Factors driving spatial and temporal variation in production and production/biomass ratio of stream-resident brown trout (*Salmo trutta*) in Cantabrian streams

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SUMMARY

1. The objective was to identify the factors driving spatial and temporal variation in annual production (*P*A) and turnover (production/biomass) ratio (*P*/*B*A) of resident brown trout *Salmo trutta* in tributaries of the Rio Esva (Cantabrian Mountains, Asturias, northwestern Spain). We examined annual production (total production of all age-classes over a year) (*P*A) and turnover (*P*/*B*A) ratios, in relation to year-class production (production over the entire life time of a year-class) (*P*T) and turnover (*P*/*B*T) ratio, over 14 years at a total of 12 sites along the length of four contrasting tributaries. In addition, we explored whether the importance of recruitment and site depth for spatial and temporal variations in year-class production (*P*T), elucidated in previous studies, extends to annual production.

2. Large spatial (among sites) and temporal (among years) variation in annual production (range 1.9–40.3 g m⁻² per year) and *P*/*B*A ratio (range 0.76–2.4 per year) typified these populations, values reported here including all the variation reported globally for salmonids streams inhabited by one or several species.

3. Despite substantial differences among streams and sites in all production attributes, when all data were pooled, annual (*P*A) and year-class production (*P*T) and annual (*P*/*B*A) and year-class *P*/*B*T ratios were tightly linked. Annual (*P*A) and year-class production (*P*T) were similar but not identical, i.e. *P*T = 0.94 *P*A, whereas the *P*/*B*T ratios were 4 + *P*/*B*A ratios.

4. Recruitment (Rc) and mean annual density (*N*A) were major density-dependent drivers of production and their relationships were described by simple mathematical models. While year-class production (*P*T) was determined (*R*² = 70.1%) by recruitment (Rc), annual production (*P*A) was determined (*R*² = 60.3%) by mean annual density (*N*A). In turn, variation in recruitment explained *R*² = 55.2% of variation in year-class *P*/*B*T ratios, the latter attaining an asymptote at *P*/*B*T = 6 at progressively higher levels of recruitment. Similarly, variations in mean annual density (*N*A) explained *R*² = 52.1% of variation in annual *P*/*B*A, the latter reaching an asymptote at *P*/*B*A = 2.1. This explained why *P*/*B*T is equal to *P*/*B*A plus the number of year-classes at high but not at low densities.

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Introduction

Production rate (sensu Ivlev, 1945) is a key measure of performance of a population in a given habitat. As emphasised by Benke (1993), production is ‘the most comprehensive representation of population ‘success’, because it is a composite of most other components of success: density, biomass, individual growth, reproduction, survival, and development time.’ Further, this vital rate is a key component of most fishery models, including the estimation of optimum harvest rate (Ricker & Foerster, 1948; Pauly, 1996) and as an input for energy budgets and trophic food webs (Benke, 1993). Mathematical descriptions of production rate and its components have been summarised in a rich literature (e.g. Ricker & Foerster, 1948; Allen, 1951; Bagenal, 1978) and, more recently, simplified formulations have been given by Mertz & Myers (1998).

The assessment of production dynamics of freshwater organisms has a long history (Waters, 1969), and relationships among production, life history traits and environmental factors have been reported for a broad array of aquatic taxa across different systems (Waters, 1977; Banse & Mosher, 1980; Plante & Downing, 1989; Benke, 1993; Randall & Mills, 2000). In particular, investigations on stream-living fish include a variety of studies relating production dynamics to the productive capacity of the stream (Kwak & Waters, 1997; Randall & Mills, 2000), geographical regions (Crisp, Mann & McCormack, 1974, 1975; Mann, Blackburn & Beaumont, 1989; Mazzoni & Lobón-Cerviá, 2000) and environmental variability (Lobón-Cerviá, 2003) and include experimental research (Warren et al., 1964; Bergheim & Hesthagen, 1990; Nislow et al., 2010).

However, the incorporation of production rates into fisheries models and other management tools remains challenging, probably because estimating these rates in the wild is costly and time-consuming. This also explains why short-cut approaches to the estimation of production recur in the literature (Waters, 1969). In particular, the notion that annual production can be approximated from the mass-specific or relative production, namely the ratio of production (P) to biomass (B) (i.e. P/B), has long been the focus of many investigations (Waters, 1969; Randall & Mills, 2000). More explicitly, the P/B ratio can be expressed on an annual (henceforth P/B_A) or a year-class basis (henceforth P/B_T). Overall, annual P/B ratios are estimated from the onset of growth (i.e. spring in temperate climates) of a particular year to the next. The reciprocal of P/B_A measures the time taken for the population to replace its own mass and, as such, provides an estimate of turnover time. Year-class P/B_T ratios refers to the production of a year-class across the entire lifetime divided by its corresponding mean biomass.

Several reviews (Chapman, 1978; Backiel, Thorpe & Kitchell, 1980; Mann & Penczak, 1986; Gibson, 1988; Kwak & Waters, 1997) have emphasised that, despite decade-long efforts, the processes underlying the production dynamics of stream salmonids (and other freshwater fish) are still poorly understood. However, those reviews have also highlighted several apparently consistent patterns: (i) maximum annual production rate is typically ≤40 g m^{-2} per year, (ii) the annual P/B_A ratio is relatively constant within the range 0.4–2.3, and (iii) variation in the P/B_A ratio may be caused by the inherent variability of population features or by environmental factors. For example, Chapman (1978) suggested a constant P/B_A ratio of 2, with slightly lower or higher values related to warmer versus cooler streams, whereas Waters, Doherty & Krueger (1990) and Kwak & Waters (1997) reported P/B_A ratios within a similar range (i.e. 0.6–2.5) with variations caused by species- or population-specific age-structure. The fewer data available for year-class P/B_T ratios also suggested a rather constant value of 5.5 within a range of 4.8–7.8 (Elliott, 1993).

