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Bret Victor[1], Bergerot Benjamin[2], Capra Hervé[3], Gouraud Véronique[1], Lamouroux Nicolas[3]

[1] EDF R&D, LNHE Department, HYNES (Irstea – EDF R&D), 6 Quai Watier, Chatou Cedex 78401, France

[2] Hepia Geneva, University of Applied Sciences Western Switzerland, Technology, Architecture and Landscape, Centre de Lullier, route de Presinge 150, CH-1254 Jussy, Switzerland

[3] IRSTEA Lyon, UR MALY, HYNES (Irstea – EDF R&D), centre de Lyon-Villeurbanne, F-69626 Villeurbanne, France

E-mails :

victor.bret@edf.fr, benjamin.bergerot@hesge.ch, herve.capra@irstea.fr, veronique.gouraud@edf.fr, nicolas.lamouroux@irstea.fr

Correspondence: Victor Bret, Tel +33130878459, victor.bret@edf.fr

Abstract

Environmental factors may cause synchronous density variations between populations. A better understanding of the processes underlying synchrony is fundamental to predicting resilience loss in metapopulations subject to environmental change. The present study investigated the determinants of synchrony in density time series of three age-groups of resident brown trout (0+, 1+ and adults) in 36 stream reaches. A series of Mantel tests were implemented to disentangle the relative effects on trout synchrony of geographical proximity, environmental synchrony in key environmental variables affecting trout dynamics (discharge, water temperature, hydraulics and spawning substrate mobility) and density-dependent dispersal. Results indicated that environmental synchrony strongly explained trout synchrony over distances less than 75km. This effect was partly due to a negative influence on 0+ trout of strong discharges during the emergence period and a more complex influence of substrate mobility during the spawning period. Dispersal between reaches had a weak influence on results. Juvenile and adult densities were strongly driven by survival processes and were not influenced by environmental synchrony. The results suggest that the environment can have general effects on population dynamics that may influence the resilience of metapopulations.

Keywords:

Moran effect; Freshwater fish; Population dynamics; Density-dependent dispersal; Mantel tests; Bypassed section

Résumé

Les facteurs environnementaux peuvent causer des fluctuations synchrones de densités entre populations. Une meilleure compréhension des processus expliquant la synchronie est fondamentale pour prédire des pertes de résilience des métapopulations sujettes à des changements environnementaux. Nous étudions la synchronie des chroniques de densités de

trois classes d'âge de la truite commune (0+, 1+ et adultes) entre 36 tronçons de cours d'eau. Nous utilisons des tests de Mantel pour discriminer les effets relatifs de la proximité géographique, de la synchronie de variables environnementales clefs (débit, température de l'eau, conditions hydrauliques et mobilité du substrat) et de la dispersion densité-dépendante. La synchronie environnementale expliquait fortement la synchronie de la truite jusqu'à des distances de 75km. Cet effet était dû en partie à l'influence négative sur les 0+ des hauts débits pendant l'émergence et une influence de la mobilité du substrat pendant la période de ponte. La dispersion entre tronçon influençait faiblement nos résultats. Les densités de juvéniles et d'adultes étaient fortement structurées par des processus de survie, mais n'étaient pas influencées par la synchronie des conditions environnementales. Les résultats suggèrent que l'environnement peut avoir des effets généraux sur la dynamique de population qui peuvent influencer la résilience des métapopulations.

Mots-clefs:

Effet Moran; Poissons d'eau douce ; Dynamique de populations; Dispersion densité-dépendante; Test de Mantel ; Tronçon court-circuité

Introduction

Temporal variations in population density depend on both abiotic (e.g., environmental) and biotic processes (e.g., density-dependent dispersal) operating at various spatial scales (Alonso et al. 2011; Richard et al. 2013). Environmental factors may cause synchronous fluctuations in density in populations with similar density-dependence structures (Moran 1953). These "Moran effects" may explain the synchronous variation in abundance of herbivorous insects and mammals in sites located as much as 1,000 km apart (Koenig 2002; Liebhold et al. 2004). Density-dependent regulation (through dispersal of individuals) can also induce

synchrony between connected populations, but these effects are generally weaker (Ripa 2000) and occur over shorter distances (Ranta et al. 1998). In many previous synchrony analyses, the influence of environmental variables (e.g., Holyoak and Lawler 1996) or density-dependent regulation (e.g., Tedesco et al. 2004) could be neglected. However, their relative influence on population synchrony needs to be analyzed to identify the general drivers of population dynamics and to better quantify the resilience of metapopulations subject to environmental change. When the main drivers of synchrony are environmental factors, metapopulations can be threatened by synchronous environmental disturbances. In contrast, populations in which synchrony is driven by density-dependent dispersal may be highly resilient to environmental disturbance. Analyzing data sets combining close and distant sites can contribute to better understanding the relative influence of the environment and of density-dependent regulation on population synchrony.

Spatial synchrony has been frequently studied and observed in riverine fish populations. Chevalier et al. (2014) studied 27 freshwater fish species commonly found throughout France. They found low but significant levels of synchrony (average correlation between pairs of reaches generally <0.1) that were related to the life-history strategies and the upper thermal tolerance limits of species. Of these species, stream-resident brown trout (*Salmo trutta*) has been especially well documented, making it useful for the study of synchrony. This species has a wide native range and is known to be sensitive to environmental conditions (e.g., high flow rates, extreme water temperatures). Synchrony in such environmental conditions may lead to synchrony in trout density. Cattanéo et al. (2003) showed the influence of hydrologic synchrony (high discharge levels during the emergence period) on the density synchrony of young-of-the-year trout in 37 stream reaches. One limitation of existing analyses of trout synchrony (e.g., Cattanéo et al. 2003; Zorn and Nuhfer 2007) is that they did not involve key habitat factors for trout population dynamics (e.g., hydraulics and water

95 temperature; Armstrong et al. 2003). They generally used proxies (e.g., air temperature,
96 discharge rate, geographic proximity) that are spatially correlated, which makes it difficult to
97 distinguish their relative influences. Studying pairs of geographically close reaches with
98 contrasting environmental characteristics (e.g., contrasting levels of discharge regulation)
99 would be particularly useful to better disentangle the relative influence of environmental
100 factors and density-dependent dispersal on synchrony. Another difficulty in interpreting
101 synchrony in fish populations is that synchrony in a given age-group may be inherited from
102 the previous age-groups (Grenouillet et al. 2001; Lobón-Cerviá 2009). Ideally, age-group
103 successions should be taken into account in analyzing synchrony.

104 The present study provides an analysis of spatial synchrony in density time series of
105 three age-groups of brown trout. The originality of the analysis lies in addressing certain
106 important limitations of previous synchrony studies. In particular, the present analyses
107 involved geographically close sites with differing environmental characteristics (disconnected
108 by dams or not, bypassed by hydroelectric plants or not), to refine analysis of the relative
109 influence of environmental factors and density-dependent dispersal on synchrony. In
110 addition, key quantitative environmental variables influencing population dynamics
111 (hydraulics, water temperature) were taken into account, as were relationships between
112 successive age-groups.

113 Materials and methods

114 In brief, the dataset covered 36 stream reaches in which trout abundance was assessed
115 annually (320 surveys: i.e., reach×year combinations) and discharge, hydraulics and water
116 temperature were described. These data were transformed into distance matrices describing
117 geographic distance, trout synchrony and environmental synchrony between pairs of reaches.
118 Series of Mantel tests were then implemented to characterize the spatial scales of trout

synchrony and environmental synchrony (step 1), and to focus on the influence on trout synchrony of environmental synchrony on the one hand (step 2) and density-dependent dispersal on the other (step 3).

