

Population fluctuations, regulation and limitation in stream-living brown trout

Martin Daufresne and Olivier Renault

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Determining causes of variation in population size and identifying factors responsible for fluctuations in species abundance are crucial questions both in theoretical and applied ecology. Based on the analysis of abundance time series, many studies have concluded that population dynamics of the stream-living brown trout (*Salmo trutta* L.) are mainly driven by year-to-year variation in the discharge level during emergence. Endogenous regulatory processes have often been considered as weak explanations for these fluctuations. This led some authors to consider that brown trout was able to persist in time with no operation of density-dependent processes. Using a model of population dynamics, we studied the influence of both discharge level during emergence and density-dependent regulatory processes on population limitation and fluctuations. We show that density-dependent and density-independent processes can act together on population density and stability at equilibrium (limitation process). We also show that the effects of internal feedbacks regulating population may often be invisible when analyzing abundance fluctuations at the interannual scale. Our results question the accuracy of studies based on the analysis of interannual fluctuations in abundance to identify processes driving population density at equilibrium.

M. Daufresne, Cemagref, 3 bis quai Chauveau, CP 220, FR-69336 Lyon Cedex 09, France (martin.daufresne@cemagref.fr). – O. Renault, Chaire d'Ecologie des populations et communautés, Inst. National Agronomique Paris-Grignon, 16 rue Claude Bernard, FR-75231 Paris cedex 05, France.

Determining sources of variation in the size of populations and identifying factors causing fluctuations in species' abundance are crucial questions in ecology (Begon et al. 1987). The relative merits of density-dependent and density-independent processes in explaining population fluctuations have been widely debated (Nicholson 1933, Haldane 1953, Andrewartha and Birch 1954). Today, these patterns are still not fully understood and retain a great deal of interest (Sinclair and Pech 1996, Ranta et al. 2000, Ricklefs and Miller 2000, Paradis et al. 2002, Kammenga et al. 2003, Lobón-Cervià and Rincón 2004). Part of the debate arises from confusion in terminology and in the questions studied. For example, the main argument

between Andrewartha and Birch (1954) and Nicholson (1958) resulted from the former being interested in population limitation, whereas the latter investigated population regulation (Sinclair and Pech 1996). Limitation is the process that sets equilibrium points; regulation is the process whereby population demographic rates decrease when population size increases (and vice versa), relative to some equilibrium. From this viewpoint, both environmental constraints and regulatory processes are likely to generate population fluctuations.

In the particular context of fish populations, recruitment has long been known to be a key factor in population fluctuations (Victor 1983, Doherty and

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Fowler 1994, Elliott 1994, Myers 2001) and it is said to be strongly influenced by environmental factors (Cushing 1995). However, internal factors also play a role. For instance, Sinclair (1989) showed that the earlier in the life cycle both density-dependent and density-independent factors affect a population, the greater the fluctuations in population abundance are. Fish populations are thus relevant subjects to study the relative influence of density-dependent and density-independent processes on population dynamics.

Salmonid recruitment has received substantial attention with respect to fisheries management. The anadromous brown trout (*Salmo trutta* L.) have been widely studied, showing that recruitment of stream-living brown trout was shrunk by winter and spring high flows (Allen 1951, Spina 2001, Cattaneo et al. 2002), especially if high flows occurred when recruits emerged from gravel nests (Allen 1951, Nehring and Anderson 1993, Nuhfer et al. 1994, Latterell et al. 1998, Liebig et al. 1999, Lobón-Cervià and Rincón 2004). In particular, Cattaneo et al. (2002) showed that this was the only hydrological constraint consistently influencing brown trout populations across 30 French streams. On the other hand, Elliott (1994) suggested that populations were regulated by a density-dependent recruit mortality. Such regulation is usually called stock-recruitment regulation because it describes the relationship between the number of recruits entering the population and the parent stock of fish (Ricker 1954). However, some authors failed to find stock-recruitment regulation in stream-living brown trout populations (Elliott and Hurley 1998, Cattaneo et al. 2002, Lobón-Cervià and Rincón 2004), which led Lobón-Cervià and Rincón (2004) to conclude that brown trout is the example of an environmentally driven animal species able to persist in time with little or no operation of density-dependent processes. These studies were well designed and greatly helped understand the factors causing population fluctuations. Nevertheless, they attempted to detect density dependence by using time series of abundance. In fact, the effectiveness of this approach is hindered by short temporal data sets (Woiwod and Hanski 1992) and measurement errors (Shenk et al. 1998), and it depends on the spatial scale of the study (Ray and Hastings 1996). In addition, studying population fluctuations alone should not be adequate to conclude on species' persistence (as was done by Lobón-Cervià and Rincón 2004), since persistence depends on both limitation and regulation.

