SPATIAL SCALE AND DEGREE OF SYNCHRONY IN BROWN TROUT (Salmo trutta) POPULATION DYNAMICS

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Spatio-temporal variability of the physical conditions in streams is known to influence freshwater population dynamics. However, the complex relationship between these physical factors (mainly available habitat, water temperature, discharge, sediment transport) and the biological response is not yet clearly understood in either natural or regulated streams. In order to investigate this relationship, it is essential to understand how the influences of these physical factors differ in time and space.

In the present study, we analyzed the spatio-temporal patterns of fluctuation in 31 brown trout populations spread across France, in both natural and regulated (i.e. bypassed sections downstream of hydroelectric water intakes) sites. This data is a result of annual fish monitoring surveys carried out continuously over a minimum of 5 years. Using statistical methods, we estimated the degree of synchrony among brown trout cohort densities (young-of-the-year, juveniles and adults) and evaluated the spatial scale at which synchrony is best identified. We also investigated whether synchrony patterns differ between natural and regulated sites. Results are then discussed according to fluctuations in local physical factors. This study demonstrates the utility of multi-site approaches for a better understanding of freshwater population dynamics. It is indeed of major importance to identify the most structuring physical factors at regional or local scales, in order to design consistent management schemes.

INTRODUCTION

Identifying the factors that regulate populations and how they influence fluctuations in population density is of crucial importance in ecology. It becomes a major challenge when natural factors are compounded by potential anthropic influences such as the presence of hydropower plants. The ecological impact of such plants on downstream reaches of the river has been widely studied (Petts [1]; Rosenberg et al. [2]). Studies on fish populations were particularly facilitated by the development in the Eighties of habitat models (IFIM/PHABSIM: Stalnaker [3]; Bovee [4]) which made it possible to link the amount of available habitat as a function of discharge to the level of fish abundance. The need for biological validation of these models, however, rapidly became evident. The models of population dynamics that emerged in the Nineties (Sabaton et al. [5]) indeed pointed out the fact that the relationship between biology and available habitat is not
simple and that other controlling factors, particularly environmental factors, are also at play. This fact was especially clear in the work of the Guaranteed Flow Working Group on populations of brown trout. (Sabaton et al. [6]; Sabaton et al. [7]).

Some authors have pointed out that the study of spatial synchrony, or synchronous fluctuation in the levels of two or more populations, is one possible approach to better understanding the mechanisms of population regulation (Ranta et al. [8]). Moreover, it is recognized that synchronisms are attributable to two types of phenomenon: on the one hand, density-dependent mechanisms such as dispersion of the individuals, and on the other, density-independent mechanisms, which are typically climatic factors (Bjørnstad et al. [9]). It is possible that each of these mechanisms influences several populations in a shared space similarly. The first, however, generally impact more limited spatial scales than the second (Ranta et al. [10]). Climatic factors can, in fact, synchronize populations over large areas through what is known as the “Moran effect” (Royama [11]). Moran [12] demonstrated that populations regulated by identical density-dependent phenomena can be synchronized by a climatic factor which is correlated over an extended area.

To our knowledge, few studies have investigated the scale on which synchrony is found in freshwater fish populations, particularly in lotic ecosystems (Grenouillet et al. [13]; Myers et al. [14]), and more particularly among brown trout (Cattanéo et al. [15]). Our aim here was to study 31 brown trout populations distributed across the three main mountain ranges of France, the Alps, the Massif Central and the Pyrenees. The ecosystems studied were both in totally or almost totally natural reaches and in by-passed sections (BPS) linked to hydropower production facilities. While a Moran effect has already been detected in a set of populations studied at sites with natural flow regimes (Cattanéo et al. [15]), our objective here was to determine at what scale it occurs, and whether or not that effect is still found if regulated sites are included in the study.

**MATERIAL AND METHODS**

**Study sites**

The 31 sites chosen for this study are situated in the three main mountain ranges of France, the Alps, the Massif Central and the Pyrenees (Fig. 1), and on 18 different streams. They represent a wide diversity in habitat for the brown trout (Table 1), at altitudes ranging from 460 to 1465 m. Their mean width varies from 4.4 m to 14.8 m, with gentle to steep slopes (0.3-10.0 %). At the level of the monitoring sites, the streams are subject to 5 different hydrological regimes out of the 8 in the classification