Study reaches and geographic distances

The 36 reaches belonged to 22 French rivers distributed across continental France (Fig. 1) and had a wide range of environmental characteristics (e.g., width ranging from 2.9 to 15.5m, median streambed particle diameter from 0.1 to 64cm; Table 1). They were selected based on the availability of hydraulic and water temperature data. In each reach, fish were sampled for at least four pairs of consecutive years (consecutive years being needed in order to take account of age-group successions). We checked that brown trout was the dominant species (relative density > 80% on at least one survey) in the eight reaches where other species were sampled. Each reach included one or several sequences of pools, runs and/or riffles. Due to changes in sampling teams (consulting firms) or harsh hydraulic conditions during some surveys, sampled length was slightly modified in half of the reaches during the study period, affecting 18% of surveys (maximum length change: 25%; median change: 13%). One reach had its length divided by two at the middle of the time series, but was kept as a single reach for analysis as its hydraulic characteristics remained unchanged. Groups of close reaches selected in the same river (Fig. 1) might or might not be disconnected by dams or bypassed by hydroelectric plants. A total of 18 reaches were bypassed, and therefore showed decreased low-flow and flood frequency. Consequently, the data set included pairs of very close reaches characterized by different hydraulic conditions. No chemical pollution was reported in these reaches.

Two kinds of geographic distance were computed between pairs of reaches: Euclidean and river network distances. Network distance is potentially more relevant to describe density-dependent dispersal, and was computed for the 93 out of 630 pairs of reaches that were not

144 separated by the sea, using a theoretical hydrographic network developed for France (Pella et
145 al. 2012). All distances were log-transformed to approximate normality.

146 **Trout data and synchrony in trout time series**

147 Between 4 and 19 surveys (mean: 8.9) were conducted per reach between 1991 and 2012.
148 Reaches were sampled by wading, using two-pass removal electrofishing sampling meeting
149 European Committee for Standardization guidelines (CEN 2003). Fish densities were
150 estimated on the Carle and Strub (1978) method. Sampling was performed without blocking
151 nets, in summer or early autumn (median date: September 13). Sampled area (between 175
152 and 2,295 m²) was computed as sampled length × reach width at median flow. All fish were
153 measured (to the nearest 1mm) and length-frequency histograms were used to distinguish
154 three age-groups: 0+ (young-of-the-year), 1+ (older than one year, generally juveniles) and
155 adult (all fish older than two years). Scales were available for 10 reaches only, but confirmed
156 the suitability of using length-frequency distributions (see Sabaton et al. 2008). Adults were
157 considered as the potential reproductive pool. Age-group densities (number of individuals per
158 100m²) were log-transformed to normalize their distributions.

159 Due to the strength of the relationship between densities of successive age-groups for brown
160 trout (Zorn and Nuhfer 2007; Lobón-Cerviá 2009), a global model of age-group succession
161 (averaged across reaches) was determined. All synchrony analyses were performed on
162 residuals of this global model, in order to reduce serial correlation and better identify the
163 causes of synchrony (e.g., Buonaccorsi et al. 2001; Santin-Janin et al. 2014). Specifically,
164 linear regressions were fitted for all age-groups (0+, 1+, Ad) relating log-transformed density
165 at year y ($D_{0+,y}; D_{1+,y}; D_{Ad,y}$) to the density of previous age-group at year y-1
166 (respectively: $D_{Ad,y-1}$; $D_{0+,y-1}$; $D_{1+,y-1}$ and $D_{Ad,y-1}$). Adults at year y depended on both
167 adults and 1+ fish at year y-1, as the adult group combined fish of several age-groups. Slopes

168 significantly lower than 1 were taken to indicate global density-dependence in population
169 dynamics (for $D_{0+,y}$ and $D_{1+,y}$).

170 To quantify the potential limits of this approach, mixed-effect linear models with a reach-
171 level random effect (i.e., with regression coefficients that could vary across reaches) were
172 also fitted to the data and compared with the global model to appreciate the generality of our
173 global models across reaches. Importantly, residuals of the mixed models were not analyzed,
174 even when they fitted better than the global models, because they could not be interpreted
175 together, not being calculated from the same regression model in all reaches. In addition, data
176 for a given individual reach were often insufficient to provide a robust model of age-group
177 succession. In other words, analyzing the residuals of the global models was a means of
178 removing average serial correlation while calculating density descriptors similarly in all
179 reaches.

180 All further synchrony analyses were made on residual densities of the global succession
181 models, hereafter noted *r0+*, *r1+* and *rAd*. For each of the three age-groups, synchrony
182 between pairs of reaches was described by 36×36 distance matrices. The elements of these
183 distance matrices were dissimilarity measures, calculated as $1 - \rho$, where ρ was the Pearson
184 correlation between age-group residual density for the corresponding pair of reaches (varying
185 between 0 and 2). Synchrony values were transformed into distance values using $1 - \rho$, as
186 distance values are conventionally used with Mantel tests ($1 - \rho$ decreases with synchrony).
187 Pairs of reaches with less than three years of simultaneous density and environmental
188 information (33% of cases) were excluded from all analyses. Finally, the average number of
189 years per reach used to calculate ρ values was 5.8.

Environmental data and synchrony in environmental time series

According to the literature, trout population dynamics may be influenced by discharge, hydraulic and thermal conditions during key periods of the trout life cycle. Therefore, for each year preceding fish sampling, environmental conditions were described for four key periods, using five environmental variables (Table 2). Only the 10 environmental descriptors (period×variable combinations) for which a causal relationship with some age-group densities was expected were considered (Table 2).

These four key periods were: (*i*) adult spawning migration (September 1st to January 31st); (*ii*) egg development (November 1st to February 29th); (*iii*) fry emergence (March 1st to April 30th); and (*iv*) the summer growth period (July 1st to September 13th, the median date of the 320 trout surveys). The dates for the first three periods (hereafter: 'spawning', 'egg', 'emergence') were estimated for France by a group of fourteen experts from several organizations on the basis of numerous trout monitoring campaigns (Gouraud et al. 2014). The 'summer' period was defined to describe low-flow conditions preceding sampling.

Two of the five environmental variables (Table 2) were daily discharge percentiles, two were hydraulic variables (flow velocity and substrate mobility), and the fifth was the frequency of low temperature. The field data and models used to calculate these environmental variables are detailed in Appendix A. In brief, field data involved daily discharge and daily water temperature measured in most reaches. Missing values were estimated using extrapolation models. For water temperature, extrapolation model tests generally indicated errors of the order of 1°C. Hydraulic conditions were derived from numerical hydraulic models or detailed hydraulic measurements (N>100) made throughout each reach.

The two daily discharge percentiles described low- and high-flow magnitude. Low-flow magnitude (Q_{90}, defined as daily discharge exceeded 90% of the time during the period, $m^3.s^-$

214 ^{1}) was used to test the effect of summer low-flows on all age-groups (see Nislow and
215 Armstrong 2012). High-flow magnitude ($Q_{10,}$ defined as daily discharge exceeded 10% of the
216 time during the period, $m^3.s^{-1}$) was used to test the effect of spates on *rAd* during spawning
217 (spawners may be more sensitive to spates during their migration), on *r0+* during egg
218 development (e.g., Unfer et al. 2011) or on residual density in all age-groups during
219 emergence. All age-groups were considered as potentially influenced by high spring floods
220 occurring during this period because spates have a major impact on 0+ fish (Jensen and
221 Johnsen 1999; Cattanéo et al. 2003; Unfer et al. 2011) and may be strong enough to influence
222 the survival and dispersal of older cohorts (Young et al. 2010).