We suggest that both external (environmental) and internal (density-dependent) processes are actually at play in driving brown trout population dynamics even if their respective effects are not easily detected by studying abundance time series. To test this hypothesis, we theoretically studied the cumulative influence of density-dependence and high-flow discharge at emergence on brown trout population dynamics by building

a matrix population model based upon its life cycle. First, we analyzed the influence of density-dependent and density-independent factors on population limitation. Then we used a stochastic version of our model to study the visibility of regulatory processes modulating interannual population fluctuations.

Methods

The model

The brown trout (*Salmo trutta* L.) life cycle is displayed in Fig. 1. Adults spawn during December (Elliott 1994, Charles 1998, Gouraud et al. 1998). We considered a prebreeding census (October) and time is discrete (Caswell 2001). The population was subdivided into three age classes (Charles et al. 1998, Chaumot et al. 2002): the young of the year (YOY), the juveniles (two summers old), and the adults (more than two summers old).

Recruitment is a function of winter/spring (January–May) discharge and is density-dependent (Fig. 1B). Elliott (1994) showed that density-dependent regulation occurred during a critical period ranging from emergence to 33–70 days after emergence. Both field and experimental works revealed that emerging trout were sensitive to the discharge up to 12 days after emergence

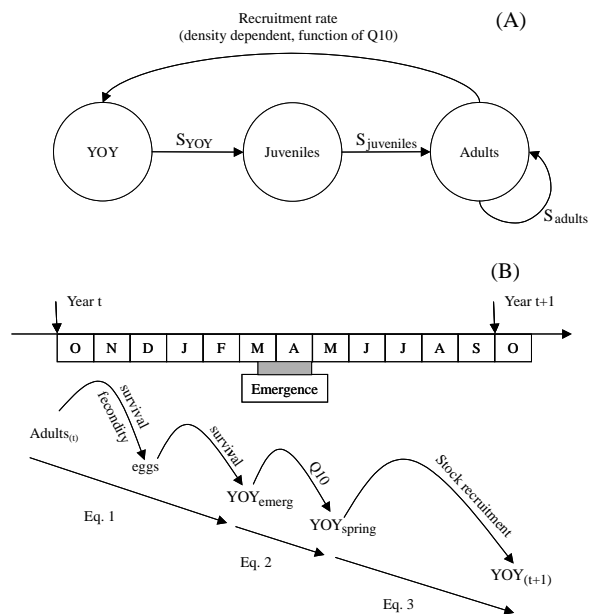


Fig. 1. (A) The brown trout life cycle was used for the construction of the matrix population model. S_{YOY} , $S_{juveniles}$, S_{adults} are survival transitions. The recruitment rate is density-dependent (the Ricker model) and depends on S_{adults} , sex ratio, female fecundity (number of eggs), and a synthetic variable of high winter–spring discharge (Q_{10}). The transition matrix of this model is provided in Appendix 1. (B) Details of the adults–YOY transition.

(Ottaway and Forrest 1983, Jensen and Johnsen 1999, Daufresne et al. 2005), suggesting that discharge constraints occur before density-dependent regulation. For each year studied, the YOY density at emergence (YOY_{emerg}) was provided by:

$$YOY_{\text{emerg}} = n_{\text{adults},t} (S_{\text{adults}})^{2/12} \sigma f (0.9) \quad (1)$$

where $n_{\text{adults},t}$, $(S_{\text{adults}})^{2/12}$, σ , f , and (0.9) were, respectively, adult density in October (year t), adult survival between October and spawning (hence the exponent $2/12$ since spawning occurs in December), sex ratio, fecundity, and under-gravel survival of eggs (Bardonnnet and Prévost 1994). Then the effect of emergence discharge was taken into account by calculating the YOY density (YOY_{spring}) as:

$$YOY_{\text{spring}} = YOY_{\text{emerg}} S_w \quad (2)$$

where S_w was the extra mortality due to high discharges during the January–May period, calculated as $S_w = \exp((-0.73) \cdot Q10)$. Following Strange et al. (1992), we derived S_w from the negative slope of the relationship (consistent across 30 French streams) between the high discharge levels during January–May (hereafter referred to as $Q10$) and the \ln -transformed abundance of YOY in early autumn established by Cattaneo et al. (2002). For a stream \times year combination, $Q10$ was the \ln transformed ratio between the 10th percentile of the daily discharges (during January–May) and the interannual median daily discharge. Finally, the density-dependent regulation was modeled by a Ricker stock-recruitment function (Ricker 1954, Caswell 2001), expressed as:

$$n_{\text{yo},t+1} = a \cdot YOY_{\text{spring}} \exp(-\gamma YOY_{\text{spring}}) \quad (3)$$

where $n_{\text{yo},t+1}$ was the YOY density in October (year $t+1$); a represented survival between spring and October at low density. The Ricker model has already been shown to describe salmonid recruitment well (Ricker 1954, 1975, 1989, Gardiner and Shackley 1991), especially for brown trout (Elliott 1994).