5. Site depth was a major determinant of spatial (among sites) variation in production attributes. All these attributes described two-phase trajectories with site depth, reaching a maximum at sites of intermediate depth and declining at shallower and deeper sites. As a consequence, at sites where recruitment and mean annual density reached minimum or maximum values, annual (P_A) and year-class production (P_T) and annual (P/B_A) and year-class P/B_T ratios also reached minimum and maximum values.

Keywords: density, production rates, recruitment, salmo trutta; site depth, streams
The present investigation is part of the long-term, large-scale monitoring of brown trout *Salmo trutta* L. across tributaries of the Rio Esva drainage, a typical coastal river in the Cantabrian mountainous corridor of north-western Spain (Asturias). Previous investigations on these same populations and year-classes emphasised the importance of endogenous, density-dependent processes in the form of recruitment (i.e. the number of juveniles commencing a new year-class; Lobón-Cerviá & Rincón, 2004) as a major driver of year-class production (Lobón-Cerviá, 2005, 2009), and exogenous factors related to habitat quality in the form of site depth as a major determinant of spatial variation in recruitment (among sites) and, hence, in year-classes production ($P_T$) across sites. The current study is an extension of those studies and is focussed on annual production ($P_A$) and turnover ratios ($P/B_A$), and their potential relationships with year-class production ($P_T$) and turnover ratios ($P/B_T$).

Specifically, this study attempted to reveal the mechanisms underlying annual production ($P_A$) and was based on a long-term monitoring of resident brown trout *Salmo trutta* across a broad scale of space and time. To this end, the present investigation (i) determined the range of variation in annual production ($P_A$) and turnover ratios ($P/B_A$), and their potential relationships with year-class production ($P_T$) and turnover ratios ($P/B_T$); (ii) explored whether annual production ($P_A$) and turnover ratios ($P/B_A$) are related to year-class production ($P_T$) and turnover ratios ($P/B_T$); and, if so, (iii) to what extent the previously determined importance of recruitment and site depth for year-class production ($P_T$) also affects the year-class turnover ratios ($P/B_T$) and (iv) whether the effect of recruitment and site depth on $P_T$ and $P/B_T$ affects annual production ($P_A$) and turnover ratios ($P/B_A$). Lastly (v), this study offers a comparison of the production-related patterns reported elsewhere versus those revealed for these Cantabrian brown trout populations.

**Methods**

The location of the study streams within the Rio Esva drainage, the sites selected for study along these streams, their major features and the sampling scheme have been described elsewhere (Lobón-Cerviá, 1991, 2007, 2009), and only details relevant for this study are covered below. The data set encompasses 128 year-classes quantified every 4 months from recruitment to complete disappearance from the study sites. The latter were selected along four contrasting streams of the Rio Esva to (i) capture the environmental and hydrological variability present across the landscape and (ii) limit the selection of stream sites to those of a size sufficient for effective electro-fishing that then allows accurate estimations of population size (Lobón-Cerviá, 1991). Two of the selected streams, Rio Chaballos (sites 1–4) and Rio Castañedo (sites 8–10), are to the west of the Rio Esva, whereas the other two streams, Río La Viella (sites 5–8) and Rio Choudral (sites 11–12), are to the east. The size and number of all brown trout individuals were quantified, based on a three-pass depletion estimation method (Lobón-Cerviá, 1991) performed, at least, in May, September and January (i.e. c. 120-day intervals). This sampling continued from 1986 to the present at three sites (S1, S3 and S4) on the Rio Chaballos, since 1988 at one site on the Rio Chaballos (S2) and since 1990 at all other sites on the Rios La Viella, Castañedo and Choudral.

Annual production ($P_A$) and turnover ratios ($P/B_A$) were estimated for the years 1986 to 1999, and year-class production ($P_T$) and turnover ratios ($P/B_T$) were estimated for the year-classes emerged in the same years 1986 to 1999. The estimation of production attributes was as follows: recruitment ($R_c$, ind m$^{-2}$) was taken as the number of juveniles in May, when these fish were 2 months old, representing the first numerical census of each year-class. Density, biomass and production were calculated for each single year-class; production were calculated for each single year-class, whereas annual density, biomass and production were calculated for each single year. Mean density of each age-class averaged across time intervals among censuses (i.e. 120 days) summed over all age-classes for a given year. The estimation of year-class production ($P_T$, g m$^{-2}$) followed Chapman (1978). To this end, the initial biomass ($B_i$, g m$^{-2}$) at the beginning of each 120-day time interval was estimated as the mean individual mass ($W_i$, g)$^*$density ($N_i$, ind m$^{-2}$), and the mean biomass ($B_{M,T}$, g m$^{-2}$) for those time intervals was $B_1 + B_2/2$, where $B_1$ and $B_2$ are the initial and final biomasses at the beginning and end of that time interval, respectively. Instantaneous growth rate ($G$) was calculated as log ($W_2/W_1$)/$T$, where $W_1$ and $W_2$ are the mean mass of
the individuals at the beginning and at the end of that time interval, respectively, and $T$ is the time interval between censuses (i.e. c. 120 days). Production for each time interval was calculated as the product of mean biomass ($B_m$) $\times$ growth rate ($G$) $\times$ number of days ($T$). Moreover, previous studies on the fecundity of these populations (Lobón-Cerviá et al., 1997), combined with quantification of the number of female spawners prior to annual spawning events, permitted the estimation of the number of eggs produced by the breeding population for each site and year (Lobón-Cerviá, 2003). Thus, year-class production ($P_{Yc}$, g m$^{-2}$ per year) was calculated by adding the production rates for every 120-day interval across age-classes over the year.