223 The other three variables, describing hydraulics and thermal conditions, were not percentiles
224 but indicated the frequency above or below quantitative thresholds of events that could
225 influence trout life cycle. Frequency of high daily velocities (*fV0.5*) was defined by a
226 threshold of 0.5 $m.s^{-1}$, corresponding to the upper end of the preferred range of current
227 velocity for 0+ (Heggenes 1996; Roussel and Bardonnet 2002). The influence of *fV0.5* on
228 *r0+* was tested during emergence, due to the reduced swimming ability of recently hatched
229 juveniles (Armstrong et al. 2003). The influence of frequency of spawning substrate mobility
230 (*fMob*, frequency of daily discharge > critical discharge; see Appendix A) during spawning,
231 egg development and emergence was tested on *r0+,* due to a potential direct influence of bed
232 mobility on mortality in early life stages (Unfer et al. 2011). Regarding the thermal threshold,
233 sub-lethal temperatures for brown trout (<0°C for all age-stages, >13°C during egg
234 development, and >22°C for older stages; Elliott and Elliott 2010) were exceptional in the
235 study reaches (only 0.7% of daily water temperatures were < 1°C and none were >19.6°C);
236 cold periods were therefore defined by temperature thresholds that occurred more frequently,
237 corresponding to the first third of the thermal preference range reported by Elliott and Elliott
238 (2010): <4.3°C for egg development and <7.3°C for older age-stages. The influence of sub-

239 optimal temperature (*fTlow*, the frequency of days with $T_{water,d}$ below threshold) on *r0+* was
240 tested during egg development ($T_{water,d}$<4.3°C) and emergence ($T_{water,d}$<7.3°C). Influence
241 on older age-groups was not tested as these fish can actively seek thermal refuge (Cunjak et
242 al. 2013).

243 Regarding biological synchrony, environmental synchrony between pairs of reaches was
244 assessed for each environmental variable on 36×36 distance matrices with dissimilarity
245 measures equal to $1 - \rho$, where ρ was the Pearson correlation of the environmental variable
246 between the corresponding pair of reaches.

247 **Data analyses**

248 Several Mantel tests (Mantel 1967) were used to analyze the relative influence of
249 environmental synchrony and density-dependent dispersal on trout synchrony. All these
250 Mantel tests analyzed the probability of the observed relationship (Mantel R) between
251 dissimilarity values of two or three distance matrices (geographic distance, trout synchrony
252 and environmental synchrony) occurring randomly (significance threshold: 0.05; 4,000
253 random permutations; "vegan" R package; Oksanen et al. 2013).

254 *Step 1: Spatial scales of synchrony*

255 The spatial scales of synchrony were first analyzed by correlating trout synchrony and
256 environmental synchrony to Euclidean distance. A strong relationship between trout
257 synchrony and geographic distance could be due to the combined influence of density-
258 dependent dispersal and environmental synchrony. However, density-dependent dispersal
259 could be expected to generate synchronous trout responses over smaller geographic distances
260 than environmental synchrony. The tests relating trout synchrony to Euclidean distance were
261 repeated using network distance: a stronger link between trout synchrony and network
262 distance than Euclidean distance would suggest an effect of dispersal.

Step 2: Influence of environmental synchrony on trout synchrony

To better analyze the influence of environmental synchrony on trout synchrony, trout synchrony was first correlated to environmental synchrony (Mantel tests for all relationship hypotheses in Table 2) and results were compared to those between geographic distance and trout synchrony (at step 1).

When univariate Mantel tests were significant with both an environmental variable and geographic distance for a given age-group, partial (multivariate) Mantel tests were performed to better distinguish their relative effects (Smouse et al. 1986). To avoid having to perform numerous tests, partial Mantel tests were performed for only one environmental variable within each type of environmental group (discharge, hydraulics, temperature). The variable selected was the most significant one found on univariate Mantel testing.

Finally, to help interpret the synchronous influence of the environment on trout density, time series of trout residual density were co-plotted against environmental variables. These time series (trout and environment) were standardized by reach and averaged between groups of reaches with synchronous trout series. The groups were obtained by hierarchical cluster analysis based on the distance matrices of trout residual density (Ward algorithm; as in Cattanéo et al. 2003).

Step 3: Influence of density-dependent dispersal on trout synchrony

To better analyze the influence of density-dependent dispersal between reaches on observed synchrony, tests that were significant at steps 1 and 2 were repeated on two subsets of data characterized by reduced possibilities of dispersal. In the first subset, 30 reaches in which dispersal was limited were selected: reaches more than 50km apart or separated by a dam preventing upstream passage; the 50 km threshold was, to the best of our knowledge, greater than the maximum distance reported for brown trout displacement (Young et al. 2010).

Dispersal between these reaches was possible only during spates (e.g., drift through the dam). The second data subset comprised only 22 reaches between which dispersal was impossible (more than 50km apart or separated by impassable dams in both directions). As there were various ways of removing reaches, tests on the two subsets were repeated 100 times with differing random selection of reaches to be removed. Thus, for each significant result of steps 1 and 2, the percentage of cases (in the 100 repetitions) in which the Mantel test remained valid on the data subsets was quantified.

Results

Trout data and synchrony in trout times series

Median trout density per reach across surveys varied between 10.3 and 51.3 individuals per 100m². On average, 38% of sampled individuals were 0+, 34% were 1+ and 28% were adult. Linear regressions indicated a significant relationship between the densities of successive age-groups (P<0.001; Fig. 2, plain lines). Model coefficients [± standard deviation] were:

(1) $\log(0+_y) = 1.37\ [\pm 0.17] + 0.34\ [\pm 0.10].\log(Ad_{y-1}) \quad (R^2 = 0.04)$

(2) $\log(1+_y) = 0.80\ [\pm 0.06] + 0.55\ [\pm 0.03].\log(0+_{y-1}) \quad (R^2 = 0.54)$

(3) $\log(Ad_y) = 0.27\ [\pm 0.08] + 0.25\ [\pm 0.04].\log(1+_{y-1}) + 0.57\ [\pm 0.03].\log(Ad_{y-1}) \quad (R^2 = 0.54)$

The global model R² for 1+ and adults indicated that the global linear model appropriately reflected an average age-group succession across reaches (>50% of variability explained). For the 0+ age-group, the model showed low explained variance. The slopes of Eqs (1) and (2) and the sum of slopes in Eq (3) were significantly less than 1, suggesting some degree of apparent density-dependence regulation in age-group successions.

Mixed models (Fig. 2, dashed lines), significantly improved fit, with R^2 values of 0.30, 0.70 and 0.71 for the three age-groups. ΔAIC between models with random effects ('mixed model') and fixed effect ('global model') were respectively 14, 23 and 9 for 0+, 1+ and adults.

Median Pearson ρ between all pairs of reaches was close to 0 (ρ_{r0+}=0.16, ρ_{r1+}=-0.01, ρ_{rAd}=0.11), indicating that there was no obvious global synchrony at the spatial scale of the whole dataset.

Step 1: Spatial scales of synchrony

Euclidean distance between pairs of reaches varied between 1.2 and 1,029.0 km, with 39 pairs of reaches less than 15 km apart. For the 93 out of 630 pairs of reaches that were not separated by the sea, distance via the river network ranged from 1.2 to 640.0km, (mean: 262.0 km), with 25 pairs of reaches less than 15 km apart.

Mantel tests showed that trout synchrony of *r0+* and *r1+* was significantly related to Euclidean distance (Fig. 3). Although significant, these tests revealed low Mantel R (R^2<0.08). For *r0+,* however, the degree of synchrony was strong (half of correlations >0.5) for reaches less than ~75 km apart, and even stronger (75% of correlations >0.5) for reaches less than 5 km apart. This effect was weaker for *r1+* (Fig. 3). Focusing on reaches for which network distance could be computed, Mantel R between *r0+* and geographic distance was lower for network distance than Euclidean distance (R^2 = 0.08 vs. 0.16; Fig. 4). Correlations between *r1+* and geographic distance were no longer significant when analysis focused on these reaches.

Environmental synchrony was also significantly related to Euclidean distance for most descriptors (7 out of 10; R^2 between 0.04 and 0.24), with particularly strong relationships for variables and periods related to high flow (see one example for each environmental group in

Fig. 3[1]). No spatial synchrony was found for only three environmental descriptors: *fTlow* during the egg period, *fMob* during the emergence period and Q_{90} during the summer. Other environmental synchronies were strong (generally >0.5) up to distances around ~75 km, except for *fTlow* during emergence (Fig. 3), which showed strong synchronies over longer distances (> 200 km).

Step 2: Influence of environmental synchrony on trout synchrony

Mantel tests relating trout synchrony to the environment were significant in 4 out of 14 tests (Table 2; Fig. 5), all concerning *r0+* residual density. Synchrony in *r0+* was related to Q_{10} (mainly during emergence and secondarily during the egg period) and *fMob* (mainly during spawning and secondarily during the egg period). Overall Mantel R was lower ($R^2 \leq 0.05$) than for Euclidean distance. Mantel test results partly depended on a substantial number of pairs of reaches in which both physical and biological synchrony were strong (Fig. 5).