Finally, we considered constant survival probabilities between two consecutive censuses for all age classes (they were labeled S_{YOY} , $S_{\text{juveniles}}$ and S_{adults} for YOY, juveniles, and adults, respectively). The transition matrix (A_n) of the model is presented in Appendix 1.

Parameter values

Parameter values were chosen in order to fit those of resident brown trout living in headwater streams to avoid interspecific competition and reproductive migratory behavior.

Survival

$S_{YOY} = 0.51$ and $S_{\text{juveniles}} = 0.50$ were derived from Elliott and Hurley (1998) (assuming a constant mortality

rate across time). These rates were consistent with values observed in other brown trout populations (Needham et al. 1945, McFadden and Cooper 1962, Hunt 1969, Mortensen 1977, Brynildson and Brynildson 1984, Olsen and Vollestad 2001, Baglinière and Maise 2002). S_{adults} was fixed at 0.50 (Needham et al. 1945, McFadden and Cooper 1962, Hunt 1969, Baglinière and Maise 2002).

Recruitment

Half the adults were considered female individuals (sex ratio $\sigma = 0.5$). All the adult females spawned. Fecundity (f) was of 208 eggs per female (average value for a 180-mm individual (mean adult size in three French headwater streams, H. Capra pers. comm.); Euzenat and Fournel 1976, Maise et al. 1987, Gouraud et al. 1998, Olofsson and Mosegaard 1999).

We considered a 0.092 mean survival for the YOY between emergence and census at low density (no density dependence) and less than average discharge conditions during emergence (Brynildson and Brynildson 1984, Elliott and Hurley 1998, Baglinière and Maise 2002). Parameter a was thus calculated as $a = (0.092) / \exp((-0.73) \cdot \bar{Q}10_{\text{mean}})$, where $\bar{Q}10_{\text{mean}}$ is the average of 30 (yearly) mean $\bar{Q}10$ provided by Cattaneo et al. (2002).

Gamma (γ) was set at 0.000279, in agreement with Elliott et al. (1997), who estimated this value from the stock recruitment relationship between egg density (number per 60 m²) and YOY density in September (number per 60 m²) in a sea trout population. This parameter is probably somewhat inaccurate to describe resident brown trout population dynamics, but to our knowledge, it has never been estimated for resident brown trout populations. We check below that population dynamics are not at all sensitive to this parameter.

Population density at equilibrium

The impact of the internal (limitation-related) factors was analyzed by computing the elasticity (i.e. relative sensitivity; Caswell 2001) of the equilibrium population density (\hat{N}) to the demographic parameters (p_i). The role of external (environment-related) factors was evaluated by studying the relative effects of $Q10$ and p_i on both level and local stability of \hat{N} . We paid particular attention to the range of $\bar{Q}10$ observed in the 30 sites studied by Cattaneo et al. (2002): 1.1–2.5.

\hat{N} was calculated solving:

$$\hat{n} = A_{\hat{n}} \hat{n} \quad (4)$$

where $A_{\hat{n}}$ is the transition matrix containing the demographic parameters and \hat{n} is the vector of population densities at equilibrium. \hat{N} was calculated as $\hat{N} = \hat{n}_{\text{YOY}} + \hat{n}_{\text{juveniles}} + \hat{n}_{\text{adults}}$, \hat{n}_{YOY} , $\hat{n}_{\text{juveniles}}$ and \hat{n}_{adults} being the densities in the different age classes at equilibrium.

The local stability of \hat{N} was assessed calculating the greatest eigenvalue ($\lambda_1^{(B)}$) of the matrix $B = A_{\hat{n}} +$

$\begin{pmatrix} 0 & 0 & \hat{n} \cdot \frac{\partial A}{\partial n_{adults}} \Big|_{\hat{n}} \end{pmatrix}$. The equilibrium is stable if $|\lambda_1^{(B)}| < 1$ (Caswell 2001).

The elasticities of \hat{N} to the demographic parameters (p_i) are proportional to the corresponding elasticities of the greatest real eigenvalue (λ) of $A_{\hat{n}}$ (Caswell 2001). The elasticities of \hat{N} to p_i are thus given by $\frac{p_i}{\hat{N}} \times \frac{\partial \lambda}{\partial p_i} \Big|_{\hat{N}}$.

Stochasticity

Environmental variation from one year to another is likely to impede the detection of population regulatory processes. This may be particularly true in studies searching to detect density-dependent processes by looking for interannual correlations in population time series. In order to investigate this question, we generated a virtual 20-year time series with a stochastic version of the model described above. To keep analysis as simple as possible, we only added stochasticity in survival of the two main components of the stock-recruitment relationship (i.e. n_{YOY} and n_{adults}) by drawing Q10 and S_{adults} in beta distributions. Densities at $t=0$ were densities at equilibrium calculated for mean Q10 and S_{adults} . The duration of 20 years was chosen to fit the maximum length of the actual time series.

