akaike Information Criterion (AIC) was markedly smaller for a negative power curve than for a linear regression (i.e.  $AIC_{\text{linear}} - AIC_{\text{power}} > 2$ ), and vice-versa for a straight line. A curve and a straight line mean that both models provided an adequate description of the data. The letters refer to the populations in Table I. Note the different x and y axes on various figures.

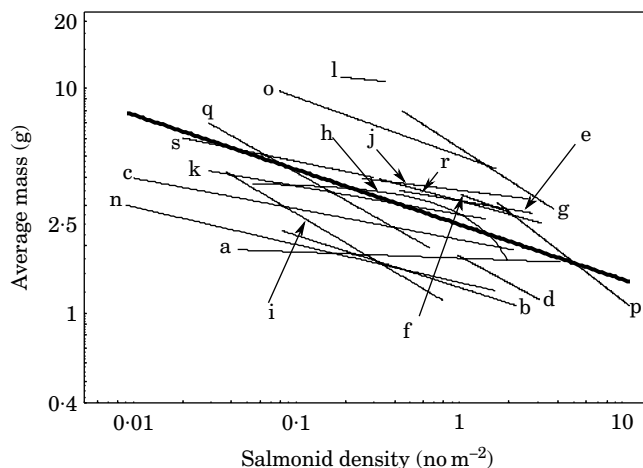


FIG. 2. Average mass of age 0+ year salmonids fishes at the end of the growing season in relation to population density for 18 stream populations (see Table I). Note the logarithmic scale on both axes. To simplify the graphical presentation, straight lines were used for all populations except h, which was markedly better described by a linear regression than a negative power curve on an arithmetic scale (see Fig. 1). The bold line is the average slope of the 18 regressions fitted through the average density and the average mass.

exhibited density-independent growth (Fig. 2). Overall, populations with and without density-dependent growth did not differ significantly in the range of population density (two-sample *t*-test,  $n = 19$ ,  $P = 0.21$ ).

Despite the considerable variation depicted in Fig. 2, all age 0+ year populations exhibited a decrease in average mass with increasing population density. The average slope of the 18 regressions was  $-0.244$  ( $n = 18$ , 95% CL =  $-0.327$ ,  $-0.161$ ). Fitting this average slope through the mean density and mean mass for the 18 populations ( $x = 0.546$  fish  $m^{-2}$ ,  $y = 2.877$  g) yielded an overall regression of:  $\log_{10} M = 0.395 - 0.244 \log_{10} \text{density}$ .

A logistic regression was used to test whether salmonid abundance affected the incidence of density-dependent growth between populations. Median per cent habitat saturation (PHS, Grant & Kramer, 1990) was used to quantify salmonid abundance in a particular study instead of population density to adjust for size differences between populations (Grant *et al.*, 1998). When comparing between populations, the occurrence of density-dependent growth was not significantly related to PHS (Fig. 3; logistic regression,  $n = 23$ ,  $P = 0.41$ ). The pattern of density-dependent growth *v.* PHS in this study differed markedly from the pattern of density-dependent growth, mortality and emigration noted in Grant & Kramer (1990; Fig. 3). At a PHS  $< 10$ , density-dependent growth was always observed in this study, whereas they were unlikely in Grant & Kramer's (1990) analysis.

## DISCUSSION

Seventy-five per cent of the populations in this analysis exhibited density-dependent growth. Nevertheless, density-dependent growth should not always

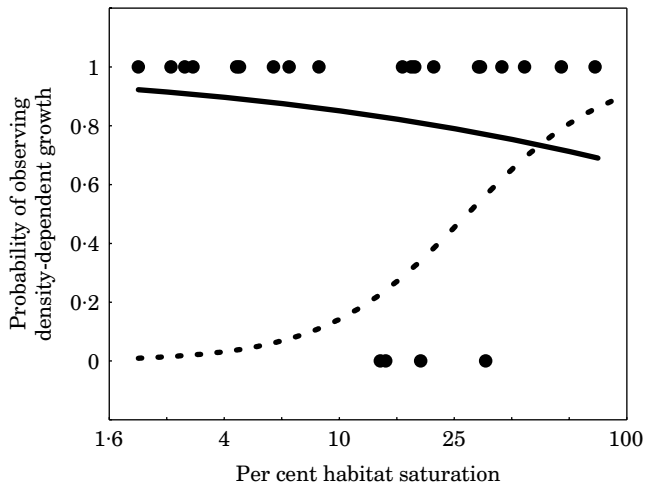


FIG. 3. The incidence of density-dependent growth in relation to median per cent habitat saturation (PHS, Grant & Kramer, 1990). ●, Populations in Table I and four others from Crisp (1995), depicting whether or not they exhibit density-dependent growth in relation to the median PHS. The solid line is the non-significant ( $P = 0.41$ ) logistic regression for these data. For comparison, the dotted line is a logistic regression depicting the occurrence of density-dependent growth, survival, and emigration versus PHS from Grant & Kramer (1990).

be expected, because other factors that affect growth, such as water temperature (Egglishaw & Shackley, 1985), food abundance (Imre *et al.*, 2004), or competition with other age-classes or species (Kennedy & Strange, 1986) may sometimes override the effects of density (Elliott, 1994).