Partial Mantel tests (Table 3) were made for combinations of Euclidean distance and each of the two main environmental descriptors that influenced *r0+*. The effect of Euclidean distance on *r0+* synchrony was significant when the environmental effect was removed, whereas the reverse was not significant ($P \geq 0.06$).

Co-plots of time series for trout residual density and the two main significant environmental descriptors in the four groups of synchronous reaches (Fig. 6) showed that Q_{10} during the emergence period was negatively associated with *r0+* (at least in the three most synchronous groups), whereas there was no clear positive or negative direction of an annual effect of *fMob*. The four groups identified by cluster analysis did not necessarily involve geographically close reaches.

[1] Relations for all environmental descriptors are presented in the supplementary material (Fig. S1)

354 **Step 3: Influence of density-dependent dispersal on trout synchrony**

355 Four of the 6 significant Mantel tests relating trout density to Euclidean distance or the
356 environment remained significant (in more than 75% of trials) when tested on the first data
357 subset, in which dispersal was limited. These concerned the relationships with Euclidean
358 distance and the two main environmental descriptors mentioned above (Q_{10} during
359 emergence and *fMob* during spawning). By contrast, only one of the six tests remained
360 significant (in 95% of trials) when tested on the second subset, in which dispersal was
361 impossible. This test concerned the relationship between *r0+* and Euclidean distance.
362 Dispersal between reaches may have influenced other results, which remained significant in
363 <35% of tests on the second data subset.

364 The results of partial Mantel tests were similar whether performed on all reaches or on the
365 limited dispersal subset, but were seldom significant when performed on the subset in which
366 dispersal was impossible (Table 3).

367 ## Discussion

368 **A Moran effect on 0+ trout**

369 The present study supports the notion that salmonid populations are frequently synchronous
370 (Copeland and Meyer 2011) and contributes to disentangling the relative influence of
371 environmental factors and density-dependent dispersal on trout synchrony. The results
372 principally suggest that a Moran effect is responsible for 0+ synchronies between
373 geographically close reaches. Synchronies in older age-groups (1+ and adults) were weaker
374 and not linked to environmental synchronies. Four elements supported the notion that 0+
375 synchrony is due to a Moran effect. Firstly, synchrony in *r0+* was particularly strong over a
376 distance of ~75km, a distance consistent with the spatial scale of environmental synchrony.
377 This distance of ~75km is greater than the 50km reported for freshwater populations in the

meta-analysis by Myers et al. (1997). We were also considering a larger geographic scale in the present study, compared with reaches < 70km apart in Hayes 1995 or <25km apart in Lobón-Cerviá 2004. Secondly, synchrony was related less to network distance than Euclidean distance, suggesting a weak influence of dispersal. Thirdly, several significant Mantel tests related 0+ synchrony to environmental synchrony (high flow during emergence and substrate mobility during spawning). And fourthly, many tests on *r0+* synchrony remained significant on the data subset where density-dependent dispersal between reaches was unlikely.

The Mantel tests showed low Mantel R values, but this statistic alone does not reflect the strength of synchrony. Mantel R is expected to be low in data sets collected over large spatial areas and with relatively short time series (see also Cattanéo et al. 2003; Chevalier et al. 2014). Pairs of reaches more than 75km apart (Fig. 3) may not be synchronized due to a variety of environmental characteristics not considered here. This inevitably generates noise in the relation between geographic distance and trout synchrony. In the present study, plots relating 0+ synchrony to Euclidean distance or environmental synchrony indicated that 0+ synchrony between geographically close reaches was frequently very strong (e.g., trout synchrony ρ was > 0.5 in 75% of pairs of reaches less than 5km apart; Fig. 3). More than the Mantel R value itself, these plots and the P-value of the Mantel tests indicated a strong, biologically significant level of synchrony between geographically close reaches.

Accounting for a global age-group succession model

A first strength of the present approach was to consider age-groups individually rather than pooled. This can increase the observed degree of synchrony (Grenouillet et al. 2001), as suggested by the present median synchrony levels (ρ_{r0+}=0.16, ρ_{r1+}=-0.01, ρ_{rAd}=0.11), which were generally higher than those obtained by Chevalier et al. (2014) after pooling age-groups (ρ=0.038).

A second strength of the present approach was to reduce serial dependence between successive age-groups, by using global models of age-group succession. Serial dependence is one of the two main statistical issues in synchrony analysis (Liebhold et al. 2004), together with the influence of temporal trends (not found in the present dataset). Global succession models for 1+ and adults explained more than 50% of density variability, confirming the strength of serial dependence and the importance of taking it into account in analyzing synchrony with the environment. The global model relating 0+ to adults explained a smaller part of variability. Nevertheless, analyses were performed on *r0+* rather than directly on 0+ density, in order to be consistent with the analyses for other age-groups. The weak serial dependence of 0+ on adults was consistent with other findings (e.g., Lobón-Cerviá 2013). Overwhelming environmental drivers may tend to make 0+ dependence on adults difficult to detect (Daufresne and Renault 2006). This relationship can also be affected by the lower catchability of small fish (e.g., Ruiz and Laplanche 2010) or by confusion between sampled adults and the actual parental stock. Actual spawning stock can depend on variability in maturity age (Olsen and Vøllestad 2005), on potential stocking issues of which the details are not well established, or on migration of adults between sampled reaches and spawning areas (Young et al. 2010).

The present global model of age-group succession for all reaches was the strongest assumption involved in accounting for serial dependence. This hypothesis was rarely tested explicitly in synchrony studies but is essential to investigating Moran effects. Liebhold et al. (2004) pointed out that the hypothesis probably does not hold in many systems, as spatial variation in population dynamics is frequent. In the present study, comparing the global models with reach-dependent mixed models suggested that a large part of population dynamics was taken into account by the global models. However, the mixed models indicated that variations in population dynamics did occur across reaches (higher explanatory power of

mixed models). This may partly lower the level of synchrony (ρ values and Mantel R) observed, because spatial variation in density-dependent dynamics reduces the synchrony caused by environmental stochasticity (Liebhold et al. 2006). Sampling error may also have lowered the observed levels of synchrony (Santin-Janin et al. 2014). However, sampling errors were unlikely to have influenced the main results, because the magnitude of sampling error was probably much lower than the magnitude of annual density variation, which can be as great as 10-fold between certain years.

The slopes of the global models for 1+ and adults were significantly less than 1, indicating an apparent global density-dependence survival for these age-groups, which was rarely previously documented (but see Richard et al. 2013). The present results also suggested a density-dependent regulation on 0+, but we remain cautious about this finding as the global 0+ model showed very low explanatory power (R^2=4%). Density-dependence mechanisms on 0+ have often been discussed in the literature, being difficult to identify (e.g., Elliott 1984; Nicola et al. 2008; Lobón-Cerviá 2013), mainly due to their high annual variability influenced by environmental conditions.

Environmental drivers of 0+ synchrony

The correlation between *r0+* and Euclidean distance was stronger than that between *r0+* and environmental synchrony, although the dataset included geographically close reaches with differing characteristics due to dams. Thus, close reaches are likely to be synchronous, even if they are separated by dams and have different flow regimes. Moreover, partial tests revealed that environmental variables did not explain *r0+* synchrony when the effect of Euclidean distance was removed. Therefore, Euclidean proximity probably accounted for a combined effect of several environmental variables including those studied here (e.g., high flow during emergence, or substrate mobility during spawning) and others not included in analysis.