Then we analyzed the influence of the mean and standard deviation of Q10 and S_{adults} on population density mean and variance, and on the residual sum of squares (RSS) of the linearized Ricker model $\ln\left(\frac{n_{YOY,t}}{n_{adults,t-1}}\right) = \ln(a) - b n_{adults,t-1}$ (Elliott 1994), where $n_{YOY,t}$ is the YOY density in October year t , and $n_{adults,t-1}$ is the adults density in October year $(t-1)$. We used RSS as a synthetic variable enlightening the ability of the Ricker model to describe trout recruitment. However, since the density-dependence could also be masked by low variation in the density of adults, we additionally analyzed the range (as a difference between maximum and minimum values) of density of adults in the 20 years simulated time series. Note that we did not

aim here to discuss statistical methods for detecting density-dependence.

Results

Elasticity analysis of equilibrium

The elasticities of \hat{N} (see Appendix 2 for literal expression) to the survival probabilities S_{YOY} , $S_{juveniles}$, S_{adults} were equal and greater than the elasticity of \hat{N} to fecundity f (Table 1). The elasticity of \hat{N} to γ was null. Actually, $1/\gamma$ was a multiplicative factor of \hat{N} and thus only influenced the level of the population density but not its relative variability.

Relative effects of discharge and demographic parameters on equilibria

Population density

For parameter values classically measured in natura, the population density at equilibrium (\hat{N}) tended to be maximized by $\bar{Q}10_{mean}$. Low and high Q10 values yielded small population densities \hat{N} (Fig. 2). Indeed, at low levels of discharge, density-dependent processes induced a strong decrease in population densities. At high levels of discharge, environmental constraints drive a population to extinction.

For $\bar{Q}10_{mean}$, \hat{N} was not absolutely maximized by survival probabilities classically measured in natura (i.e. a , S_{YOY} , $S_{juveniles}$, S_{adults}) (Fig. 2). However, it is worth noting that on the range of $\bar{Q}10$ observed on 30 French streams (i.e. 1.1–2.5), \hat{N} was not very sensitive to an increase in survival probabilities.

Conversely, for $\bar{Q}10_{mean}$, the classically observed fecundity value (f) led to a maximized population density at equilibrium (Fig. 2, bottom-right panel). Moreover, we found that on the observed range of $\bar{Q}10$ (i.e. 1.1–2.5), \hat{N} was sensitive to fecundity.