Linear and nonlinear models were used to describe functional relationships among production-related attributes and/or habitat-related factors. These included linear and power regressions in the form:

$$\hat{Y} = A + BX$$  \hspace{1cm} (Model1)

and

$$\hat{Y} = AX^B$$  \hspace{1cm} (Model2)

Moreover, the relationships between $P/B$ ratios versus recruitment ($R_c$) and annual density ($N_A$) both approached asymptotes and we explored a model of the form:

$$\hat{Y} = AS[1 - e^{-K(X+U)}]$$  \hspace{1cm} (Model3)

where $A$ is the asymptotic value of $Y$, $K$ is the rate at which $Y$ increases with increasing $X$ and $U$ is the intercept on the $Y$-axis when $X = 0$. Moreover, production-related attributes versus site depth (cm) described nonlinear, two-phase trajectories with an increase up to a threshold followed by a continuous decline beyond that threshold. For these cases, we explored two different models, a parabolic function in the form:

$$\hat{Y} = A + BX + CX^2$$  \hspace{1cm} (Model4)

and a two-phase linear regression in the form:

$$\hat{Y} = A_1 + B_1D(D<U) + A_2 + B_2D(D \geq U)$$  \hspace{1cm} (Model5)

For computational purposes, Model 5 can be rewritten as:

$$\hat{Y} = (A_1 + B_1D) \times (D<X) + [A_1 + (B_1X + B_2D - B_2X)] \times (D \geq X)$$

which has the advantage that only one intercept ($A_1$) and two slopes ($B_1$ and $B_2$) must be estimated.

To assess the suitability of a model to fit a single data set, nonlinear models were firstly compared with linear regressions and secondly with more simple nonlinear models based on the Akaike's information criterion (AIC, Motulsky & Christopoulos, 2004). Overall, when comparing two models, the one with a lower AIC score best fits the data set. However, we further calculated the likelihood that one out of two competing models is the best. This likelihood is based on the differences between corrected AIC$_c$ values, where a difference between AIC$_c > 2$ implies a $\geq 75\%$ probability that the model is the best (Motulsky & Christopoulos, 2004). Once suitable models were selected for single data sets, they were fitted with Quasi-Newton least-squared algorithms.

### Results

#### Population age-structure

All populations were composed of age-0 to age-3 individuals, with the exception of the two sites on the Rio Choudral where the oldest age-class (age-3) was occasionally missing. Overall, there was a consistent pattern in the contribution of each age-class (mean contribution averaged across years) to the annual production rates ($P_{A}$, Fig. 1a), with age-0 and age-1 contributing $>75\%$ to the total production, with only a weak contribution from age-2 and age-3 individuals. However, there were at least five exceptions to this pattern, occurring at the least productive sites of the four streams: site 4 on the Rio Chaballos, site-5 on the La Viella, site 10 on the Castaño and sites 11 and 12 on the Rio Choudral (Fig. 1). At these sites, the production of age-0 and age-1 individuals was consistently low, and their contribution to total annual production was only slightly greater than age-2 and age-3 (Fig. 1a).

Annual $P/B_A$ ratios (Fig. 1b) declined consistently with age and were greater for age-0 > age-1 > age-2 > age-3, and the relative contribution of each age-class showed no significant difference among sites ($F_{10} = 0.68$, $P = 0.72$ for age-0; $F_{10} = 0.93$, $P = 0.52$ for age-1; $F_{10} = 1.98$, $P = 0.10$ for age-2 and $F_{10} = 0.70$, $P = 0.72$ for age-3).
Spatial and temporal variations in production (P) and P/B ratios

Overwhelming temporal and spatial variations typified annual production (\( P_A \)) and \( P/B_A \) ratios as much as year-class production (\( P_T \)) and \( P/B_T \) ratios (Fig. 2). A nested ANOVA (year within sites within streams) highlighted that ‘site’ and ‘year’ effects were significant, and their combined effect explained c. 60% of the variation in production and 38.5% and c. 60% of the variations in year-class \( P/B_T \) and annual \( P/B_A \) ratios, respectively (Table 1). However, the effect of ‘stream’ only was almost significant for both year-class (\( P_T, P = 0.10 \)) and annual (\( P_A, P = 0.08 \)) production and explained a substantial amount of variation (18.2% for \( P_T \) and 24.1% for \( P_A \)) but had no effect on turnover (Table 1).

Interestingly, several sites where annual production was highest also showed remarkably wide temporal variation (Fig. 2). For example, at the most productive sites (sites 1 and 2 on the Rio Chaballos), annual production averaged across years was \( P_A = 15.5 \text{ g m}^{-2} \text{ per year} \), but varied substantially more temporally (CV% = 83.2 and 52.2) than that at the least productive sites (sites 11 and 12 on the Rio Choudral), where mean annual production averaged only \( 3.4 \text{ g m}^{-2} \text{ per year} \) and was less temporally variable, i.e. \( \text{CV}_A = 24 \) and 25.8, respectively. Variation was intermediate at all other sites (Fig. 2).

