The Ghost of Density-Dependence: Environmental (Hydrological) Factors Drive the Numerical Changes of Young Migratory Trout *Salmo trutta* in a Lake District Stream (UK), 1966–1996

Javier Lobón-Cerviá and Gorm Rasmussen

Abstract Finding empirical support for the "paradigm of density-dependence" has been a major focus of ecological and fishery research. Quantifying relationships between the abundance of spawners and the subsequent recruitment is essential for testing the key prediction of density-dependent population regulation: that the number of recruits is mechanistically, but non-linearly, dependent on the number of reproducing individuals. Long-term data are required to explore such relationships, but such data are rare. Elliott and colleagues used a 30-year study of brown trout, *Salmo trutta* L. in a small UK stream to construct a stock–recruitment relationship suggesting remarkably severe density-dependent mortality of recruits at high spawners' abundance. In marked contrast, more recent studies on other brown trout populations, suggest environmental (hydrological) factors play a principal role in driving variation in recruitment. These disparate results underscore the more general controversy regarding the relative roles of density-dependent *versus* density-independent population regulation. The objective of this study was to revisit and re-analyze the data reported by Elliott in light of recent results from other trout populations. The results suggest that variation in stream discharge soon after emergence drives variation in recruitment and early survival rates, and produces the same two-phase, threshold-like recruitment patterns observed in other brown trout populations. These results cast doubt on the original interpretation of the data, and add to a growing body of evidence that environmental (hydrological) factors are the principal drivers of recruitment variation in stream-rearing salmonids.

J. Lobón-Cerviá (✉)
National Museum of Natural Sciences (CSIC), Madrid, Spain
e-mail: MCNL178@mncn.csic.es; jlobon@mncn.csic.es

G. Rasmussen
Institute of Aquatic Resources. DTU, Silkeborg, Denmark
e-mail: GR@aqua.dtu.dk

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1 Introduction

Identifying the causes of temporal fluctuations in animal populations is a central goal of ecology and fishery research. The fundamental challenge is to understand the relative importance of density-dependence (Nicholson 1933) *versus* density-independent or environmental drivers (Andrewartha and Birch 1954). Therefore, finding empirical support for the "paradigm of density-dependence"—that the populations are regulated by density-dependent feedback loops—has been a major focus of ecological research for decades (Coulson et al. 2004).

Fishes provide useful systems for exploring mechanisms of population regulation. Fish populations are typically characterized by high mortalities rates following hatching and emergence (Bradford and Cabana 1997), so the number of recruits is generally dramatically lower than the number of eggs produced by spawners, and the magnitude of recruitment is deemed to be set at, during or soon after that time period (Cushing 1996). Identifying the factors responsible for mortality during the egg-to-recruit stage is thus essential for understanding fish population dynamics (Houde 1989; Hilborn and Walters 1992; Chambers and Trippel 1997; Walters and Martell 2004). Nevertheless, distinguishing between the roles of density-dependent *versus* density-independent factors in driving recruitment remains a sufficiently elusive "*enigma*" (Frank and Leggett 1994) to warrant calls for a "*Science of Recruitment in Fish Populations*" (Cushing 1996).

The key quantitative basis of the "paradigm of density-dependence" is that the number of recruits is mechanistically but not linearly linked to the abundance of the reproductive component of the population. It follows that regardless of the factors causing mortality during the egg-to-recruit stages, the number of spawners is the principal predictor of recruitment (Trippel et al. 1997). Therefore, exploring relationships between the number of spawners and the subsequent recruitment is an essential tool for testing population regulation hypotheses.

Long-term data series with accurate estimates of the parental (ST) and recruitment (RC) abundances are required to meaningfully quantify such stock-recruitment relationships (Walters and Martell 2004). Such data are rare, but an exceptional example is a 30-year study on Brown Trout, *Salmo trutta* L. inhabiting a small UK stream. The analyses of these data by Elliott (1984, 1985, 1987, 1989, 1993, 1994), Elliott et al. (1997) and Elliott and Elliott (2006) provide evidence for remarkably dramatic density-dependent mortality in the youngest juveniles at high spawners abundance. The dome-shaped stock–recruitment curve is one of the most influential and widely cited empirical examples of density-dependent population regulation in the ecological and fishery literature (citations compiled by major scientific literature databases corroborate this statement). Nevertheless, studies based on similar spawner–recruit time series from other stream-rearing brown trout populations in Spain (Lobón-Cerviá and Rincón 2004; Lobón-Cerviá 2006, 2007; Lobón-Cerviá et al. 2017), France (Cattanéo et al. 2002) and Denmark (Lobón-Cerviá and Mortensen 2005) point rather to the primacy of environmental (hydrological) factors in driving recruitment variations. Such results are seemingly at odds with the stock–recruitment relationships highlighted by Elliott and colleagues and, in combination, obscure more than clarify the long-standing controversy on the relative roles of density-dependence *versus* density-independence underpinning population growth, persistence, and resilience in stream salmonids and other fish populations.