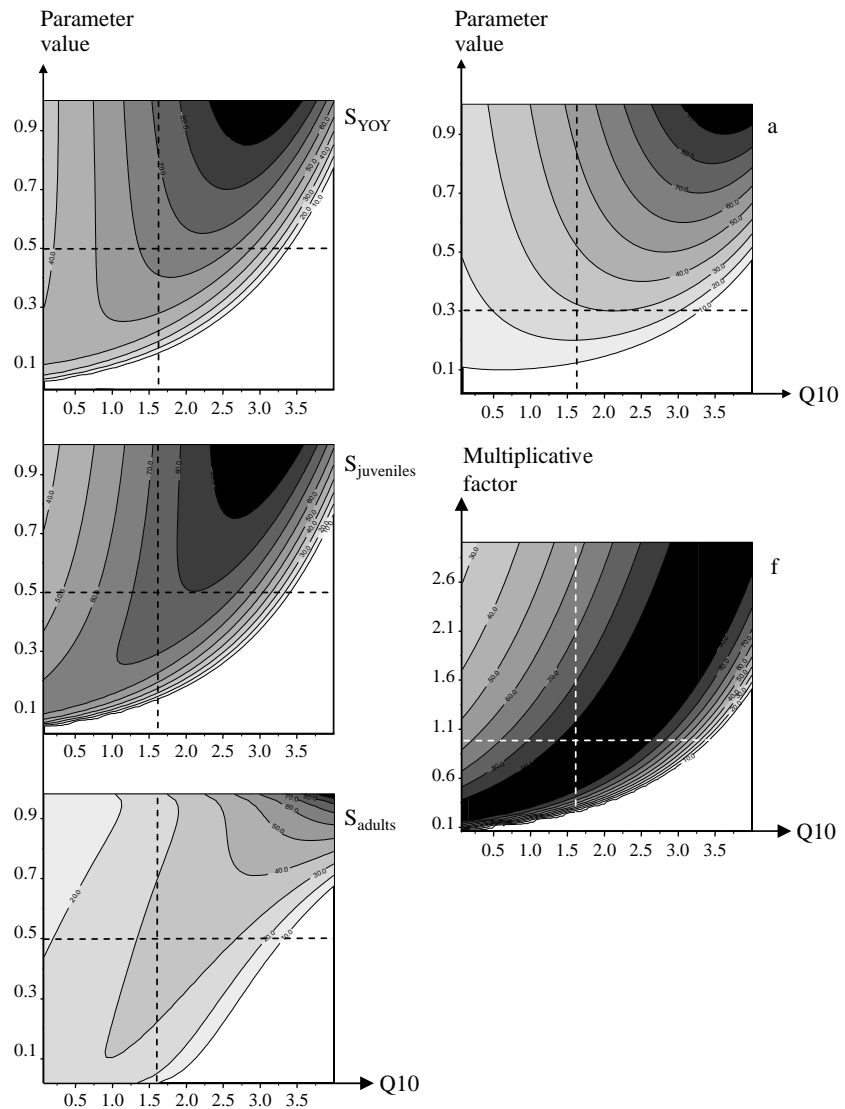
Local stability

Areas of instability associated with high Q10 and low demographic parameter values correspond to extinction zones (Fig. 3). For high S_{YOY} , $S_{juveniles}$, f , a values and low Q10, we observed quasi-periodic equilibrium.

Table 1. Elasticities (i.e. relative sensitivities, Caswell 2001) of the population density at equilibrium (\hat{N}) to demographic parameters. S_{YOY} , $S_{juveniles}$, S_{adults} are the survival of the YOY, juveniles, and adults, respectively. f is the fecundity of adult females. γ and a are parameters of the stock-recruitment Ricker model. The parameters' actual values are in parentheses.

	S_{YOY} (0.5077)	$S_{juveniles}$ (0.5030)	S_{adults} (0.5000)	f (208)	γ (0.000279)	a (0.2950)
Elasticity of \hat{N}	0.0013	0.0013	0.0012	-0.0005	0	0.0013

Fig. 2. Contour plots of the population densities at equilibrium as a function of demographic parameter values and a synthetic variable of high winter–spring discharge (Q10). For each graph, densities are expressed as percentages of the maximum density obtained over the Q10 and demographic parameter range. Densities increase from white (0–10%) to dark zones (>90%) by 10% intervals. The dashed line represents observed demographic parameter values and the average value of the 30 average (from yearly values) $\bar{Q}10$ by site ($\bar{Q}10_{mean}$) studied by Cattaneo et al. (2002). Parameter descriptions are given in the legend to Table 1.



Effects of interannual stochasticity of adult survival and level of discharge

Mean and standard deviation of population density

Interannual stochasticity of S_{adults} and Q10 slightly decreased the population density as compared to \hat{N} predicted by the deterministic model (for instance, mean population density ranged from 80% to 100% of \hat{N} for $\bar{Q}10=1.6$ and mean S_{adults} (\bar{S}_{adults})=0.5). This effect was most pronounced for low and highly variable S_{adults} (e.g. mean population density could drop to 15% of \hat{N} at $\bar{S}_{adults}=0.2$ and S_{adults} standard deviation = 0.3).

The standard deviation of population density increased when both S_{adults} and Q10 standard deviations increased. Again, this effect was more pronounced for

low and highly variable S_{adults} (e.g. $\bar{S}_{adults}=0.2$ and S_{adults} standard deviation = 0.3).

The ability to detect density-dependent recruitment

For $\bar{S}_{adults}=0.5$ and $\bar{Q}10=1.6$ (which are values observed in the field) and for high S_{adults} standard deviations and low Q10 standard deviations, RSS were low (Fig. 4A) and ranges of density of adults were high (Fig. 4B). The Ricker model thus described the recruitment of brown trout rather well (Fig. 4C). Conversely, the model was quite inaccurate for high Q10 standard deviations (low RSS, Fig. 4A), especially for high S_{adults} standard deviations (Fig. 4D, black diamonds). Finally, for low S_{adults} standard deviations and low Q10 standard deviations, both RSS and ranges of density of adults were low (Fig. 4D, grey