Variance of annual production across the years (\( s^2 \)) typically greatly exceeded the mean (\( P_A \)), except at the two sites on the Rio Choudral. When considering temporal variation in streams (sites within streams pooled), the variances were also much greater than the means for Rio Chaballos: \( s^2 = 92.7 > \mu = 14.6 \); Rio La Viella: \( s^2 = 17.6 >> \mu = 10.1 \) and Rio Castanedo: \( s^2 = 20.3 >> \mu = 8.4 \), whereas the opposite occurred at Rio Choudral where \( s^2 = 0.8 < \mu = 3.1 \). Patterns of variances >> means unequivocally indicated that annual production (\( P_A \)) did not fluctuate randomly over the years, but rather clustered into groups of years. A more detailed analysis of the time series highlighted several sets of common years: a set of four successive years (1986–1989) when production was twice that in any other year (i.e. mean \( P_A = 25.4 \text{ g m}^{-2} \text{ per year} \)); a set of 2 years of markedly lower rates included 1990 and 1991 (mean \( P_A = 9 \text{ g m}^{-2} \text{ per year} \)); and a second set with still lower rates (mean \( P_A = 6 \text{ g m}^{-2} \text{ per year} \)) included 1998 and 1999. A set of intermediate productive years (mean \( P_A = 11.6 \text{ g m}^{-2} \text{ per year} \)) included 1992, 1993 and 1994, and yet another set of intermediate years with slightly lower rates (mean \( P_A = 8.5 \text{ g m}^{-2} \text{ per year} \)) included 1995, 1996 and 1997.

A further exploration for evidence of temporal covariation or synchrony in annual production (\( P_A \)) was performed through Spearman rank correlations among sites. Pairwise correlations (all sites versus all other sites; Table 2) revealed that, among the 66 possible pairwise combinations, 55 were significant at least at \( P < 0.05 \); in 10 instances, the significant levels were at 0.05 > \( P < 0.010 \). And, in only one instance was the significance level \( P > 0.10, R = 0.19 \) (Table 2). These results support the hypothesis of a strong temporal synchrony in annual production across sites and streams and that, despite the disproportionally different temporal variability in annual production among sites, there was a strong covariation with...
concurrent years of high, low or intermediate rates fluctuating synchronously across the entire river drainage over the years.

Relationships among annual ($P_A$) and year-class production ($P_T$) and annual ($P/B_A$) and year-class ($P/B_T$) ratio

An exploratory analysis based on correlations revealed that year-class production during the lifetime ($P_T$) was similar in magnitude to annual production ($P_A$) and appeared closely related. The fit of a linear regression (Fig. 3b) confirmed the strength of this relationship ($R^2 = 79.9$, $P < 0.001$) and further showed that the intercept was not significantly different from zero ($F_{1,128} = 0.83$, $P = 0.36$). A new fit of the same data with the intercept set to zero yielded ($R^2 = 79.9$, $P < 0.001$):

$$P_T = 0.94P_A$$

Despite the similarity between the estimated slope $B = 0.94$ and equality (i.e. $B = 1$), the null hypothesis could not be rejected ($F_{1,129} = 1579$, $P < 0.001$), implying that $P_A$ and $P_T$ are similar, but annual production increases at a slightly greater rate than year-class production (Fig. 3).
Moreover, annual and year-class \( P/B \) ratios were positively, linearly related (Fig. 3a), and the corresponding fit was significant (\( R^2 = 30.1, P < 0.001 \)) and yielded:

\[
P = B_T = 3.0 + 1.35 P_A
\]

When the slope of this regression \( B = 1.3 \) was tested for differences from equality (i.e. \( B = 1 \)), the \( F \)-value was almost significant (\( F_{1,129} = 3.16, P = 0.08 \)), suggesting that the null hypothesis could not be rejected. Nonetheless, we explored a regression with slope \( B = 1 \) to fit these data and yielded (Fig. 3a; \( R^2 = 28.5, P < 0.001 \)):

\[
P = B_T = 3.5 + P_A
\]

We could not reject the null hypothesis that the intercept (i.e. 3.5) differed significantly from a value of four (the number of age-classes).

Consequently, the annual production rate (\( P_A \)) for any given year was quite similar to the production of a single year-class during its lifetime, whereas annual turnover ratios (\( P/B_A \)) were the year-class turnover ratios (\( P/B_T \)) plus 3.5 (years). Note, however, that if we consider the actual range of \( P/B_A \) values instead of the mathematical fit, then the annual \( P/B_A \) ratio was simply the year-class \( P/B_T \) ratio plus the number of age-classes (i.e. four).

The importance of density-dependence for production (\( P \)) and \( P/B \) ratios

For all year-classes pooled, year-class production (\( P_T \)) was strongly linked to recruitment (\( R_c \)). A comparison
of Akaike’s (AIC\textsubscript{c}) values between a linear and a power model suggested a 99.7\% probability that the power model was the correct model. A fit of this model to data was highly significant (Fig. 4a, \( R^2 = 70.1 \), \( P < 0.001 \)) and yielded:

\[ P_T = 23.0Rc^{0.606} \]

In contrast, annual production (\( P_A \)) was positively and linearly related to mean annual density (\( N_A \)) (Fig. 4c, \( R^2 = 60.3 \), \( P < 0.001 \)):

\[ P_A = 3.08 + 56.1N_A \]

Year-class (\( P/B_T \)) ratios increased with increasing levels of recruitment. A comparison of Model 3 versus Model 2 yielded an 85\% probability that Model 3 was the correct one and a fit of this model to data gave:

\[ PB_T = 5.95[1 - e^{-4.34(Rc-0.21)}] \]

indicating that at low values of recruitment, year-class (\( P/B_T \)) ratios increased rapidly with increased recruitment up to an asymptote at \( PB_T = 6 \) and then remained fairly constant at high values of recruitment (Fig. 4b; \( R^2 = 55.2 \)).

Annual \( P/B_A \) ratio against mean annual density (\( N_A \)) indicated a similar relationship. Again a comparison between Models 3 and 2 revealed a 72\% probability that Model 3 was better and its fit to the data yielded:

\[ P/B_A = 2.13[1 - e^{-5.65(N_A-0.10)}] \]

with an asymptote at \( P/B_A = 2.1 \) (Fig. 4d; \( R^2 = 52.1 \)).