452 Nevertheless, *r0+* synchrony correlated significantly with Q_{10} during emergence and with
453 *fMob* during spawning. These results are consistent with the observation of a negative
454 influence of high flow on small individuals during emergence (e.g. Hayes 1995; Cattanéo et
455 al. 2003; Nicola et al. 2009), due to higher mortality and/or drift. Effects of spawning
456 substrate mobility on 0+ were more rarely mentioned in the literature (but see Jensen and
457 Johnsen 1999). Unfer et al. (2011) suggested that these effects could be positive (reshaping
458 spawning grounds due to substrate turnover) or negative (scouring redds and destroying eggs)
459 according to their timing. This could explain why the positive or negative direction of the
460 annual effect of *fMob* was harder to identify.

461 The other environmental descriptors implemented in analysis, including the frequency of high
462 current velocity, did not explain trout synchrony. However, using velocity percentiles instead
463 of discharge (Q_{10}) percentiles would have led to comparable results, due to the monotonic
464 relationship between discharge and velocity in reaches. Therefore, an influence of hydraulics
465 on trout synchrony cannot be ruled out. The non-significant effect of temperature may be due
466 to local adaptation to the thermal regime (Filipe et al. 2013). It is also possible that the
467 present dataset covered a larger range of hydraulic than thermal conditions (e.g., median flow
468 velocity ranged from 0.1 to 0.7 $m.s^{-1}$ while median water temperature ranged from 6.6° to
469 11.5°C; Table 1).

470 Including additional environmental descriptors could have increased understanding of trout
471 synchrony. For example, food availability and oxygen concentration were not monitored in
472 the study reaches, but may contribute to synchrony. Other descriptors of the available
473 environmental regimes could also have been used (relating to magnitude, frequency, duration,
474 timing or rate of change; Poff et al. 1997). For example, other thresholds, such as 2-year high
475 seasonal discharge as used by Cattanéo et al. (2002), could have been tested. Finally,
476 averaged physical conditions within a given reach could have been translated into hydraulic

habitat values that account for the heterogeneity of microhabitat conditions within the reach (Lamouroux and Capra 2002). However, to ensure statistical power, we only considered the variables that were most likely to explain density synchrony.

Influence of density-dependent dispersal on 0+ synchrony

In previous papers, density-dependent dispersal between study populations was often ruled out *a priori* because pairs of populations were totally disconnected (Tedesco et al. 2004) or too distant (network distance >50km for 95% of the pairs of reaches in Cattanéo et al. 2003). In contrast, the present results on *r0+* synchrony remained significant when density-dependent dispersal between reaches was unlikely (tests on the first subset, where reaches could be connected by downstream drift only). Thus, *r0+* synchrony was linked to environmental synchrony and not to density-dependent dispersal. The limited density-dependent dispersal of 0+ reported in the literature also supports this conclusion. For example, Vollestad et al. (2012) mentioned a scale of dispersal of 200m while Dieterman and Hoxmeier (2011) and Vatland and Caudron (2015) estimated that only a small proportion of the 0+ population was involved in emigration from reaches due to density-dependence (≤10%).

By contrast, except for the test linking *r0+* and Euclidean distance, the present tests were no longer significant when dispersal between reaches was totally impossible, even by drift (tests on the second subset). This may partly be due to reduced statistical power (i.e., fewer reaches involved). However, this suggests that the possibility of drifting from one reach to another can explain synchronous emigrations from reaches that are not explained by high flow variables. Drift between reaches would potentially explain synchronous immigration, but cannot reasonably explain synchronous emigration of 0+. Therefore, this result again suggests that synchrony between geographically close reaches is not perfectly explained by the present high flow variables.

Synchrony in 1+ and adults

For older age-groups, except for a weak relation linking *r1+* synchrony and geographic distance, the present results were not able to explain trout synchrony. Authors often failed to identify constraining abiotic conditions for juveniles and adults (e.g., Cattanéo et al. 2002) except after exceptional events (e.g., a 50-year flood in Young et al. 2010). As they grow, stream-resident salmonids show increased swimming ability and may move more easily to avoid stressful conditions, reducing the influence of the environment (Unfer et al. 2011; Nislow and Armstrong 2012). Accordingly, movements of juveniles and adults toward sheltered areas during high flows (Bunt et al. 1999) or toward cold waters during droughts (Elliott 2000) have been reported. Moreover, movements of older individuals can occur at distances much larger than the reach (Ovidio et al. 1998), partially masking the links between trout density and the environment through sink/source recolonization processes (Zorn and Nuhfer 2007). The synchrony of *r1+* was related to Euclidean distance only, suggesting that environmental variables other than those studied here are likely involved.

In summary, the present study confirmed a Moran effect on 0+ trout density, operating mainly over distances <75km. A negative influence of high discharge was identified during emergence and a more complex relationship with spawning substrate mobility during the spawning period. Nevertheless, other environmental variables than those tested are likely involved. By contrast, dispersal between reaches had a weak influence on 0+ synchrony. The synchrony analyses provide useful information for building models of brown trout population dynamics integrating both biotic aspects (e.g., density-dependent and density-independent survival, dispersal) and abiotic mechanisms (e.g., the effects of high flow and spawning substrate movement). The results also suggest that brown trout populations may show low resilience in case of more frequent high flows over a given area (e.g., watershed). In a context

of global environmental change, further synchrony analyses are needed to better quantify the risk of extinction and potential resilience of freshwater fish metapopulations.

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707

708 ## Tables

709 **Table 1.** Physical characteristics of the 36 stream reaches.

Physical characteristics	Min	Mean	Max
Width at median discharge (m)	2.9	8.2	15.5
Reach slope (%)	0.3	3.4	13.2
Elevation (m)	15.0	787.7	1370.0
Distance from source (km)	3.0	17.9	49.0
Basin area (km²)	9.0	135.1	605.0
Median daily discharge Q_{50} ($m^3.s^{-1}$)	0.1	1.0	2.7
Median diameter of streambed particle (cm)	0.1	16.6	64.0
Reach flow velocity ($m.s^{-1}$) at Q_{50}	0.1	0.4	0.7
Median daily water temperature (°C)	6.6	8.3	11.5

710

711 **Table 2.** Environmental variables used in Mantel tests relating trout synchrony to environmental
712 synchrony (discharge, hydraulics or temperature regime).

Variable group		Periods			
Code	**Definition**	**Spawning**	**Egg**	**Emergence**	**Summer**
Discharge					
Q_{90}	daily discharge exceeded 90% of the time				*r0+; r1+; rAd*
Q_{10}	daily discharge exceeded 10% of the time	*rAd*	***r0+***	***r0+***; *r1+; rAd*	
Hydraulics					
fV0.5	Frequency of current velocity > 0.5m.s^{-1}			*r0+*	
fMob	Mobility frequency of the spawning substrate	***r0+***	***r0+***	*r0+*	
Temperature					
fTlow	Frequency of $T_{water,d}$ below threshold		*r0+* (<4.3°C)	*r0+* (<7.3°C)	

713 **Note**: Univariate Mantel tests relating synchrony in residual density of each age-group (*r0+*,
714 *r1+*, *rAd*) and environmental synchrony were made for a subset of environmental descriptors
715 (variables×periods). Bold values correspond to significant associations (p-value <0.05) and
716 the most significant association for a given variable group is underlined.

717 **Table 3.** Results of Partial Mantel tests analyzing the association of *r0+* synchrony, geographic
718 distance and synchrony of one environmental descriptor.

Effect tested	Effect removed	Partial p-value	Partial r²	% tests still significant on first subset	% tests still significant on second subset
Log(Euclid dist)	$Q_{10\ Emergence}$	<0.01	0.06	100	35
$Q_{10\ Emergence}$	*Log(Euclid dist)*	0.20			
Log(Euclid dist)	$fMob_{\ Spawning}$	<0.01	0.07	100	11
$fMob_{\ Spawning}$	*Log(Euclid dist)*	0.06			

719 **Note**: For significant partial tests, partial R^2 was computed and we indicate the percentage of
720 significant tests when the Mantel test was repeated on two subsets of reaches (first subset:
721 limited dispersal between reaches; second subset: no dispersal).

Figures

Fig. 1. Locations of the 36 reaches (18 in bypassed sections).