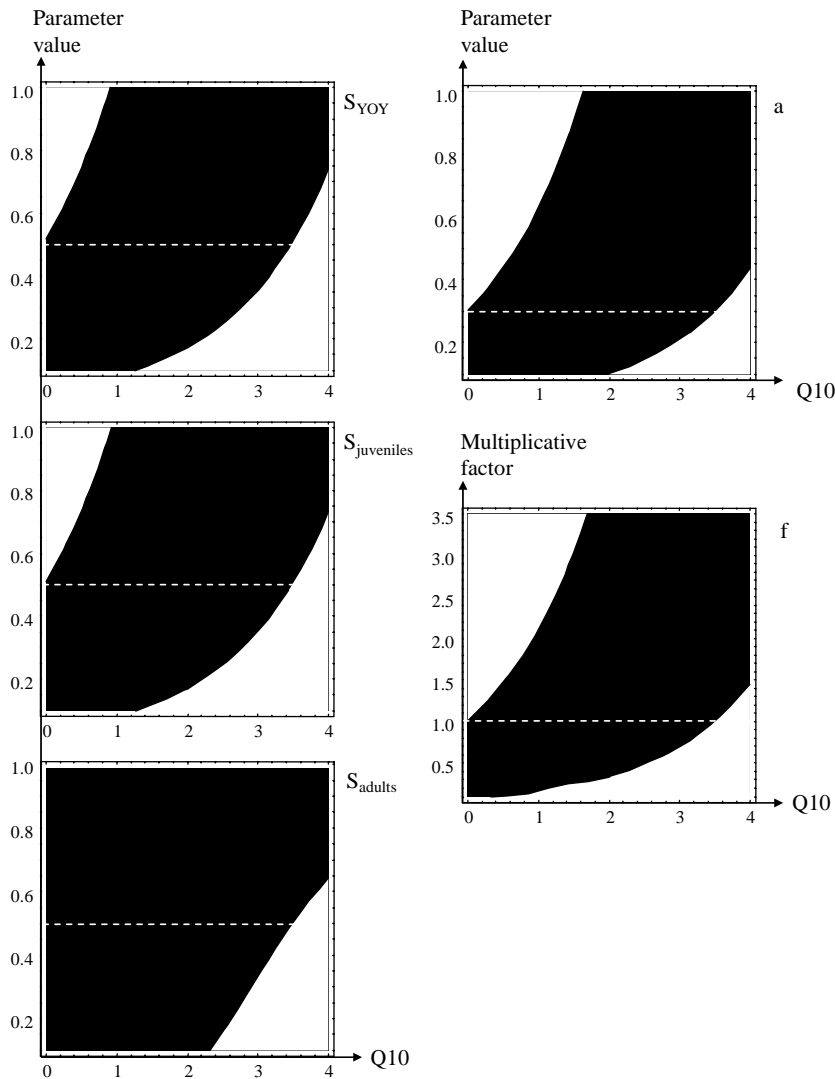


Fig. 3. Contour plots of the local stability of equilibrium as a function of demographic parameter values and a synthetic variable of high winter-spring discharge (Q10). Dark zones correspond to stable equilibrium. The dashed line represents observed demographic parameter values. Parameter descriptions are given in the legend to Table 1.

squares). Despite a good fit of the Ricker model, it was impossible to conclude about the density-dependence of the recruitment because of the low variation in the density of adults (and recruitment).

A proportional increase or decrease of $\bar{Q}10$ and \bar{S}_{adults} simultaneously provided results closer to those observed at $\bar{Q}10 = 1.6$ and $\bar{S}_{adults} = 0.5$.

For fixed \bar{S}_{adults} , the area for which the Ricker model accurately described the recruitment (low RSS) decreased when the $\bar{Q}10$ increased, especially for high standard deviations of S_{adults} (Fig. 4A). Area for which it was possible to detect density-dependent processes thus tended to decrease.

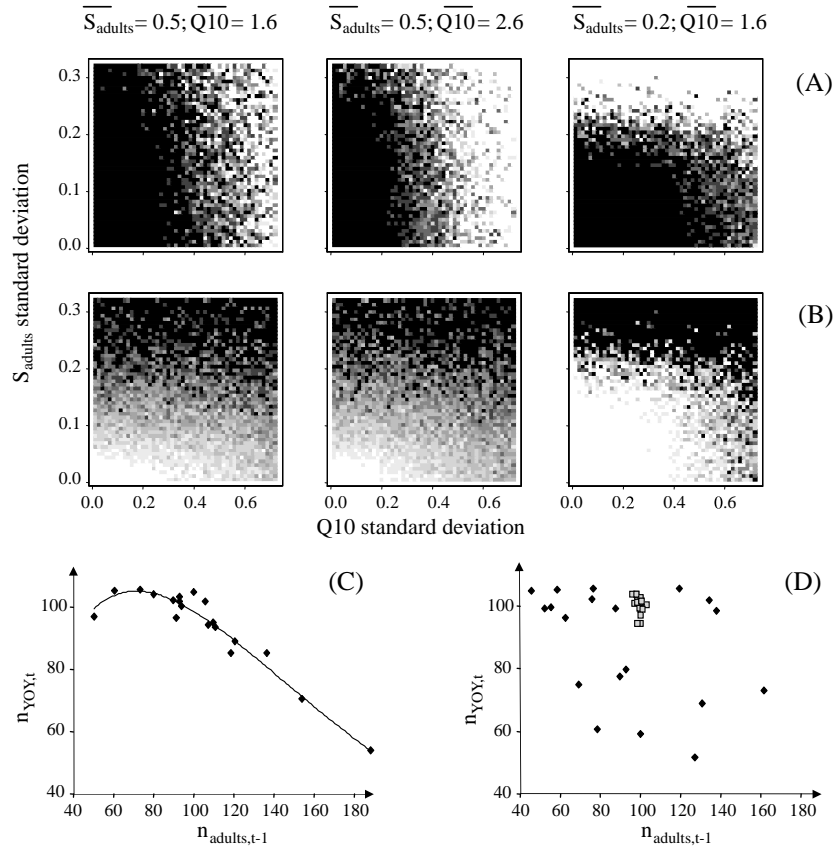
Similar results were found for fixed $\bar{Q}10$ when \bar{S}_{adults} decreased. Overlapping of low RSS and high ranges of density of adults conditions was almost inexistent (Fig. 4A, 4B). It was thus nearly impossible to detect density-dependent recruitment.