The fits of Model 3 to the \( P/B \) ratios versus recruitment (\( Rc \)) and mean annual density (\( N_A \)) offered evidence of strong density-dependent effects on \( P/B \) ratio (that became negligible when the ratio reached a threshold after which increased density had no further effect). While year-class \( P/B_T \) ratio reached an asymptote of about 6 at a recruitment of c. 0.35 ind m\textsuperscript{-2}, annual \( P/B_A \) ratio reached an asymptote of c. 2.1 at a mean annual density of about 0.15 ind m\textsuperscript{-2}. Both ratios then remained constant over a broad range of values of recruitment and density beyond these thresholds. These relationships further inferred, as noted previously, that year-class \( P/B_T \) ratio was simply the annual \( P/B_A \) ratio plus the number of year-classes (i.e. four). This relationship, however, holds only at high densities or above the threshold after which density had no further effects.

The importance of site specificity in determining spatial variations in production (\( P_A \) and \( P_T \)) and turnover (\( P/B_A \) and \( P/B_T \))

The strong effect of ‘site’ on density, as highlighted by the nested ANOVA, and the density-dependent nature of production, \( P_A \) and \( P_T \), and turnover, \( P/B_T \) and \( P/B_A \), suggested that site specificity [in the form of site depth, recruitment (\( Rc \)) and annual density (\( N_A \))] should have explained, at least partly, variation among sites.

Visual inspection of plots of the mean (averaged across sites) values of \( Rc \), \( P_t \) and \( P/B_T \) and \( N_A \), \( P_A \) and

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**Fig. 4** Relationship between (a) year-class production (\( P_T \), g m\textsuperscript{-2}) versus recruitment (\( Rc \), ind m\textsuperscript{-2}): the regression is \( P_T = 23.0Rc^{0.61} \) (\( R^2 = 0.66 \), \( P < 0.001 \)); (b) year-class turnover ratios (\( P/B_T \)) versus recruitment (\( Rc \), ind m\textsuperscript{-2}): the regression is \( P/B_T = 5.95[1 - e^{-4.34(Rc-0.21)}] \) (\( R^2 = 0.55 \), \( P < 0.001 \)); (c) annual production (\( P_A \), g m\textsuperscript{-2} per year) versus mean annual density (\( N_A \), ind m\textsuperscript{-2}): the regression is \( P_A = 3.08 + 56.1N_A \) (\( R^2 = 0.60 \), \( P < 0.001 \)); and (d) annual turnover ratios (\( P/B_A \)) versus mean annual density (\( N_A \), ind m\textsuperscript{-2}): the regression is \( P/B_A = 2.13[1 - e^{-5.65(N_A-0.10)}] \).
$P/B_A$ versus site depth (cm) highlighted consistent two-phase patterns (Fig. 5). The values of these six variables increased linearly from the lowest values attained at the shallowest sites (c. 15 cm) to maximum values at sites with mean depth (21.5 cm). Beyond this point, this suite of density and production variables then declined with increased site depth beyond the mean to attain similarly low values at the shallowest (c. 15 cm) and at the deepest sites (c. 27 cm). In sum, the two sets of data, including year-class recruitment ($Rc$), production ($P_T$) and turnover ($P/B_T$) and annual density ($N_A$), production ($P_A$) and turnover ($P/B_A$), reach maximum values at sites of mean depth and declined at both shallower and deeper sites. For the six instances, two-phase linear regressions (i.e. Model 5) were compared with parabolic functions (Model 4) and revealed probabilities $>75\%$ for the two-phase regressions, indicating that this model was the best for the six instances, and fits for all six variables to site depth were all significant (Table 3).

Moreover, plots of site-specific means (averaged across year-classes) of year-class production ($P_T$) and turnover ($P/B_T$) versus recruitment ($Rc$; Fig. 6a,b), and also of site-specific means (averaged over years) of annual production ($P_A$) and turnover ($P/B_A$) versus site depth (cm). Regression coefficients and other details are given in Table 3; sites as in Fig. 2.

Fig. 5 Two-phase linear regressions fitted to (a) recruitment ($Rc$, ind m$^{-2}$), (b) year-class production ($P_T$, g m$^{-2}$), (c) year-class $P/B_T$ ratios, (d) mean annual density ($N_A$, ind m$^{-2}$), (e) annual production ($P_A$, g m$^{-2}$ year$^{-1}$) and (f) annual $P/B_A$ ratios (year$^{-1}$) versus site depth (cm). Regression coefficients and other details are given in Table 3; sites as in Fig. 2.
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Table 3 Coefficients of two-phase regressions in the form $Y = (A_1 + B_1X)(D < X) + [A_2 + B_2X + B_1X^2 + B_2X^2](D > X)$ fitted to recruitment ($R_c$, ind $m^{-2}$), mean annual density ($N_A$, ind $m^{-2}$), mean annual turnover ($P_A$, g $m^{-2}$ per year) and mean (annual turnover ($P_A$, g $m^{-2}$ per year) and =annual turnover ($P_A$, year$^{-1}$) versus the site depth (cm) of the 12 study sites as depicted in Fig. 5.