<table>
<thead>
<tr>
<th>Physical characteristics</th>
<th>Minimum</th>
<th>Mean</th>
<th>Maximum</th>
</tr>
</thead>
<tbody>
<tr>
<td>Elevation (m)</td>
<td>460.0</td>
<td>798.0</td>
<td>1465.0</td>
</tr>
<tr>
<td>Basin area (km²)</td>
<td>18.0</td>
<td>185.0</td>
<td>613.0</td>
</tr>
<tr>
<td>Mean width (m)</td>
<td>4.4</td>
<td>9.1</td>
<td>14.8</td>
</tr>
<tr>
<td>Reach slope (%)</td>
<td>0.3</td>
<td>2.8</td>
<td>10.0</td>
</tr>
<tr>
<td>Distance from the source (km)</td>
<td>2.0</td>
<td>21.0</td>
<td>49.0</td>
</tr>
</tbody>
</table>
established by Sauquet et al. [16] according to Pardé [17], from nival to pluvial with intermediate regimes. The monitoring stations were at the head of the hydrologic basin, at distances between 2 and 39 km from the source, in watersheds ranging in size from 17 to 605 km². Of the 31 sites, 15 were on streams considered to be little or not at all influenced by hydropower installations, and 16 were in by-passed sections downstream of hydropower plants.

Fish data came from two different sources: first, a national database held by the Office National de l’Eau et des Milieux Aquatiques (ONEMA) grouping about 800 stream reaches sampled annually across France; second, the database built up in the framework of the Guaranteed Flow Working Group (Sabaton et al. [7]) which includes sites near hydropower production facilities (control sites upstream of the hydroelectric facilities, and BPS sites downstream of the facilities) and which was augmented for the present study. The study sites were selected for the study using different criteria. First, the annual inventory had to be in summer or early autumn when discharge is low to get a good count since estimations of densities tend to drop when flow increases (Jensen and Johnson [18]). In addition, it is quite easy at that time of the year to capture all life stages, particularly the young-of-the-year, which are large enough in summer/early fall to be efficiently caught. A further consideration was always to perform the sampling on a given site at the same time each year, to avoid any bias linked to the sampling date, and inventories had to have been conducted at the site at least 5 times over the period from 1999-2007. The time series chosen in light of these criteria then had to have at least one

**Year-to-year monitoring of trout populations**

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inventory showing more than 80% brown trout, or at least one with only brown trout (Salmo trutta fario), bullhead (Cottus gobio) and common minnow (Phoxinus phoxinus). Lastly, the fishing protocol required two successive passes, for efficient estimation of the real fish density at each site.

Fish were sampled by means of two-pass electrofishing, enabling application of the Carle and Strub method [19] to estimate real densities. Using size histograms, we determined the 3 age classes – fry (0+), juveniles (1+) and adults (>1+) - for each site and each year which gave us estimated annual densities expressed in number of individuals per 100m² for each site and each cohort.

Analysis of spatio-temporal variation in densities

Spatio-temporal variations in density were examined using standardized data so as to simplify comparison between the monitoring stations. For each age class, the densities observed were distributed over three equidistant classes: the lower third, the median third and the upper third. These three classes successively reflect a level of abundance that is below the mean, at the mean, and above the mean at a given site.

Analysis of synchronisms

To evaluate the degree of synchrony between sites, we calculated the Spearman rank correlation coefficient using densities (nb ind.100m²) for all pairs of sites for which common inventories were available for at least 5 years per age class. For this analysis, density data was not transformed. So as to avoid measuring any synchrony linked to dispersion, we voluntarily eliminated pairs of sites between which migration of individuals was possible; dams were all considered as barriers. The overall average synchrony was estimated by computing the arithmetic mean of any of the pairwise correlation coefficients (Buonaccorsi et al. [20]) for different groups : all sites pooled together, for each geographical region, and for each stream. We also computed the average synchrony for all BPS/control site pairs. For the site pairs ultimately selected, we also calculated the great circle distance between them. Using these results, we traced a correlogram for each age class, representing the correlation coefficient as a function of distance. We then fitted a model of exponential decrement (Myers et al. [14]) (Eq. 1) to evaluate the spatial scale of occurrence of the synchronism:

\[
\rho(d) = \rho_0 e^{-d/v}
\]  

(1)

Coefficients \(\rho_0\) and \(v\) were evaluated using the least square method.

The quality of the model fit to the data was evaluated by linear regression between the values predicted by the model and the observed values. In addition, to visually evaluate the real general trend in the data, we synthesized the information by distance class: 0-200 km, 200-400 km and 400-637 km, in the form of box-and-whisker plots.