This study re-visits the data from Black Brows Beck described by Elliott and colleagues. The results bring into doubt the importance of the density-dependent mechanisms in driving variation in recruitment. Instead, these new analyses suggest that stream discharge operating during or soon after emergence drives variation in recruitment, a pattern consistent with those observed in other stream-rearing brown trout populations.

2 The Study Population and Data Collection

Demographic data on brown trout inhabiting a stream section of Black Brows Beck was reported by Elliott (1984, 1985, 1987, 1989, 1993, 1994), Elliott et al. (1997) and Elliott and Elliott (2006). This small stream enters Dale Park Beck, a tributary of the River Leven in northern England, and is a highly productive nursery for sea-migratory trout (Elliott 1984). Over three decades, the number of recruits was quantified at the end of May or early June in a 75 m long (60 m^2) section of the stream. The number of fertilized eggs as a proxy of the spawners' abundance, was estimated in a 45-m long (32 m^2) section downstream of the recruitment section. Further details of the study site and methods are given in Elliott (1984).

Parental density and recruitment were reported in two different studies. Elliott (1984, 1985) presents data from the 1966–1983 cohorts as eggs and recruits m^{-2}, or as the total number of eggs and recruits at the 60-m^{-2} study site. The second data set includes 13 additional cohorts (1984–1996) to complete 30 years from 1966 to 1996 and was reported in figures by Elliott et al. (1997). For this study, Figs. 1 and 2 in Elliott et al. (1997, p. 1232–1233) were scanned with an image analyzer. The data from 1966 to 1983 obtained *via* image analyzer matched the data reported by Elliott (1984, p. 340) and Elliott (1985, p. 620), confirming the accuracy of the method.

Stream discharge data were obtained from a local gauging station that recorded daily flows in m^3/s over the entire study period. The identification of this station and the corresponding data set is: National River Flow Archive; Database, nrfa_public name; Station: 73010; name: "Leven at Newby Bridge, FMS". Grid reference SD367863. Daily data were used to calculate the cumulative stream discharge over the 30 days of April. Spring rainfall data were reported by Elliott et al. (1997, Fig. 1) as the total spring rainfall with March, April and May pooled together.