<table>
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<tr>
<th></th>
<th>$A_1$</th>
<th>$B_1$</th>
<th>$K$</th>
<th>$B_2$</th>
<th>$R^2$</th>
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<td>-0.07</td>
<td>66.1</td>
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<td>2.21</td>
<td>20.7</td>
<td>-0.88</td>
<td>46.6</td>
</tr>
<tr>
<td>Year-class turnover ratios</td>
<td>2.4</td>
<td>0.15</td>
<td>21.0</td>
<td>-0.20</td>
<td>53.6</td>
</tr>
<tr>
<td>Mean annual density</td>
<td>-0.8</td>
<td>0.06</td>
<td>21.2</td>
<td>-0.05</td>
<td>67.3</td>
</tr>
<tr>
<td>Annual production</td>
<td>-35.8</td>
<td>2.49</td>
<td>20.5</td>
<td>-1.01</td>
<td>53.7</td>
</tr>
<tr>
<td>Annual turnover ratios</td>
<td>0.51</td>
<td>0.06</td>
<td>21.0</td>
<td>0.10</td>
<td>73.1</td>
</tr>
</tbody>
</table>

$A_1$ is the intercept and $B_1$ and $B_2$, the left-side positive and right-side negative slopes of the two-phase lines, respectively. $K$ is the breakdown point (i.e. site depth, cm) upon which the slope changes direction and $R^2$ is the variance explained. All fits are significant at least at $P < 0.01$.

Annual densities, $N_A$ (Fig. 6c,d), highlighted consistently positive linear trends across the entire range of variation. Linear regressions for these relationships were all highly significant (Table 4).

These two sets of regressions offered compelling evidence that, independent of the stream where a site was located, those of mean depth supported not only greater recruitment but also higher density, production and $P/B$ ratios. At the opposite extreme, shallower and deeper sites typically supported lower recruitment and, correspondingly, lower density, production and $P/B$ ratios.

Discussion

This long-term, large-scale study highlighted a very wide range of variation in brown trout production across streams and sites and over a long timescale, 14 years across 12 sites spread along four different tributaries of the Rio Esva (Lobón-Cerviá, 2009). The production potential of the Rio Esva drainage appears spatially heterogeneous, with streams differing in their productive potential, from highly productive (i.e. Rio Chaballos) to unproductive (i.e. Rio Choudral), with streams in between (Rio La Viella and Rio Castañedo) interspersed throughout the river drainage.

Further, annual production ($P_A$, g $m^{-2}$ per year) and $P/B_A$ ratios varied so widely among streams, sites and years that the data reported here actually includes all the variation reported for streams inhabited by one or more salmonid species worldwide (Mann & Penczak,

![Fig. 6 Positive linear regressions fitted to the relationships between the site specific (a) mean year-class $P/B_T$ ratios averaged across years versus mean recruitment ($R_c$, ind $m^{-2}$) averaged across years: the regression is $P/B_T = 4.24 + 2.34 R_c$ ($R^2 = 80.2$, $P < 0.001$); (b) mean year-class production ($P_T$, g $m^{-2}$) averaged across years versus mean recruitment ($R_c$, ind $m^{-2}$): the regression is $P_T = 3.24 + 21.5 R_c$ ($R^2 = 67.4$, $P = 0.001$); (c) mean annual $P/B_A$ (year$^{-1}$) ratios versus the mean annual density ($N_A$, ind $m^{-2}$) averaged across years: the regression is $P/B_A = 1.09 + 1.17 N_A$ ($R^2 = 50.3$, $P = 0.01$); and (d) mean annual production ($P_A$, g $m^{-2}$ per year) averaged across years versus mean annual density ($N_A$, ind $m^{-2}$): the regression is $P_A = -1.53 + 33.2 N_A$ ($R^2 = 79.6$, $P < 0.001$).](https://www.blackwellpublishing.com/doi/10.1111/j.1365-2427.2011.02616.x)
1986; Kwak & Waters, 1997) and, with a few exceptions, almost all the variation in production rates reported for stream-living fishes (Mazzoni & Lobón-Cerviá, 2000). Despite such extreme variation, the maximum annual production rates observed here \( P_A = 38.3 \text{ g m}^{-2} \text{ per year} \) was similar, or only slightly higher, than the greatest annual rates reported for any other stream-dwelling salmonid. For example, for populations within the European distributional range of brown trout, the greatest annual production rates were 35.0 and 33.9 g m\(^{-2}\) per year for a resident and a sea-migratory population, respectively, in U.K. streams (Crisp et al., 1975; Elliott, 1993) and 33.2 g m\(^{-2}\) per year for a Danish lake-migratory population (Mortensen, 1982). These maximum rates are also similar to those reported for non-native populations in North America, where values of annual production 36.0 and 32.2 g m\(^{-2}\) per year were reported for streams in Pennsylvania and Minnesota, respectively (Brynildson & Brynildson, 1984; Waters, 1999), and for other stream-living salmonids worldwide (Kwak & Waters, 1997). The few data available for year-class production precluded comparisons but, again, a maximum year-class production (\( P_T \)) of 40.2 g m\(^{-2}\) for our Cantabrian populations was only slightly higher than the highest reported in the literature (33.9 g m\(^{-2}\) for a sea-migratory population in a U.K. stream; Elliott, 1993). This comparison can be extended to \( P/B \) ratio, which reached a maximum annual \( P/B_A \) of 2.1 and year-class \( P/B_T \) of 6.0, values that are very similar to \( P/B_A = 2.7 \) and \( P/B_T = 5.5 \) also reported for sea-migratory brown trout (Elliott, 1993) and to all other stream salmonid populations (Mann & Penczak, 1986).

Table 4 Coefficients for the linear regressions \( Y = A + B \times X \) fitted to the relationships between site-specific mean year-class \( P/B_T \) ratios and mean year-class production (\( P_A \), g m\(^{-2}\)) versus mean recruitment (\( R_C \), ind m\(^{-2}\)) (as depicted in Fig. 6a,b) and mean annual \( P/B_T \) ratios and mean annual production rates (\( P_A \), g m\(^{-2}\) per year) versus mean annual density (\( N_A \), ind m\(^{-2}\)) (as depicted in Fig. 6c,d). \( R^2 \) is the variance explained and \( P \) is the significance level.