Discussion

The detection of density-dependent and/or density-independent factors acting on brown trout population dynamics usually relies on the analysis of time series fluctuations performed at the interannual scale. Using such methods, Lobón-Cervià and Rincón (2004) reached the conclusion that the brown trout was mainly an environmentally driven species able to persist with no or few internal biological feedbacks. Our results provide evidence that endogenous mechanisms are also likely to play an important role in this species dynamics. Actually, density-dependent and density-independent processes probably act together to determine population density and stability at equilibrium.

A simple model fitted with demographic data from the literature showed that population density and

Fig. 4. (A) Levels plots of the residual sum of square (RSS) of the linearized Ricker model as a function of mean (μ) and standard deviation (SD) of a synthetic variable of high winter–spring discharge (Q10) and adult survival (S_{adults}). All statistics were calculated for 20-year densities simulated time series. To homogenize the plots, RSS were expressed as percentages of the 10th percentile of the RSS values calculated for mean Q10 and S_{adults} observed in nature (i.e. 1.6 and 0.5 respectively; upper-left panel values). The RSS decrease from white (0–10%) to dark zones (>90%) by 10% intervals. (B) Ranges of $n_{adults,t-1}$ (expressed as percentages of densities at equilibrium of adults) in simulated time series used to calculate the RSS. Ranges increase from white (0–10%) to dark zones (>90%) by 10% intervals. (C) Example of the relationship between $n_{YOY,t}$ and $n_{adults,t-1}$ (expressed as percentages of densities at equilibrium of YOY and adults, respectively) for low RSS and high range of $n_{adults,t-1}$ [Q10 ($\mu = 1.6$; $SD = 0.1$); S_{adults} ($\mu = 0.5$; $SD = 0.3$)]. The curve fitted is estimated from the linearized Ricker model. (D) Examples of the relationship between $n_{YOY,t}$ and $n_{adults,t-1}$ for low RSS and low range of $n_{adults,t-1}$ [squares; Q10 ($\mu = 1.6$; $SD = 0.1$); S_{adults} ($\mu = 0.5$; $SD = 0.01$)] and for high RSS and high range of $n_{adults,t-1}$ [diamonds; Q10 ($\mu = 1.6$; $SD = 0.7$); S_{adults} ($\mu = 0.5$; $SD = 0.3$)]. Note that for a 0.32 SD and 0.5 mean S_{adults} , the beta distribution used is close to a uniform distribution between 0 and 1. For a 0.72 SD and 1.6 mean Q10, the beta distribution used is close to the observed Q10 distribution (Cattanéo et al. 2002) but with a higher variance and roughly a uniform distribution between 1 and 2.



stability are optimal over ranges of stream discharge (our variable Q10 above) commonly observed in the field (Cattanéo et al. 2002). A level of discharge that is too high would induce substantial mortality within the YOY class that used to emerge from under-gravel nests during winter–spring floods. If these high levels of discharge were maintained for a long period of several years, they would substantially lower the population growth rate (hence the population density at equilibrium) and probably lead the population to extinction (Fig. 2 and 3, bottom-right-hand corner of all panels). Discharge levels that are too low also do not seem

suitable for this species. Emerging YOY survivorship would then be too high, driving the populations into smaller and highly variable population densities due to density-dependent regulation (Fig. 2, 3).

Our results support the hypothesis that density-dependent processes predominate in benign environments, whereas density-independent processes predominate in harsh environments (Haldane 1953). The introduction of stochasticity on two parameters of the model (the adult survival probability and a synthetic measure of winter–spring discharges) did not change the results above, except that mean population sizes

were slightly smaller than predicted at equilibrium because populations became extinct. This effect seemed important only for highly variable and low mean adult survival, but this type of situation is probably rare in natural headwater streams. The studies conducted by Elliott and Hurley (1998) and Lobón-Cervià (2003) indicated that variability in adult survival was low. Moreover, mean survival after the first year is generally high, ranging from 27% to 55% (Needham et al. 1945, McFadden and Cooper 1962, Hunt 1969, Mortensen 1977, Elliott and Hurley 1998, Olsen and Vollestad 2001, Baglinière and Maisse 2002). The lowest estimates are probably underestimated because of technical difficulties (catchability, tag loss, migration) or interspecific competition (Olsen and Vollestad 2001).