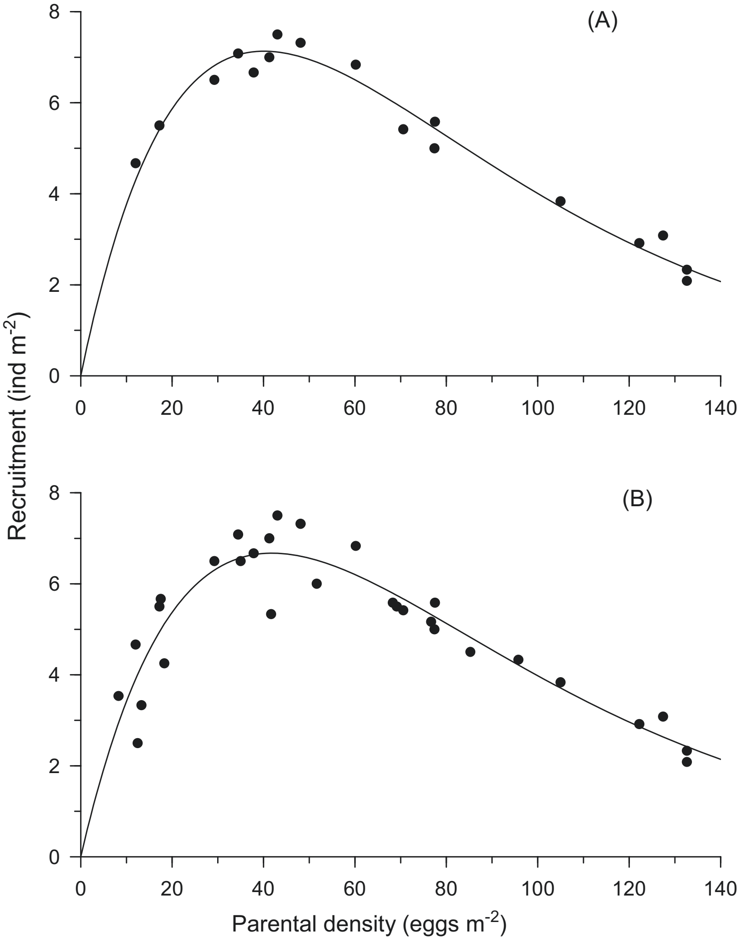

Fig. 1 Stock–recruitment relationships for Black Brows Beck brown trout with a Ricker model fitted to data. Redrawn from Elliott (1984, 1985) and Elliott et al. (1997). (**a**) Recruitment of the 1966–1983 cohorts with constants and variance explained: $A = 0.49$, $B = 0.025$ and $R^2 = 0.997$. (**b**) Recruitment of the complete data set (1966–1996) with a Ricker model fitted to data with constants and variance explained: $A = 0.042$, $B = 0.0004$ and $R^2 = 0.87$. All significant at $p < 0.001$

3 Results

3.1 Elliott's Findings: Density–Dependent Recruitment Regulation

During the 1966–1996 study period, recruitment in May/early June (stage R1 in Elliott 1985), varied between 2.1 and 7.5 m^{-2}, which is equivalent to approximately 125–450 individuals in the 60 m^{-2} study section. Spawners' density varied between

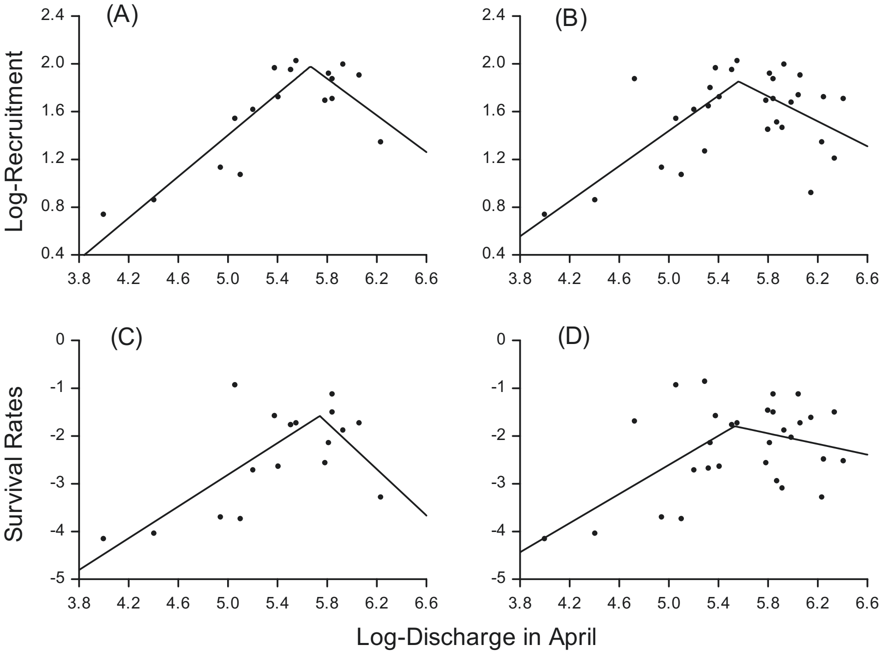

Fig. 2 Log-transformed recruitment RC, ind m^{-2} and survival rates SR = Log (RC/ST) *versus* log-transformed discharge in April (m^3/s) with two-phase linear regressions fitted to data: (**a**) Log-transformed recruitment for the 1967–1983 cohorts. Constants, variance explained and significance levels: $A = -2.92, B = 0.87, X = 5.67$ and $K = -0.77$; $R^2 = 0.81, p < 0.001$. (**b**) Log-transformed recruitment for the complete data set (1967–1996), with constants, variance explained and significance levels: $A = -2.24$, $B = 0.74$, $X = 5.56$ and $K = -0.52$; $R^2 = 0.45$, $p < 0.01$. (**c**) Survival rates for the first data set, 1967–1983, with constants, variance explained and significance levels: $A = -11.1$, $B = 1.66$, $X = 5.74$ and $K = -2.42$ ($R^2 = 0.53$, $p < 0.001$). (**d**) Survival rates for the complete data set (1967–1996), with constants, variance explained and significant level: $A = -10.2$, $B = 1.53$, $X = 5.53$ and $K = -0.56$; $R^2 = 0.30$, $p < 0.01$