Within populations, the literature data provided broad general support for the hypothesis that the density-dependent growth rate of individual salmonids in streams is stronger at low rather than at high population densities. Ironically, the data from Jenkins *et al.* (1999) provided only equivocal support for their own hypothesis. The present analysis, however, only included one of their data sets; it may be that other data sets in their paper provided strong support for the hypothesis of a negative power curve.

Jenkins *et al.* (1999) also hypothesized that the failure of Elliott (1984*a, b*) to detect density-dependent growth was related to the narrow range and the high mean density of fish in Black Brow's Beck. Of the two explanations, the former seems more likely because Elliott's (1984*a, b*) population ranked 18th out of 19 in terms of range of density, but only sixth in terms of median density and fifth in PHS. Alternatively, Elliott's (1984*a, b*) result may have occurred because the brown trout in Black Brow's Beck were growing at maximal rates for the ambient water temperature (Elliott, 1994), and hence were unaffected by density. Although populations exhibiting density-independent growth tended to have narrow ranges in density and higher salmonid abundance (Fig. 3), as predicted by Jenkins *et al.* (1999), neither comparison was significant.

This comparative analysis supports the hypothesis that stream salmonid populations are regulated in two ways: density-dependent growth *via* exploitative competition at low densities and density-dependent mortality and emigration *via*



interference at high densities. In 10 of 11 populations whose patterns of growth were best described by a negative power curve, most of the decrease in growth rate occurred at densities  $<1$  fish  $m^{-2}$ . At these low densities, space should not normally be limiting (Grant & Kramer, 1990), suggesting that density-dependent growth is caused by exploitation rather than interference competition. The contrasting patterns of logistic regressions in Fig. 3 provide further support for this hypothesis. Growth data accounted for only 29% of the data in Grant & Kramer's (1990) analysis and the dramatic increase in compensatory responses at high PHS in their study was caused primarily by high rates of emigration at high PHS.

A paired analysis of populations in which both growth rate and loss rate were measured over a broad range in population density would provide a powerful test of this two-mechanisms hypothesis. Such an analysis would also aid fisheries managers in evaluating the trade-off between the density of fishes in a stream and the growth rate and mortality rate of each fish. The average slope ( $-0.244$ ) of the mass *v.* density regressions in Fig. 2 indicates that the average mass of a fish decreases by *c.* 15% for every doubling in fish density. At low densities when mortality rate is probably density independent, this decrease in individual growth rate is more than compensated by an increase in density: the biomass of age 0+ year fishes would increase by *c.* 1.7 times for every doubling in density. At higher densities, however, the joint effects of density-dependent growth and mortality on the population dynamics of the cohort needs further exploration.

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## References

- Armstrong, J. D., Kemp, P. S., Kennedy, G. J. A., Ladle, M. & Milner, N. J. (2003). Habitat requirements of Atlantic salmon and brown trout in rivers and streams. *Fisheries Research* **62**, 143–170.
- Close, T. L. & Anderson, C. S. (1992). Dispersal, density-dependent growth, and survival of stocked steelhead fry in Lake Superior tributaries. *North American Journal of Fisheries Management* **12**, 728–735.
- Crisp, D. T. (1993). Population densities of juvenile trout (*Salmo trutta*) in five upland streams and their effects upon growth, survival and dispersal. *Journal of Applied Ecology* **30**, 759–771.
- Crisp, D. T. (1995). Dispersal and growth rate of 0-group salmon (*Salmo salar* L.) from point-stocking together with some information from scatter-stocking. *Ecology of Freshwater Fish* **4**, 1–8.
- Dodson, J. J., Gibson, R. J., Cunjak, R. A., Friedland, K. D., de Leaniz, C. G., Gross, M. R., Newbury, R., Nielsen, J. L., Power, M. E. & Roy, S. (1998). Elements in the development of conservation plans for Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences* **55** (Suppl. 1), 312–323.
- Egglishaw, H. J. & Shackley, P. E. (1985). Factors governing the production of juvenile Atlantic salmon in Scottish streams. *Journal of Fish Biology* **27** (Suppl. A), 27–33.
- Elliott, J. M. (1984a). Numerical changes and population regulation in young migratory trout *Salmo trutta* in a Lake District stream, 1966–83. *Journal of Animal Ecology* **53**, 327–350.