<table>
<thead>
<tr>
<th></th>
<th>( A )</th>
<th>( B )</th>
<th>( R^2 )</th>
<th>( P )</th>
</tr>
</thead>
<tbody>
<tr>
<td>( P/B_T ) versus ( R_C )</td>
<td>4.24</td>
<td>2.34</td>
<td>80.2</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>( P_T ) versus ( R_C )</td>
<td>3.24</td>
<td>21.5</td>
<td>67.4</td>
<td>0.001</td>
</tr>
<tr>
<td>( P/B_A ) versus ( N_A )</td>
<td>1.09</td>
<td>1.17</td>
<td>50.3</td>
<td>0.01</td>
</tr>
<tr>
<td>( P_A ) versus ( N_A )</td>
<td>-1.53</td>
<td>33.2</td>
<td>79.6</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>

Although these general consistencies, a more detailed analysis highlighted a strong tendency for production rates to be site specific, with consistently highly productive sites alternating with consistently low and intermediate productivity sites along the stream length. Importantly, at sites where production was greatest, temporal variability in annual production among years was greater than that at other sites.

Apparently, habitat quality varies sufficiently among sites within streams for production to be highly site specific. However, the temporal (among years) variability in habitat quality at the site scale was less than temporal variability in annual production. Assessments of the physical structure of sites (based on systematic mapping) and water chemistry during the study years (unpublished) showed that the physical habitat was temporally persistent whereas water chemistry varied predictably with season and annual fluctuations in discharge, offering little evidence that inter-annual variation in production is driven by fluctuations in the potential productive capacity of the sites. Clearly, other factors than the habitat quality must contribute to inter-annual variations in production rates.

Previous studies on these very same populations and year-classes demonstrated that the magnitude of annual recruitment is determined by interactions between local and regional factors. Rainfall-induced stream discharge soon after the time of emergence interacts with channel structure to determine the availability of space suitable for the youngest juveniles, which ultimately determines site-specific recruitment (Lobón-Cerviá & Rinconcón, 2004; Lobón-Cerviá, 2007). However, rainfall is also year specific and operates across the entire river drainage; as such, annual stream discharge ultimately determines year-specific recruitment. These processes generate strong temporal synchrony in recruitment across streams and sites throughout the entire river drainage (Lobón-Cerviá, 2004, 2007) and result in consecutive years of relatively high, intermediate or low recruitment and associated strong, intermediate or weak year-classes. Thus, when data for all sites and years were pooled, recruitment, as a single factor, explained 71% of all the variation in year-class production (\( P_T \)). This is similar to that described by Elliott (1993) for a sea-trout population in a U.K. stream, where the combined effect of density-dependent survival (57%) and density-independent growth (17.5%) accounted for 74.5% of the variation in production among year-classes. In addition, recruitment alone accounted for...
>55% of the variation in year-class $P/B_T$ ratios. These results strongly support the hypothesis that new recruits to a year-class at any site or year is a primary determinant of the subsequent year-class production ($P_T$) and turnover ($P/B_T$) over the entire lifetime (Lobón-Cerviá, 2009).

Moreover, heterogeneity in the spatial structure of sites along the stream length has profound effects on recruitment. In years favourable for recruitment, and independently of the stream where they are located (for example, site 1 and site 3 in Rio Chaballos and site 6 and site 7 in La Viella), sites of average depth had disproportionately more recruits than shallower or deeper sites. In unfavourable years, recruitment was low even at sites of overall average depth and was similar to that observed at shallower or deeper sites, where year-to-year variations in recruitment were minor. Thus, favourable years enhanced among-site differences in recruitment, whereas unfavourable years minimised differences among sites (i.e. 1990, 1993 and 1995), to the extent that among-site differences in recruitment were completely obscured.

The two-phase effect of depth on recruitment was sufficiently strong to drive year-class production ($P_T$) and $P/B_T$ ratios but also importantly had strong effects on annual density ($N_A$), production ($P_A$) and turnover ($P/B_A$). In particular, shallow and deep sites not only produce fewer recruits, but also density, production and $P/B$ ratios were low relative to sites of intermediate depth. As a consequence, differences among sites in production and $P/B$ ratio appeared to be driven directly by site-specific recruitment, and ultimately by site depth. Since recruitment is site specific and varies widely across the years, and temporal variation is also site specific, year-class production ($P_T$) and $P/B_T$ ratio are also site specific and vary widely across the years, while the range of temporal variation is also site specific. Mean annual density ($N_A$) is concurrently determined by the combined effect of recruitment in addition to the recruitment-dependent density of three accompanying age-classes, with a predominant contribution from the two youngest age-classes (age-0 and age-1). As a consequence, short-term combinations of favourable and unfavourable years for recruitment may dramatically change the contribution of age-0 and age-1 individuals and bring about strong variations in annual density ($N_A$) and, hence, in annual production ($P_A$) and turnover ($P/B_A$) over the years.

Overall, the results emphasise the importance of site specificity as a major driver of spatial variation in recruitment along streams and, in turn, confirm the role of density-dependence of both recruitment and annual density as major drivers of year-class and annual production and $P/B$ ratios. The relative importance of these drivers has been the topic of much research. For example, Le Cren (1969) identified site depth as a major determinant of spatial variation in brown trout production in U.K. streams, as did Newman & Waters (1989) for introduced brown trout in Minnesota streams. Further, Carlile (1977) emphasised the importance of recruitment for the production of brook trout *Salvelinus fontinalis* (Mitchill) in U.S. streams, whereas Randall & Chadwick (1986) stressed the importance of annual density for Atlantic salmon (*Salmo salar* L.) production in Canadian streams. Clearly, the strong links between recruitment, density, year-class ($P_T$) and annual production ($P_A$) highlighted in this study and elsewhere emphasise the important role of these factors across species and populations and across scales of space and time.