We estimated the spatial scale of synchrony according to two methods. It is either given readily by the \(v\) parameter of the model, which corresponds to the distance over which the correlation \(\rho(d)\) is reduced by a factor \(e^{-1}\) (Myers et al. [14]). Or it is given by
the distance over which the correlation $\rho(d)$ equals the overall mean pairwise correlation (Bjørnstad et al. [9]).

RESULTS

Spatio-temporal variations in density for the 3 age classes

Considerable spatio-temporal variability was found in the 31 populations over the study period, particularly in the case of fry: their mean year-to-year densities vary, depending on the site, from 0.7 to 21.4 ind.100m$^{-2}$ for an annual variability of between 0.1 and 56.3 ind.100m$^{-2}$. This variability for juveniles is of the same order, with mean year-to-year densities between 0.7 and 39.2 ind.100m$^{-2}$ for an annual variability between 0.1 and 57.3 ind.100m$^{-2}$. For adults, variability is slightly lower with mean year-to-year densities varying from 0.5 to 24.6 for an annual variability between 0.3 and 31.8 ind.100m$^{-2}$.

In 2006, most of the Pyrenees sites reached a level of abundance higher than the mean (78%, n=14) (Figure 2). In 1999, 95% (n=13) of the Massif Central and Alps sites had low abundance levels. Similarly, in the Pyrenees in 2003 and 2007, all but one site for which data are available had a low relative level of abundance (93%, n=14). Such clear results are not found for juveniles and adults, for which there do not seem to be parallel trends in density except for sites located on the same stream.

The Spearman rank correlation coefficient was calculated for 411 site pairs with 5 years of monitoring in common. Six of these pairs corresponded to sites on the same stream with a possibility of migration, and were eliminated, reducing our sample to 405 pairs. The overall mean correlation coefficient for these 405 pairs is low for all 3 age classes (fig. 2a-b-c), thus indicating low synchrony. At a regional scale, the degree of synchrony is higher for fry and juveniles, and even higher when looking at a same stream for the 3 age classes. Furthermore, the degree of synchrony is generally higher for fry than for adults. These statements are however not true for the Massif Central. For this particular region, regional mean correlation coefficients are higher than at the stream scale, and are the highest for adults. Regarding correlations between BPS sites and control sites located upstream, they are 0.52 for fry, 0.40 for juveniles and 0.04 for adults in average.

Analysis of the scale of synchrony

The correlograms (Figure 3) show significant dispersion in the scatter diagram, with no clear general trend. The distances between the study sites vary from 1.3 to 637 km. The degree of correlation varies from -0.77 to 0.98 for fry, from -0.81 to 0.93 for juveniles, and from -0.94 to 0.98 for adults, for mean correlations of 0.18, 0.09 and 0.12 respectively. The box plots give a better picture of the overall downward trend for fry and juveniles. The fit of the exponential decrement model is significant for these two age classes (at the $\alpha=0.01$ threshold). The model explains respectively 18 and 17% of the total variability in data. On the other hand, no trend is found for adults, and the model fit is not significant (p=0.30).
Figure 2. Evolution in standardized densities for fry (a), juveniles (b) and adults (c)

- Density lower than the mean for the site (class 1)
- Density on a level with the mean for the site (class 2)
- Density higher than the mean for the site (class 3)
- No data

Each column represents the temporal trend at one site over the study period. The color for a given year shows the density class to which the density observed at that site in that year corresponds. The narrow line separates two sites far from each other on a same stream. Dotted lines separate the streams. Solid lines separate the 3 study regions. BPS sites are coded with b. ρ values give mean pairwise correlations for each group: all sites pooled together (ρ₁), mountain ranges (ρ₂) and streams (ρ₃).

Streams: AD = Adour; AUD = Aude; GA = Gave d’Azun; GG = Gave de Gavarnie; REB = Rebenty; CLA = Clarée; REA = Réallon; ROI = Roizonne; BESB = Besbre; COU = Couzepavin; DOU = Dourbie; SEN = Senouire.
Figure 3. Correlations of fish densities (a : fry, b : juveniles, c : adults) between pairs of sites as a function of the distance between them (km), summarized in the form of box plots for each distance class (0-200 km, 200-400 km and 400-637 km).

The box represents the interquartile distance divided in two by the median; the whiskers represent the minimum and maximum if they are less than 1.5 times the interquartile distance. The outliers are represented by . The curve represents the model fit: $\rho(d) = \rho_0 e^{-d/v}$.