Fig. 2. Relationships between raw densities of successive age-groups. Recruitment is linked to the adult density of the previous year (1st column) and 1+ are linked to previous density of 0+ (2nd column). Adult densities are linked to previous density of 1+ and adults (3rd and 4th columns); they are represented here after setting one of the two explanatory variables at its mean value across reaches. These relations are shown for all reaches pooled (1st row) and 5 randomly selected reaches (2nd to 5th rows). The solid lines correspond to a global linear regression and the dashed lines to linear mixed-effects models with a reach-level random effect.

Fig. 3. Trout synchrony (1st column) or environmental synchrony (2nd column) related to geographic distance. Linear relationships (full lines) correspond to the Mantel tests. Local polynomial fittings (dashed lines) present the smoothed spatial evolution of synchronies. For significant Mantel tests, Mantel R^2 and p-values are given. The environmental variables showing the strongest relation to geographic distance (with highest R^2) are shown for each environmental group (Table 2).

Fig. 4. Synchrony of *r0+* related to geographic distance (Euclidean or network distance), as in Figure 3 but restricted to 93 pairs of reaches for which a network distance could be computed.

Fig. 5. Significant relationships (on Mantel tests) between the synchrony of *r0+* and the synchrony of environmental descriptors.

Fig. 6. Time series of *r0+* trout residual densities and environmental descriptors illustrating the most significant Mantel tests. Series were standardized by reach and grouped according to the results of a cluster analysis on trout synchrony. The cluster analysis was performed on the 18 (out of 36) reaches with more than 5 sampling year between 1999 and 2006. Q_{10} time series were multiplied by -1 to facilitate interpretation. The histograms in the right column represent the frequency distributions of ρ_{r0+} between all pairs of reaches within the groups.

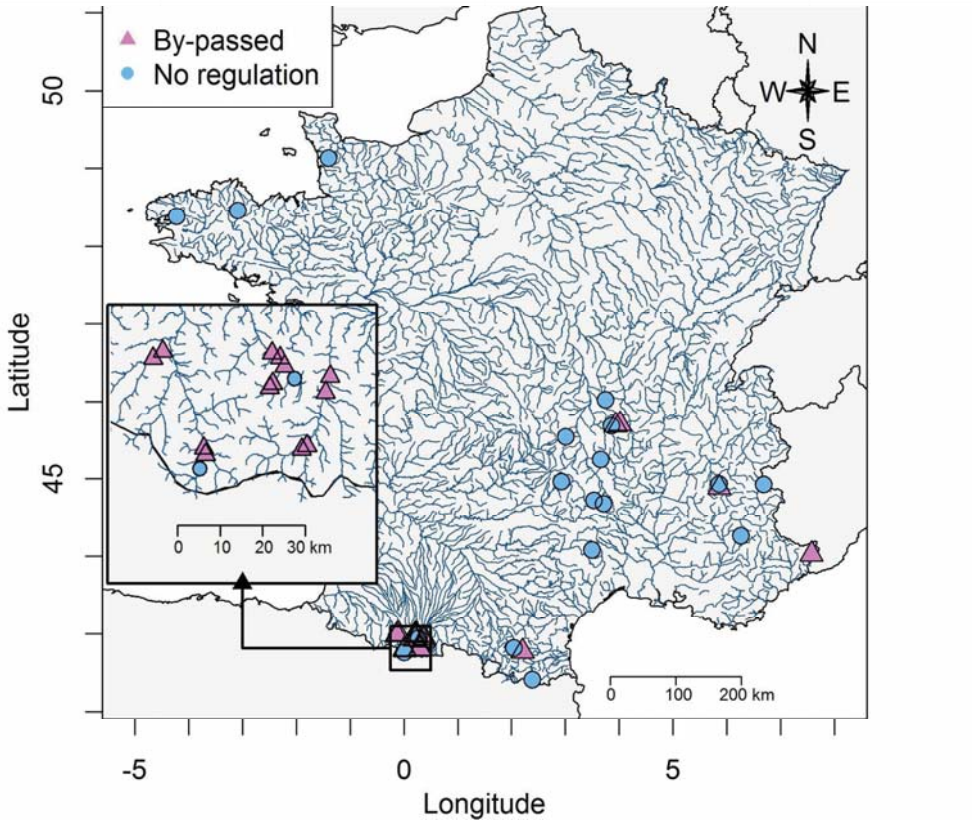

Fig. 1. Locations of the 36 reaches (18 in bypassed sections).
169x159mm (300 x 300 DPI)

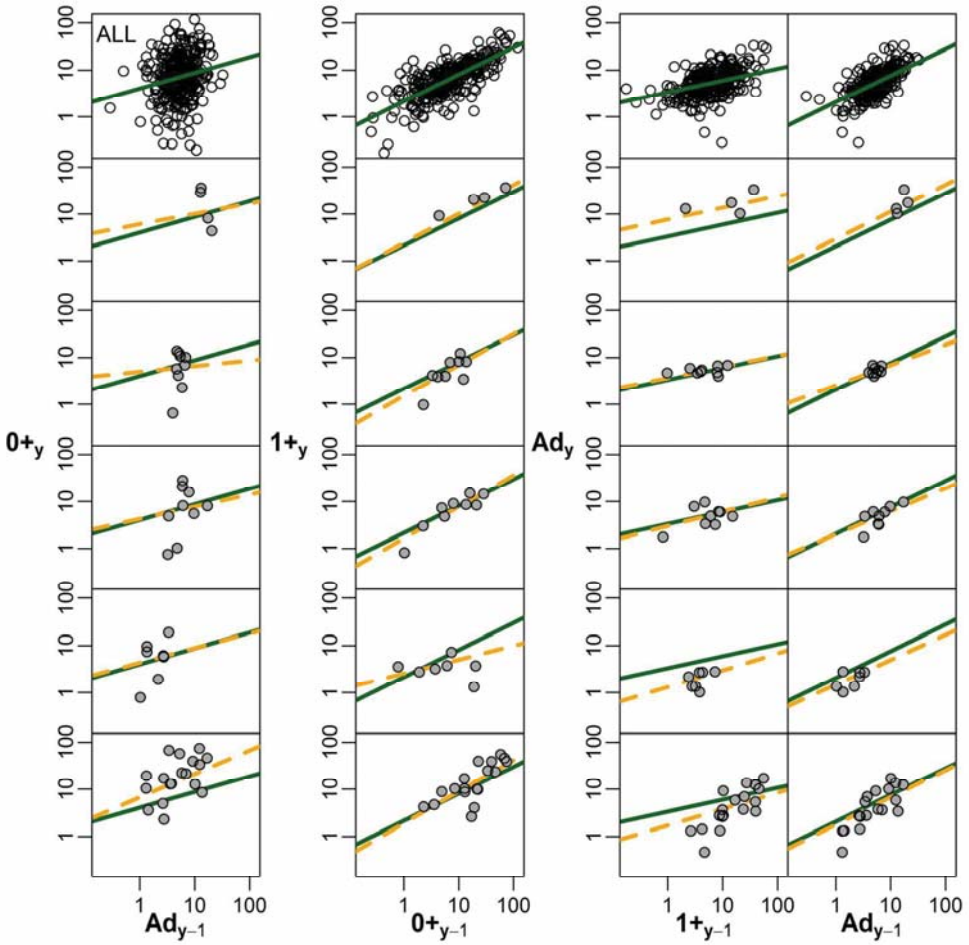

Fig. 2. Relationships between raw densities of successive age-groups. Recruitment is linked to the adult density of the previous year (1st column) and 1+ are linked to previous density of 0+ (2nd column). Adult densities are linked to previous density of 1+ and adults (3rd and 4th columns); they are represented here after setting one of the two explanatory variables at its mean value across reaches. These relations are shown for all reaches pooled (1st row) and 5 randomly selected reaches (2nd to 5th rows). The solid lines correspond to a global linear regression and the dashed lines to linear mixed-effects models with a reach-level random effect.
179x179mm (300 x 300 DPI)