5 and 140 eggs m^{-2}. Elliott (1984, 1985, 1987, 1989, 1993, 1994), Elliott et al. (1997) and Elliott and Elliott (2006) constructed parental density (ST)—recruitment (RC) relationships using a Ricker model (Ricker 1954) of the form:

$$RC = aST\,e^{-bST}$$

The result was a strikingly dome-shaped relationship indicative of strong density-dependent mortality during the egg-to-recruit life stage. For the first part of the study (1966–1983, Fig. 1a), Elliott (1984) reported that the Ricker model explained essentially all the variation in recruitment ($R^2 = 0.997$). For the extended data set (1966–1996), Elliott et al. (1997) reported that the model still explained a remarkable amount of recruitment variation ($R^2 = 0.87$) (Fig. 1b).

3.2 New Insight: Stream Discharge Explains Recruitment Variation

Based on evidence from other stream-rearing brown trout populations (Lobón-Cerviá 2006, 2007; Lobón-Cerviá and Rincón 2004, Lobón-Cerviá and Mortensen 2005, Lobón-Cerviá et al. 2017), we explored whether variation in recruitment in Black Brows Beck was related to stream discharge in April, a critical month covering hatching, emergence and recruitment settlement.

A visual exploration of the relationships between recruitment (RC, ind m^{-2}) *versus* discharge in April (henceforth, DIS, m^3/s) for the two data sets 1967–1983 and 1967–1996 highlighted strongly consistent patterns (Fig. 2). For the first data set, log-transformed recruitment *versus* log-transformed discharge demonstrated a continuous ascend/descent pattern over the whole range of discharge values. Recruitment was low in years of low discharge, increased with increased discharge up to a maximum, and then declined with further increases in April discharge (Fig. 2a). The complete data set (1967–1996) followed the same pattern (Fig. 2b). Similar two-phase, threshold relationships between the survival rates, calculated as SR = ln (RC/ST), and discharge suggest the relationship between recruitment and discharge is mechanistic (Fig. 2c, d).

We quantified these patterns using split-line, two-phase linear regressions of the form:

$$\mathrm{RC} = a_1 + b_1\,\mathrm{DIS}\left(\mathrm{DIS} \le k\right) + a_2 + b_2\,\mathrm{DIS}\left(\mathrm{DIS} > k\right)$$

with the restriction for continuity $a_1 + b_1 * k = a_2 + b_2 * k$ at the threshold point k,where the slope changes direction. For computational purposes this two-phase regression can be re-written as:

$$\mathrm{RC} = \left(a_1 + b_1\,\mathrm{DIS}\right)\left(\mathrm{DIS} \le k\right) + \left(a_1 + \left(b_1\,k + b_2\,\mathrm{DIS} - b_2\,k\right)\right)\left(\mathrm{DIS} > k\right)$$

This re-formulation has the advantage that only one intersect "a", the positive and negative slopes "b_1 and b_2", and the threshold "k", upon which the trajectory changes direction from positive to negative, need to be estimated.

For the first data set (1967–1983), the two-phase regression was highly significant ($p < 0.001$); April discharge explained 80% of the variation in recruitment (Fig. 2a). For the full data set (1967–1996) the two-phase model was still significant ($p < 0.01$), but April discharge explained less of variation in recruitment ($R^2 = 0.45$, Fig. 2b). Importantly, the same model applied to the survival rates (SR) *versus* log-transformed discharge also showed highly significant fits (Fig. 2c, d).

A very small stream like Black Brows Beck might be extremely sensitive to rainfall episodes. Therefore, I explored how spring rainfall (March, April and May pooled together as reported by Elliott) might be related to stream discharge and recruitment. Before exploring potential effects of spring rainfall on recruitment, I examined whether spring rainfall was a good predictor of discharge in April. During the study years, spring rainfall varied widely (110–570 mm). However, a rainy spring with high discharge does not necessarily imply a rainy April with high discharge. In any given year, rainy *versus* dry months may alternate with each other so that a rainy month with high discharge may be preceded or followed by a dry month with low discharge thus, yielding a spring of intermediate conditions. This complexity is revealed by plotting discharge in April *versus* spring rainfall (Fig. 3). For example, the 2 years with the lowest April discharge, 1974 and 1982, were associated with relatively dry and wet springs. Despite such variability, discharge in April was significantly related to the total spring rainfall over the study period ($R^2 = 0.29$, $p = 0.002$, Fig. 3).