The power of an ecological process, operating at a single but critical life stage that only lasts for several days after emergence (i.e. recruitment; Lobón-Cerviá & Rinco, 2004; Lobón-Cerviá, 2007), to regulate the productive dynamics of stream salmonids is notable. Further, the ability of recruitment to regulate the dynamics of production across sites, and to be foremost among the various processes that may occur across the lifetime (e.g. the effects of density-dependent and density-independent factors operating on growth and mortality), is also remarkable.

Interestingly, year-to-year variation in the (discharge dependent) carrying capacity of sites to sustain recruits, in combination with the effects of short-term conjunctions of favourable and unfavourable years, results in population densities that rarely attain the potential maximum of the sites. Across the study years, recruitment reached maximum values in 1987 and then only once more in 1996, but neither of these two years was followed or preceded by other years of maximum recruitment. Thus, mean annual density ($N_A$), which includes the density of four successive age-classes, only scarcely reaches the overall carrying capacity (i.e. the maximum density expected if four successive years maximise recruitment and, subsequently, year-classes density).
Moreover, density-dependent annual production follows the same temporal pattern and, as a consequence, only rarely attains the full productive potential of sites, thus corroborating the views of Mann & Penczak (1986) and Kwak & Waters (1997) about stream-dwelling salmonids in general.

An essential aim of ecological research (Clark et al., 2001), and the impetus for long-term investigations on the production dynamics of stream salmonids (Elliott, 1994; Waters, 1999) and other freshwater fish (Bagenal, 1978), is to reach a better understanding of complex population dynamics but also to develop models capable of predicting population changes induced either by natural events (i.e. environmental or climatic changes over temporal scales) or by human activities. This predictive ability is relevant for the management, recovery, restoration and conservation of salmonids and other populations that, with few exceptions, are over-exploited or threatened in other ways (Kemp, 2010). While many models have attempted to link population density and dynamics to habitat capacity, most are based on short-term studies and have identified a plethora of different predictive variables that are not always internally consistent and cannot be extrapolated to different environments and/or broader geographical scales (for a review see Fausch, Hawkes & Parsons, 1988).

This and other long-term studies (Hunt, 1974; Egglishaw & Shackley, 1977; Elliott, 1994; Waters, 1999; Lobón-Cerviá & Mortensen, 2005) provide compelling evidence that populations of stream-living salmonids vary in magnitude over both time (over the years) and space (within and among streams) much more than previously suspected, and neglecting such variability may hinder the development of predictive models. For example, within the context of this study, shorter-term research that, by chance, selected only a few successive years unfavourable for recruitment and, hence, with consequent low density and production rates, would highlight factors that may be irrelevant to the process concerned, limiting the inference that can be drawn regarding key drivers of population attributes. This phenomenon may also explain why quantitative relationships between factors related to habitat quality and population traits remain so elusive (Rose, 2000) and, in turn, why the salmonid literature is characterised by an overall lack of consistent patterns across populations, within and among species and regions.

Unlike density and standing crop, there are considerably fewer predictive models based on production. Kwak & Waters (1997) suggested two equations to predict annual production based on alkalinity (Model 1: \( P_A = 40.7 + 0.48 \times \text{alkalinity} \)), and annual \( P/B_A \) ratios from the number of year-classes (Model 2: \( P/B_A = 2.10 - 0.20 \times \text{number of year-classes} \)). These two models have been tested successfully with field data for other North American streams differing in alkalinity (i.e. Clark & Scruton, 1999). The Cantabrian streams in this study flow over quartz and alkalinity is extremely low or negligible; given values of alkalinity near zero, Model 1 predicts an annual production \( P_A \) of 40 kg ka\(^{-1}\), a 10% of the maximum production observed here. Moreover, for our populations with four age-classes, the Model 2 of Kwak & Waters (1997) predicts an annual turnover \( P/B_A \) of 1.3. While this value is also fairly close to the observed mean \( P/B_A \) of 1.5 for our Cantabrian populations, this value was actually predicted for populations composed of only three age-classes. Moreover, in four of the study sites, the mean \( P/B_A \) ratios were >1.5 and, for the most part, reached an asymptote of 2.1. Thus, in summary, it appears that only the prediction of Chapman (1978) that the annual \( P/B_A \) ratio should be 2 and (slightly higher in warm water streams) appeared to be fully consistent with our observations.

Despite the great spatial and temporal variation in production rate and the related difficulty in developing predictive models, we show here that relationships among production attributes can be summarised by simple mathematical models suggesting, for example, that the conventional importance given to the annual \( P/B_A \) ratio for predicting annual production \( P_A \) could be replaced by recruitment \( R_c \) and/or mean annual density \( N_A \). This recognition has important implications, as quantifying recruitment and density in the field is considerably more cost and time-effective. Both recruitment and density may, for example, be accurately estimated with one field visit at or near the end of the growing season. These measures may be readily used to predict annual production \( P_A \) and, hence, year-class production \( P_T \) given that \( P_T \) and \( P_A \) are strongly linked. In turn, year-class \( P_T \) and \( P/B_T \) ratios can be predicted from annual production \( P_A \) and \( P/B_A \) ratio. Also, \( P_T \) and \( P_A \) are similar, and the \( P/B_T \) ratio at a relatively high density is simply the \( P/B_A \) ratio plus the number of age-classes. Clearly, these production attributes have
a variety of applications to both fishery and stream management. Cross-validations of these predictive models across populations and eco-regions or different environmental conditions would provide further insight into their future applications.

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References


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