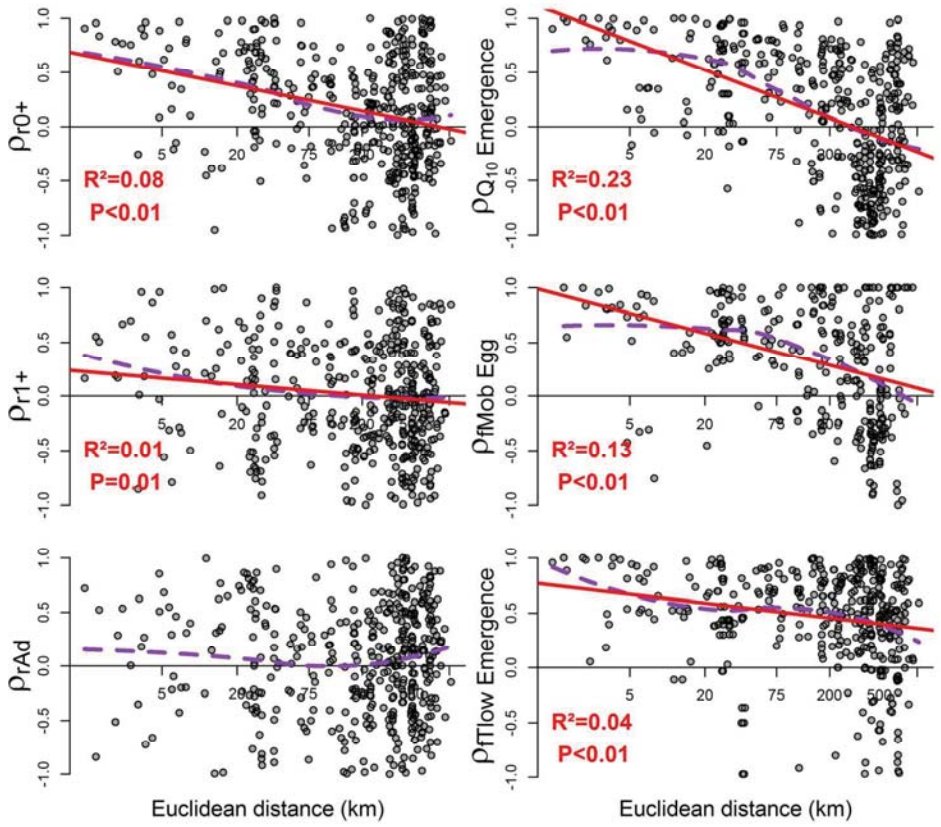

Fig. 3. Trout synchrony (1st column) or environmental synchrony (2nd column) related to geographic distance. Linear relationships (full lines) correspond to the Mantel tests. Local polynomial fittings (dashed lines) present the smoothed spatial evolution of synchronies. For significant Mantel tests, Mantel R^2 and p-values are given. The environmental variables showing the strongest relation to geographic distance (with highest R^2) are shown for each environmental group (Table 2).
159x142mm (300 x 300 DPI)

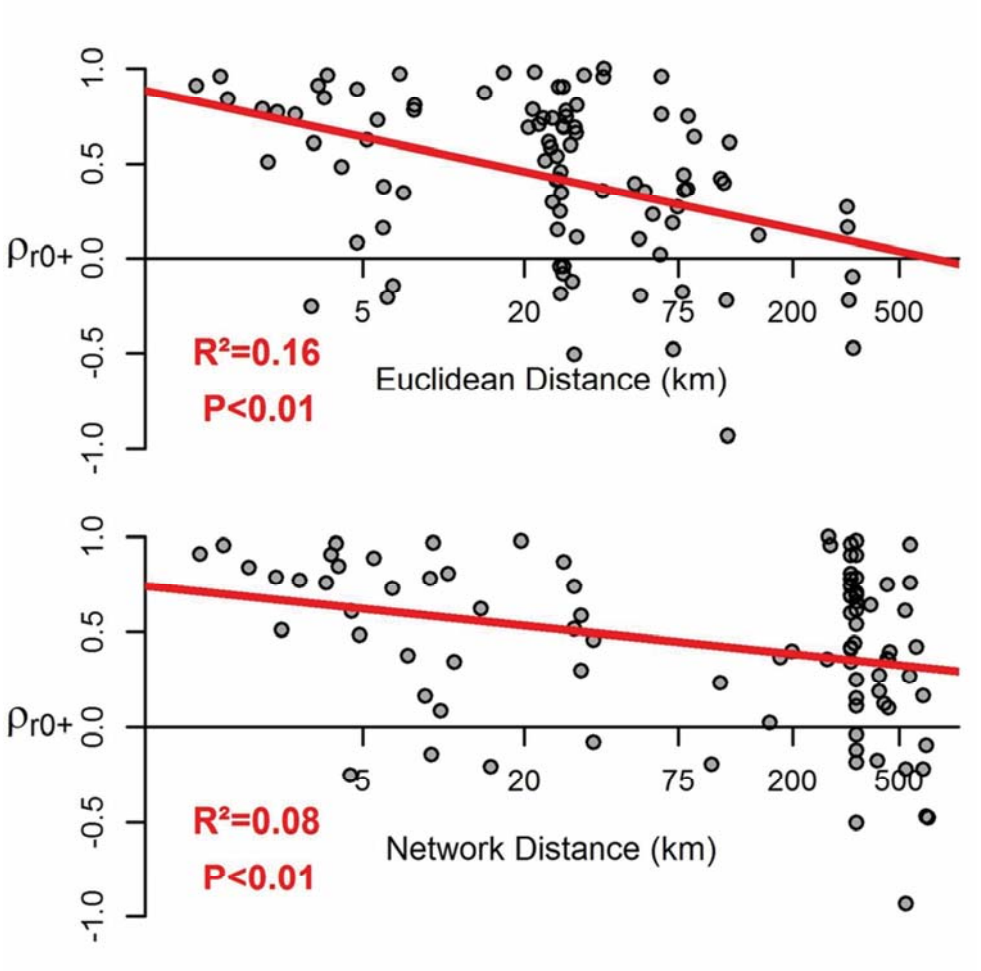

Fig. 4. Synchrony of r0+ related to geographic distance (Euclidean or network distance), as in Figure 3 but restricted to 93 pairs of reaches for which a network distance could be computed.
79x79mm (300 x 300 DPI)

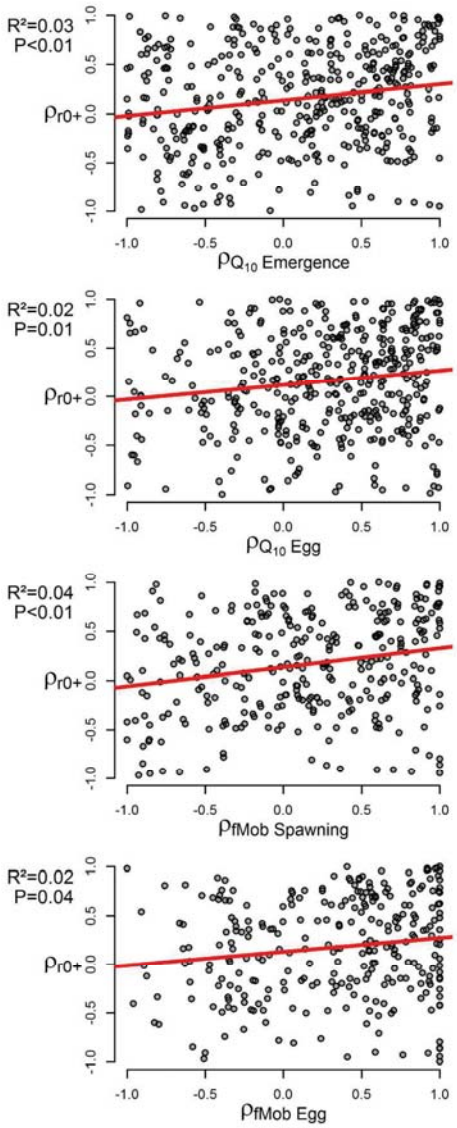

Fig. 5. Significant relationships (on Mantel tests) between the synchrony of r0+ and the synchrony of environmental descriptors.
199x500mm (300 x 300 DPI)