Recruitment plotted *versus* spring rainfall also demonstrated a consistent ascending/descending relationship, but the outliers highlight the role of April discharge in driving recruitment (Fig. 4). Recruitment in 1982, is unexpectedly low because it corresponds to one of the lowest discharge in April recorded over the 30 study years (Fig. 2). Alternatively, the 1984 recruitment is unexpectedly high, because that year had the driest spring but a more moderate April discharge (Figs. 2 and 4). After omitting these 2 years, the data conformed to a two-phase relationship that explained 44% of the variation in recruitment ($p < 0.05$). Consequently, both discharge in April and spring rainfall appeared to drive variation in recruitment over the study

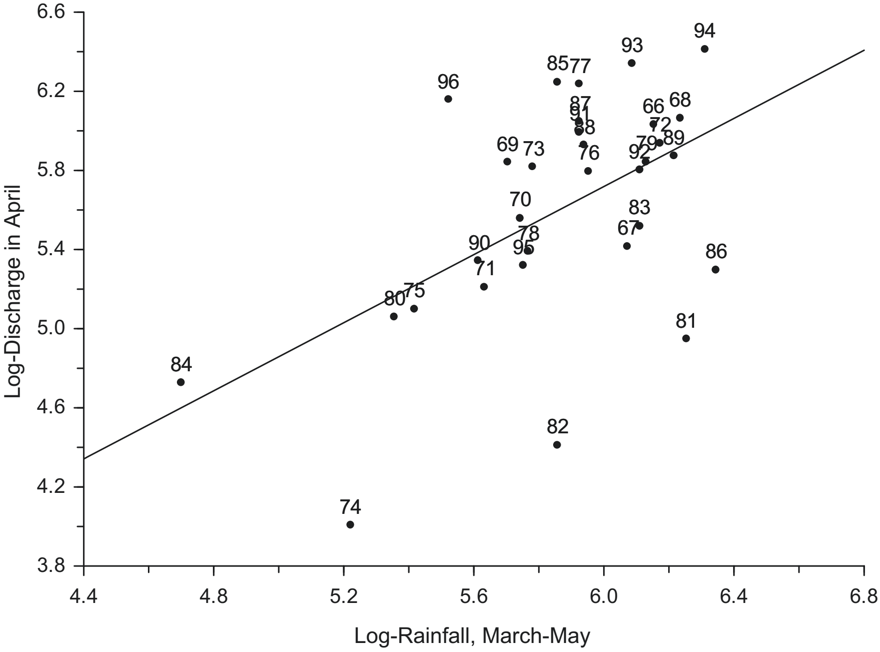

Fig. 3 Positive linear relationship between log-transformed discharge in April (m^3/s) *versus* log-transformed rainfall (mm) over the spring months (March, April and May pooled together). Constants for the linear regression, variance explained and significant level: $A = 0.55$, $B = 0.86$, $R^2 = 0.30$, $p = 0.002$

period. Collectively, these relationships offer compelling evidence to support a major role of rainfall/discharge conditions soon after emergence as a major determinant of recruitment abundance.

We applied the corrected Akaike's Information Criterion (Burham and Anderson 2002; Motulsky and Christopoulos 2004) to explore the relative strength of the Ricker (spawners) *versus* two-phase (environmental) models. The AICc values were calculated for each model (AICc_1 and AICc_2). The differences between the two AICc values (ΔAIC) provide an estimate of how many times more likely a particular model is. Overall, the model with a lower AICc score is more likely to be correct. The difference between the AICc scores can be further used to calculate the probability that a model is correct. A difference $\mathrm{AICc}_2 - \mathrm{AICc}_1$ =/0 indicates that the two models have an equal probability of being correct. A difference $\mathrm{AICc}_2 - \mathrm{AICc}_1 = 2$ indicates a 73% probability and those between 5 and 10 indicate 90–100% probability that the preferred model is correct.