Finally, we found that brown trout fecundity optimized population size at equilibrium and that elasticity of the population density at equilibrium to fecundity was low. However, assuming no density-dependent recruitment regulation, the elasticity of the population growth rate (dominant eigenvalue λ of the transition matrix) to fecundity increased and equal positive elasticity of the population growth rate to survivals. Density-dependent recruitment thus probably made it possible to cope with recruit mortality due to harsh environmental conditions during emergence without an intuitive increase in fecundity. This could explain the low fecundity of the brown trout compared to other European fish species (Bruslé and Quignard 2001) despite harsh conditions during early stages of development, which generally refer more to r-environments than to K-environments (Reznick et al. 2002).

Maximization of the population density at equilibrium under mean discharge conditions during emergence is probably helpful to prevent population extinction. Thus, contrary to the conclusions reached by Lobón-Cervià and Rincón (2004), internal regulatory mechanisms might play a significant role in persistence of brown trout populations. We showed that the visibility of density-dependent and density-independent processes at the interannual scale was context-dependent. This could explain the paradoxical conclusions on the main factors that drive population fluctuations in the brown trout (e.g. Elliott 1994 compared to Lobón-Cervià and Rincón 2004). We found that the Ricker model was quite inaccurate in describing brown trout recruitment under highly variable discharge conditions. The observed standard deviation of the variable Q_{10} was 0.47 (Cattaneo et al. 2002). Considering also that interannual variability of adult survival is often low, it is not surprising that many authors have failed to find stock-recruitment relationships by studying the fluctuation in abundance of the YOY and adult brown trout (Fig. 4). With this level of average discharge variability,

the fluctuations in population size are mainly driven by environmental constraints, as revealed by numerous studies (Allen 1951, Solomon et al. 1980, Nehring and Anderson 1993, Nuhfer et al. 1994, Liebig et al. 1999, Spina 2001, Cattaneo et al. 2002, Lobón-Cervià and Rincón 2004).

Our results add weight to those of Ranta et al. (2000), who symmetrically showed that regulatory processes could mask the effect of environmental noise on population dynamics. Clearly, these findings suggest that studies based on analysis of interannual abundance fluctuations could result in biased conclusions on the relative influence of density-dependent and density-independent mechanisms on population limitation. Consequently, this also questions the relevance of the classical suggestions made concerning population management. Regarding the brown trout, such suggestions are usually based upon analyses highlighting interannual hydrological constraints on abundance fluctuations, and often recommend limitations of the flow downstream from dams during the emergence period in regulated streams (Cattaneo et al. 2002). This proposal could be valuable at the interannual scale to increase the strength of a single cohort. However, our results suggest that, at least for fixed demographic parameters, a decrease in the mean discharge level during emergence could induce a decrease in the population size at the long-term scale (i.e. at equilibrium) due to the effects of endogenous regulatory mechanisms (Fig. 2).

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Appendix 1

Transition matrix of the model. S_{YOY} , $S_{juveniles}$, S_{adults} are the survival of the YOY, juveniles, and adults, respectively; f is the fecundity of adult females; σ is the sex ratio; S_w is the extramortality due to high discharges in January–May; γ and a are parameters of the stock-recruitment Ricker model.

$$A_n = \begin{pmatrix} 0 & 0 & a(0.9)(S_{adults})^{2/12} \sigma f S_w \exp(-\gamma(0.9)(S_{adults})^{2/12} \sigma f S_w n_{adults}) \\ S_{YOY} & 0 & 0 \\ 0 & S_{juveniles} & S_{adults} \end{pmatrix}$$

Appendix 2

Literal expression of the population density at equilibrium (\hat{N}). S_{YOY} , $S_{juveniles}$, S_{adults} are the survival of the YOY, juveniles, and adults, respectively; f is the fecundity of adult females; σ is the sex ratio; $Q10$ is a synthetic variable of high discharges in January–May; γ and a are parameters of the stock-recruitment Ricker model. \hat{n}_{adults} is the adults density at equilibrium.

Equation 1 gives:

$$\hat{n}_{adults} = 0, \text{ or, for } S_{adults} \neq 0 \text{ and } S_{adults} \neq 1: \hat{n}_{adults} = \frac{\exp(0.73 Q10)}{-\gamma S_{adults}^{1/6} \sigma} \left(0.73 Q10 - \ln \left(\frac{a f S_{YOY} S_{juveniles} S_{adults}^{1/6} \sigma}{1 - S_{adults}} \right) \right),$$

and

$$\hat{N} = 0, \text{ or, for non-null age-class survivals and } S_{adults} \neq 1: \hat{N} = \hat{n}_{adults} \left(1 + \frac{1 - S_{adults}}{S_{juveniles}} + \frac{1 - S_{adults}}{S_{YOY} S_{juveniles}} \right).$$