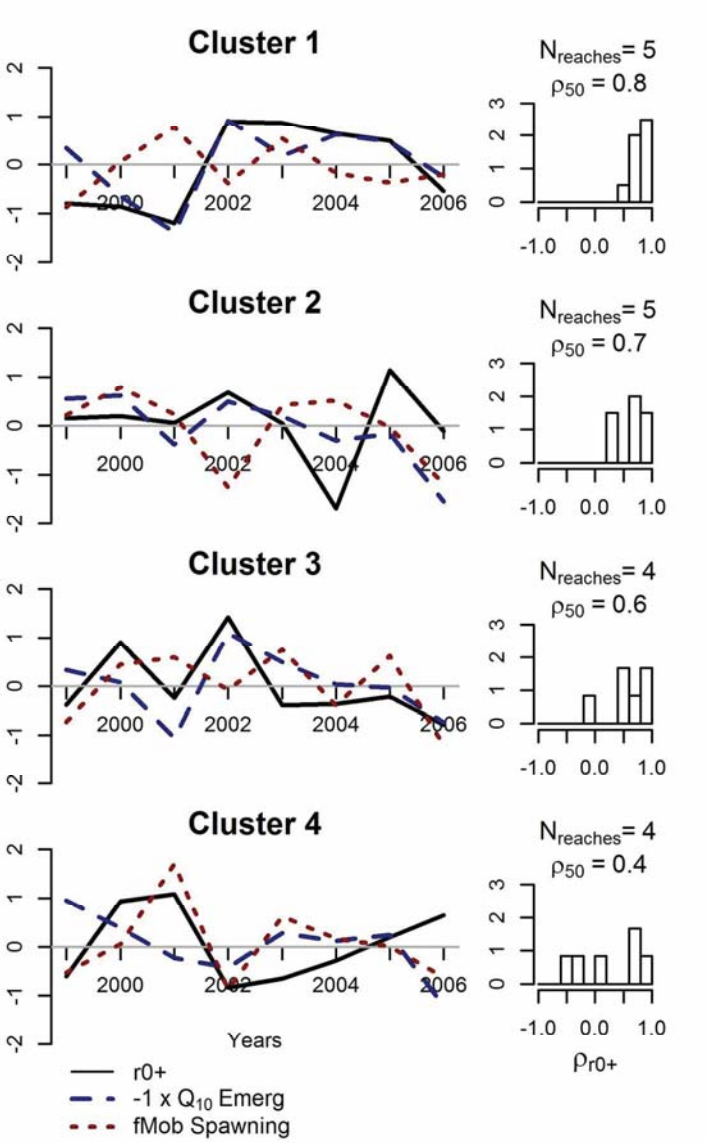

Fig. 6. Time series of r0+ trout residual densities and environmental descriptors illustrating the most significant Mantel tests. Series were standardized by reach and grouped according to the results of a cluster analysis on trout synchrony. The cluster analysis was performed on the 18 (out of 36) reaches with more than 5 sampling year between 1999 and 2006. Q10 time series were multiplied by -1 to facilitate interpretation. The histograms in the right column represent the frequency distributions of ρr0+ between all pairs of reaches within the groups.
129x211mm (300 x 300 DPI)

Appendix A: Daily data series

A.1 Discharge

Daily discharge ($m^3.s^{-1}$) was continuously gauged in 23 reaches (SP2T pressure probes). For seven reaches close to a gauging station (<40 km via the stream network), daily discharge was spatially extrapolated after correcting for drainage area. In the remaining six reaches, which were all below dams, daily discharge was calculated from the upstream discharge and the operating schedule of the dam. Less than 5% of the selected surveys had missing daily discharge values within the preceding year (with < 33% of missing values for key periods used in analysis).

A.2 Hydraulic conditions: flow velocity and substrate mobility

Reach daily current velocities ($m.s^{-1}$) were estimated as the ratio between daily discharge and the corresponding cross-section area (average depth × average width). This required estimating depth-discharge and width-discharge relationships for the reach (i.e., at-a-reach hydraulic geometry relationships; Stewardson 2005). For this purpose and for 24 reaches, hydraulic geometry relationships were fitted to conventional power laws (Leopold and Maddock 1953) using estimates of depth and width made at two distinct discharges (median ratio between the two discharges: 5.1). For each measured discharge, the wetted widths of regularly spaced cross-sections (n > 15) and the water depth at regularly spaced points along cross-sections (n> 100 across the reach) were measured. For five reaches, the same method was used, except that cross-sections were not regularly spaced but weighted by the length of streams they represented. In the seven remaining reaches, the mean velocity was obtained from a numerical hydraulic model calibrated in the reach for habitat modeling purposes (Ginot et al. 1998).

Spawning substrate mobility was defined as the number of days with discharge above the critical discharge theoretically moving particles of diameter 0.02 m (typical size for spawning; Kondolf and Wolman 1993). This critical discharge was estimated using the classical Shields' criterion (Shields 1936).

A.3 Water temperature time series

Depending on the availability of water temperature data for a given reach, three procedures were used to estimate missing water temperature values.

Twenty-two reaches with available water temperature measurements

These reaches had at least one year of daily water temperature data measured in the reach (on average, 5.4 years of data per reach). To predict missing values in these reaches (29% of time series), daily water temperature on day d ($T_{water,d}$) was modeled from air temperature during the three previous days ($T_{air,d-2}$ to $T_{air,d}$), partly accounting for inertia and hysteresis effects. A logistic model (used on a weekly time-step in Mohseni et al. 1998) was implemented:

$$\text{(A1)} \quad T_{water,\,d} = \mu + \frac{(A-\mu)}{\left(1+\exp\left[\Gamma.\left(B-(0.5\,x\,T_{air,\,d}+0.3\,x\,T_{air,\,d-1}+0.2\,x\,T_{air,\,d-2}\right)\right]\right)}$$

T_{air} was recorded at meteorological stations close to our reaches (median Euclidean distance: 6.8 km, maximum: 31.1 km). Parameters corresponded to minimal (μ) and maximal (A) water temperature and air temperature at inflection point (B) or were linked to the slope at inflection point (Γ). Each reach model was fitted using least-squares criteria ("nls" function of R 3.1.1 software; R Core Team 2014).

Following Mohseni et al. (1998), Root Mean Squared Error (RMSE) and Nash-Sutcliffe coefficients (NSC; Nash and Sutcliffe 1970) were computed for each reach to estimate accuracy and goodness of fit. Water temperature models calibrated on these 22 reaches with

calibration data had a low RMSE (min: 0.7; mean: 1.0; max: 1.5 °C) and explained a large part of variability (min NSC: 0.82; mean: 0.90; max: 0.95). Fitting the parameter μ (minimal water temperature) or setting it at 0 hardly changed the results (maximal variation: +2.8% in RMSE and -0.54% in NSC); it was therefore set at 0 in all reaches. Using lagged air temperature over three days instead of daily air temperature reduced the RMSE of the model by 14.6% on average.

Five reaches close to another reach with water temperature data

Five additional reaches were close to another reach (< 5km; mean: 2.6 km, with no tributary between reaches) with similar physical properties (<15% difference in flow or width; <10% difference in median grain size); the two were then considered to have similar water temperatures.

Nine reaches without water temperature data

For the nine remaining reaches, water temperature was predicted from air temperature using a global logistic model, fitted simultaneously on the 22 reaches with water temperature data. The global logistic model used had the same formulation as in Eq. (A1) but parameters μ, A, B and Γ depended linearly on parameters that could explain differences between water and air temperatures (longitude, latitude, distance from the source, and difference in altitude between the reach and the air temperature recorder).

The RMSE of this global model was calculated when fitted on all available data. The global water temperature model had an RMSE of 1.3 and an NSC of 0.87. Cross-validation was then used (leaving one reach out in turn) to estimate the average residual absolute error on water temperature using the global model. Cross-validations indicated a mean absolute error of less than 1°C in 59% of cross-validations (maximum: 2.3°C for one reach).

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