For the first data set (1967–1983), the ΔAIC scores were $\mathrm{AIC}_{\mathrm{RC}} = -37.47$ and $\mathrm{AIC}_{\mathrm{DIS}} = -43.9$, and as a consequence, $\Delta\mathrm{AIC} = 6.9$, indicating a > 90% probability that the two-phase discharge model is the most plausible. For the whole data set, 1966–1996, the AICc scores were $\mathrm{AIC}_{\mathrm{RC}} = -22.59$ and $\mathrm{AIC}_{\mathrm{DIS}} = -69.32$ and as a

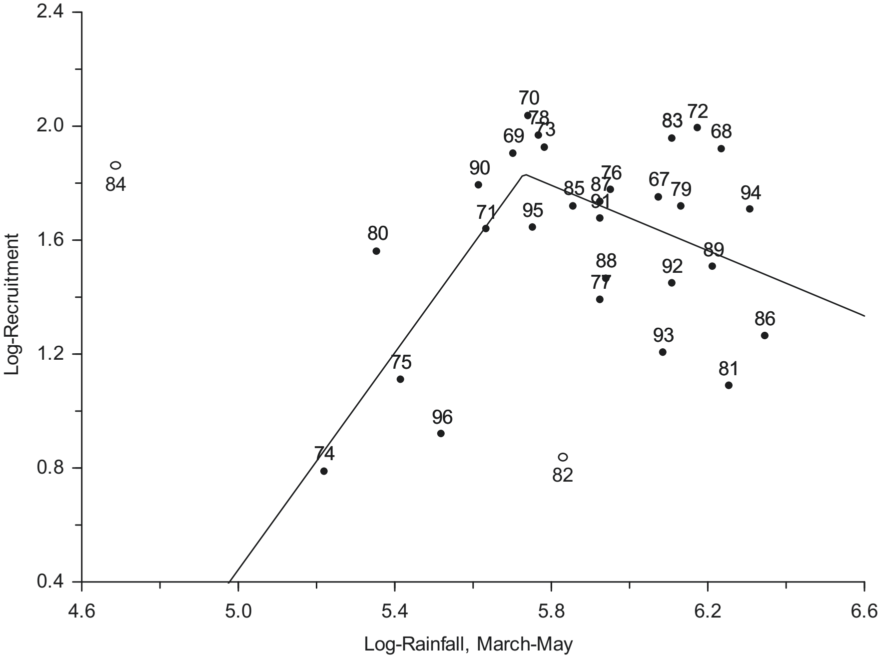

Fig. 4 Ascent/descent relationship depicted by log-transformed recruitment (ind m^{-2}) *versus* log-transformed spring rainfall (March, April and May pooled together) with a two-phase regression fitted to data. After omitting the 1982 and 1984 observations (open circles), the constants, variance explained and significant level are: $A = -9.07$, $B1 = 1.9$, $K = 5.72$ and $B2 = -0.57$, $R^2 = 0.42$, $p < 0.01$

consequence, ΔAIC = 46.7, demonstrating the discharge-dependent recruitment model is far more likely to be the most plausible than the density-dependent model.

3.3 Elliott's Findings Revisited

Evidence that environmental conditions drive variation in recruitment and survival rates requires a critical re-evaluation of the stock–recruitment relationships reported by Elliott and colleagues. It is seriously questionable that the operation of two, essentially opposing and for most incompatible factors as discharge- and density-dependence may operate simultaneously to generate two different and contradictory patterns. How can we cope with this serious discrepancy?

Inherent in the stock–recruitment relationships reported by Elliott (Fig. 1) is that: (1) recruitment is density-dependent; it follows that (2) recruitment is largely independent of the large variation in the environmental (hydrological) conditions, particularly at high parental density; (3) at low spawners abundance, recruitment increases with increased parental density up to a threshold assumed to be the carrying capacity. (4) The carrying capacity that sustains maximum recruitment magnitudes is constant over time. However, (5) along the right-side wing, recruitment attains values far below the threshold upon which recruitment declines abruptly with increased parental density and (6) the slope of the right-side wing is sufficiently steep to predict that a minor increase in parental density would result in population extirpation (i.e. RC = 0). Based on the preceding re-analysis of Elliott's original data, we consider the following points in turn:

Elliott (1984) argued that recruits are highly territorial. In other words, the youngest juveniles compete for and defend territories after emerging from the gravel and moving across the water column in search of feeding positions. Even if the territories were exclusive, their number likely depended on discharge soon after emergence, which varied from 54.9 m^3/s to 610 m^3/s during the study period. If habitat availability drives competition and fry mortality, it is unclear how recruitment was similar (i.e. 2.0–3.5 recruits m^{-2}) in 1993 and 1996. when the parental density was lowest, with only 13 and 12 eggs m^{-2} but discharge was highest with 567.5 and 471.7 m^3/s and, at the opposite extreme, in 1974, 1975, 1981 and 1982, when the parental density was ten times higher with 122.2, 127.4 and 132.6 eggs m^{-2} but the discharge was an order of magnitude lower. Such inconsistency is explained by a simple visual inspection of the two-phase, discharge-dependent recruitment relationships (Fig. 2), in which the years located at the opposing extreme of discharge with very low *versus* very high discharge conditions result in similarly low recruitment levels including exactly 1974, 1975, 1981, 1982, 1993 and 1996.