- Elliott, J. M. (1984b). Growth, size, biomass and production of young migratory trout *Salmo trutta* in a Lake District stream, 1966–83. *Journal of Animal Ecology* **53**, 979–994.
- Elliott, J. M. (1994). *Quantitative Ecology and the Brown Trout*. Oxford: Oxford University Press.
- Fraser, F. J. (1969). Population density effects on survival and growth of juvenile coho salmon and steelhead trout in experimental stream-channels. In *Symposium on Salmon and Trout in Streams* (Northcote, T. G., ed.), pp. 253–266. Vancouver: University of British Columbia.
- Fretwell, S. D. & Lucas, H. L. (1970). On territorial behaviour and other factors influencing habitat distribution in birds. *Acta Biotheoretica* **19**, 16–36.
- Gee, A. S., Milner, N. J. & Hemsworth, R. M. (1978). The production of juvenile Atlantic salmon, *Salmo salar* in the upper Wye, Wales. *Journal of Fish Biology* **13**, 439–451.
- Girard, I. L., Grant, J. W. A. & Steingrímsson, S. Ó. (2004). Foraging, growth, and loss rate of young-of-the-year Atlantic salmon (*Salmo salar*) in relation to habitat use in Catamaran Brook, New Brunswick. *Canadian Journal of Fisheries and Aquatic Sciences* **61**, 2339–2349.
- Grant, J. W. A. & Kramer, D. L. (1990). Territory size as a predictor of the upper limit to population density of juvenile salmonids in streams. *Canadian Journal of Fisheries and Aquatic Sciences* **47**, 1724–1737.
- Grant, J. W. A., Steingrímsson, S. Ó., Keeley, E. R. & Cunjak, R. A. (1998). Implications of territory size for the measurement and prediction of salmonid abundance in streams. *Canadian Journal of Fisheries and Aquatic Sciences* **55** (Suppl. 1), 181–190.
- Hartman, G. F. & Scrivener, J. C. (1990). Impacts of forestry practices on a coastal stream ecosystem, Carnation Creek, British Columbia. *Canadian Fisheries and Aquatic Sciences Bulletin* **223**.
- Harvey, B. C. & Nakamoto, R. J. (1996). Effects of steelhead density on growth of coho salmon in a small coastal California stream. *Transactions of the American Fisheries Society* **125**, 237–243.
- Hume, J. M. B. & Parkinson, E. A. (1987). Effect of stocking density on the survival, growth, and dispersal of steelhead trout fry (*Salmo gairdneri*). *Canadian Journal of Fisheries and Aquatic Sciences* **44**, 271–281.
- Hunt, R. L. (1974). Annual production by brook trout in Lawrence Creek during eleven successive years. *Wisconsin Department of Natural Resources Technical Bulletin* **82**.
- Imre, I., Grant, J. W. A. & Keeley, E. R. (2004). The effect of food abundance on territory size and population density of juvenile steelhead trout (*Oncorhynchus mykiss*). *Oecologia* **138**, 371–378.
- Imre, I., Grant, J. W. A. & Cunjak, R. A. (2005). Density-dependent growth of young-of-the-year Atlantic salmon (*Salmo salar*) in Catamaran Brook, New Brunswick. *Journal of Animal Ecology* **74**, 508–516.
- Jenkins, T. M. Jr, Diehl, S., Kratz, K. W. & Cooper, S. D. (1999). Effects of population density on individual growth of brown trout in streams. *Ecology* **80**, 941–956.
- Keddy, P. A. (1989). *Competition*. London: Chapman & Hall.
- Kennedy, G. J. A., & Strange, C. D. (1986). The effects of intra- and inter-specific competition on the survival and growth of stocked juvenile Atlantic salmon, *Salmo salar* L., in an upland stream. *Journal of Fish Biology* **28**, 479–489.
- LeCren, E. D. (1965). Some factors regulating the size of populations of freshwater fish. *Mitteilungen der Internationalen Vereinigung für theoretische und angewandte Limnologie* **13**, 88–105.
- LeCren, E. D. (1973). The population dynamics of young trout (*Salmo trutta*) in relation to density and territorial behaviour. *Rapports et Procès-Verbaux des Réunions Conseil International pour l'exploration de la Mer* **164**, 241–246.
- Motulsky, H. & Christopoulos A. (2004). *Fitting Models to Biological Data Using Linear and Nonlinear Regression: a Practical Guide to Curve Fitting*. Oxford: Oxford University Press.

- Nislow, K. H., Sepulveda, A. J. & Folt, C. L. (2004). Mechanistic linkage of hydrologic regime to summer growth of age-0 Atlantic salmon. *Transactions of the American Fisheries Society* **133**, 79–88.
- Palmer, A. R. (2000). Quasi-replication and the contract of error: lessons from sex ratios, heritabilities and fluctuating asymmetry. *Annual Review of Ecology and Systematics* **31**, 441–480.
- Post, J. R., Parkinson, E. A. & Johnston, N. T. (1999). Density-dependent processes in structured fish populations: interaction strengths in whole-lake experiments. *Ecological Monographs* **69**, 155–175.
- Randall, R. G. (1982). Emergence, population densities, and growth of salmon and trout fry in two New Brunswick streams. *Canadian Journal of Zoology* **60**, 2239–2244.
- Sokal, R. R. & Rohlf, F. J. (1995). *Biometry*, 3<sup>rd</sup> edn. New York: W. H. Freeman and Company.
- StatSoft (2004). *Statistica, Version 7*. Tulsa, OK: Statsoft, Inc.
- Whalen, K. G. & LaBar, G. W. (1994). Survival and growth of Atlantic salmon (*Salmo salar*) fry stocked at varying densities in the White River, Vermont. *Canadian Journal of Fisheries and Aquatic Sciences* **51**, 2164–2169.