**DISCUSSION**

Annual trout densities observed during this study vary widely from one year to another and from one stream to another, as is often the case for this species when monitored over a long period and on a large number of sites (Cattanéo et al. [21]; Sabaton et al. [27]). Despite this variability, our study shows patterns of spatio-temporal trends in densities common to several sites when they are situated on the same stream. For the young of the year, these patterns may even be common to entire geographical regions. In particular, levels of abundance higher or lower than the mean for the period of monitoring are often reached synchronously at the majority of sites in a single mountain range. In the case of fry, the mean degree of synchrony within each range is greater than the mean synchrony for all populations taken together (Ranta [22]). For adults, we also find patterns in spatio-temporal density trends common to several sites on a single stream, but the phenomenon is not as marked on the scale of an entire mountain range. Among juveniles, we find that
high relative levels of abundance are found on most of the sites in the Alps and Massif Central in 2003, and in the Pyrenees in 2007. In each of these three cases, observations in the preceding year had pointed out high relative levels of abundance for the 0+ fishes. We can suppose that the degree of synchrony within an age class in year \( n \) is responsible for a certain degree of synchrony in the next higher age class in year \( n+1 \). Indeed, it has been shown that the abundance of juveniles in one year is in part linked to the abundance of fry in the preceding year (Gouraud et al. [23]; Cattanéo et al. [21]). These results show the importance of studying phenomena of synchrony in any type of population by age class. The different cohorts in the life cycle of rheophilic fish species have different habitats, and the mechanisms regulating the corresponding age classes are thus most probably also different, with the result that the phenomena of synchrony differ in terms of both the form they take and their spatial scale (Reyjol et al. [24]).

A regional synchrony was also highlighted by Cattanéo et al. [15] in France, but not for the same geographical regions. In our case, the synchrony is still noticeable despite the fact that regulated sites (BPS) were also taken into account. Furthermore, our results suggest a certain degree of synchrony between sites located upstream and downstream of hydroelectric facilities for early-life stages. We can reasonably suppose that some of the factors regulating these age classes and which are responsible for the observed synchrony are the same in regulated and unregulated streams. The next step is to determine what could have caused this regional synchrony. Dispersion could be a factor responsible for synchrony but in our case, we voluntarily eliminated that possibility by eliminating the pairs of sites between which migration was possible. The synchrony observed would rather seem to be caused by a disruptive influence which similarly affected the entire region. According to Cattanéo et al. [15], this Moran effect is related to hydrology. Indeed, climatic events (rise in temperature, spring melt, rain, etc.) produce similar regional hydrological signals, particularly in the case of flood episodes. The effect of flooding on young age classes of trout has been widely demonstrated (Nehring and Andersen [25]; Latterell et al. [26]; Jensen and Johnsen [27]; Cattanéo et al. [21]; Sabaton et al. [6]).

With respect to our study of the spatial scale of synchrony, our results point out a general trend toward a declining correlation between sites as distance between them increases for young of the year and juveniles. This trend is not found with adults, however, which is consistent with the patterns of spatio-temporal density trends for this age class, which are not common to several sites unless they are situated on the same stream. The number of site pairs concerned (22) is, however, probably insufficient for such to be detectable in relation to the total number of pairs studied (406). This fact is all the more true in that site pairs where migration was possible from one to the other were eliminated from the study, although they show similar trends. For fry and juveniles, our results indicate a spatial scale of correlation on the order of 150 km. This scale is consistent with a synchronizing effect attributable to climatic events and tends to confirm the idea that a Moran effect is influencing the young age classes. The scale we posit is greater than that proposed by Myers [14] for other freshwater species, but close to that
found by Grenouillet [13] for roach (*Rutilus rutilus*). The latter author, however, conducted his study on populations distributed throughout a single stream.

Surprisingly, our analyses showed a strong correlation between populations distant from each other, at all life stages. We also found negative correlations. One possible reason for this is, in the case of some site pairs, too few years of monitoring in common (minimum 5). Complete and longer time series might better highlight the pairs of sites which really show synchronous trends, particularly since densities vary considerably at all sites. It would be interesting to eliminate the effect of local variability linked to available habitat (Jowett [28]) in order to determine whether the synchrony becomes more evident.

Next steps in this study will be to search for the possible causes of the observed synchrony: spring hydrological conditions, bedload mobilisation frequency,… Moreover, as our results suggested that synchrony operates at a regional scale, it would be more consistent to identify the response of trout populations according to the regional context of their stream (reach slope, hydrological regime, distance from the source,…).

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