A similar argument applies to the temporal persistence of the carrying capacity. This can be defined by the amount of suitable space capable of sustaining a maximum number of recruits (assuming sufficient food availability). This being the case, the carrying capacity might necessarily be mediated, once more, by the discharge conditions offering an overwhelming variability of space suitable for recruits over the study years. This is, unequivocally demonstrated by (1) the discharge-dependent recruitment relationships where the annual-specific discharge in April represents the annual-specific carrying capacity to sustain recruits and eventually determines an annual-specific recruitment strength. Concurrently, (2) the 10 years of maximum recruitment in the stock-recruitment relationships are exactly those matching intermediate discharge conditions within the range, log (discharge) 5.2–6.1 or between 200 and 450 m^3/s (see Fig. 1 *versus* Fig. 2). That is, the highest recruitment recorded during the study years did not maximize at a temporally persistent carrying capacity *vis-a-vis* appropriate levels of parental densities but, on the contrary, when the space suitable for recruits maximize in years of intermediate discharge.

In regards to issue #6, the right-side wing of the fitted stock–recruitment curve is steep enough to predict that a small increase in the parental density would result in population extirpation. A line drawn over the declining subset of data (Fig. 5) predicts an intersection (i.e. RC = 0) at a parental density of little more than 10,000 eggs. Given female fecundity ranges from 500 to 1800 eggs (Elliott 1984, 1994), this right-side wing predicts serious risks for the population if the parental density increases with the simple addition of one large-sized (spawning, for example 1800 eggs) or two medium-sized females (spawning, for example 2000 eggs).

At the opposite extreme, the recruitment of the seven cohorts located at the left-side wing is associated with parental densities below 1000 eggs (or <30 eggs m^{-2} in Fig. 1). Again, given the fecundity range reported by Elliott (1984, 1994) implies that recruitment of those cohorts may well derive from the successful spawning of just one female. This observation is actually documented in Elliott et al. (1997, Fig. 2, p. 1233) and Elliott and Elliott (2006, Fig. 18.2) where the surviving females in November/December (life stage R_5 in his key-factors analysis) are exactly one female in 6 years and two females in 3 years.

Apparently, during the 30 years of study, the population of Black Brows Beck persisted when only one or two females successfully reproduced, whilst, at opposite extreme, the single extra female predicted to drive recruitment to zero never materialized. The question still remains as to which mechanism, other than the innate upstream migratory behaviour of sea trout, may actually guarantee the temporally persistent "en route" colonization of just one or two females to spawn successfully at the study site. The discharge–recruitment relationship contains no such inconsistency; whatever number of females spawn successfully at the study site, the subsequent recruitment is determined by the discharge conditions.

4 Discussion

The relationship between rainfall/discharge and recruitment/survival rates elucidated in this study for Black Brows Beck brown trout provide compelling evidence that environmental (hydrological) conditions drive recruitment and combined with

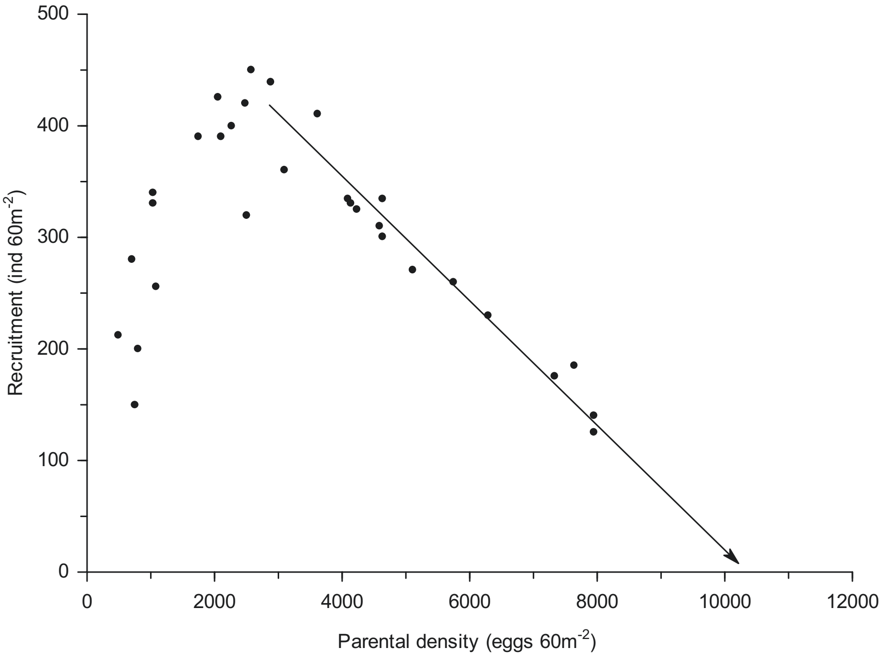

Fig. 5 Re-calculated and redrawn from Fig. 1b. A linear line drawn over the declining recruitment values of the stock–recruitment relationship indicates an intersect at the parental stock-axe of 10,300 eggs 60 m^{-2}

the biological inconsistencies of the stock–recruitment curves, cast doubt on the interpretations offered by Elliott and colleagues.

Interestingly, Elliott focused on the stock–recruitment relationships but also considered rainfall/discharge conditions on several occasions. In an early study, Elliott (1984, p. 329) concluded that, over the summer (June to August), "*rainfall and hence the discharge remained fairly constant from 1966 to 1982*". Later on, Elliott (1985, p. 630) explored relationships between recruitment and spring rainfall, and stated that: "*Neither water temperature nor rainfall significantly affected loss-rates except those for 1+parr …*". More assertively, Elliott et al. (1997, p. 1233) stated that "*the densities for 0+ parr in late May or early June* (i.e., recruitment in this study), *could be affected by spring droughts for the period March to May but this did not occur".*

Clearly, for one or another reason, Elliott overlooked the effects of the rainfall/discharge conditions in April, the critical time of fry emergence. This oversight together with the re-analysis of the stock-recruitment relationships makes the proposed dramatic density-dependent regulation of recruitment in Black Brows Beck most unlikely.

In contrast, the rainfall/discharge-recruitment relationship for Black Brows Beck matches patterns previously found in other stream-rearing brown trout populations

(Lobón-Cerviá and Rincón 2004; Cattanéo et al. 2002; Lobón-Cerviá and Mortensen 2005; Lobón-Cerviá 2007; Lobón-Cerviá et al. 2017). All these studies emphasize the "*modus operandi*" of a single environmental (hydrological) factor on recruitment, and further highlight that the effects of rainfall/discharge describe the very same, ascent/descent pattern where recruitment strength is weaker in the driest years of lowest discharge, higher in years of increased discharge up to a threshold in years of intermediate discharge, and lower again in years of highest discharge.

Nevertheless, environmentally determined recruitment is not incompatible with the operation of density-dependence in post-recruitment stages. For example, recent investigations have reported density-dependent mortality in adults, but not in juveniles in contrasting populations of brown trout (Lobón-Cerviá 2012). This appears also the case in North-American stream-rearing salmonids (Grossman et al. 2010, 2012; Kanno et al. 2015). However, even if density-dependence operates on post-recruitment stages over the lifetime, its role as a "Nicholsonian population regulator" might be minor, irrelevant or non-existent; simply because whatever number of spawners survive to the operation of density-dependence, the subsequent recruitment will be determined by the discharge conditions soon after emergence. And, given that recruitment is the major determinant of year-class strength (Lobón-Cerviá et al. 2011), the population size will fluctuate once more, tracking the vagaries of the rainfall/discharge conditions over time.

In perspective, these environmentally-determined recruitment patterns clash with the "paradigm of density dependence" and, more specifically, with the temporal stability expected to occur under the operation of density-dependence in the form of stock-recruitment relationships. Instead, these patterns offer evidence that stream-rearing salmonid populations vary through time due to density-independent variation in recruitment. Such temporal instability is consistent with the notion of non-equilibrium populations that fluctuate temporally tracking the environmental/climatic randomness (Andrewartha and Birch 1954) and further adds to the Krebs (2002)' claim: "*The assumption that we can uncover invariant relationships between population growth rate and some other variables is an "article of faith". Numerous commercial fishery applications have failed to find invariant relationships between stock and recruitment as predicted by the density paradigm"* and *"Environmental variation is the rule, and non-equilibrium dynamics should force us to look for the mechanisms of population change"*.

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