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1 Influence of discharge, hydraulics, water temperature and dispersal on
2 density synchrony in brown trout populations (*Salmo trutta*)

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21

22 **Abstract**

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

38 **Keywords:**

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

41 **Résumé**

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

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

58 **Mots-clefs:**

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

61

62 **Introduction**

63 Temporal variations in population density depend on both abiotic (e.g., environmental) and
64 biotic processes (e.g., density-dependent dispersal) operating at various spatial scales (Alonso
65 et al. 2011; Richard et al. 2013). Environmental factors may cause synchronous fluctuations
66 in density in populations with similar density-dependence structures (Moran 1953). These
67 "Moran effects" may explain the synchronous variation in abundance of herbivorous insects
68 and mammals in sites located as much as 1,000 km apart (Koenig 2002; Liebhold et al.
69 2004). Density-dependent regulation (through dispersal of individuals) can also induce

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

82 Spatial synchrony has been frequently studied and observed in riverine fish populations.
83 Chevalier et al. (2014) studied 27 freshwater fish species commonly found throughout
84 France. They found low but significant levels of synchrony (average correlation between
85 pairs of reaches generally <0.1) that were related to the life-history strategies and the upper
86 thermal tolerance limits of species. Of these species, stream-resident brown trout (*Salmo*
87 *trutta*) has been especially well documented, making it useful for the study of synchrony.
88 This species has a wide native range and is known to be sensitive to environmental conditions
89 (e.g., high flow rates, extreme water temperatures). Synchrony in such environmental
90 conditions may lead to synchrony in trout density. Cattaneo et al. (2003) showed the
91 influence of hydrologic synchrony (high discharge levels during the emergence period) on the
92 density synchrony of young-of-the-year trout in 37 stream reaches. One limitation of existing
93 analyses of trout synchrony (e.g., Cattaneo et al. 2003; Zorn and Nuhfer 2007) is that they did
94 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

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

122 **Study reaches and geographic distances**

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

141 Two kinds of geographic distance were computed between pairs of reaches: Euclidean and
142 river network distances. Network distance is potentially more relevant to describe density-
143 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 r_{0+} , r_{1+} and r_{Ad} . 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.

190 **Environmental data and synchrony in environmental time series**

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

197 These four key periods were: (i) adult spawning migration (September 1st to January 31st); (ii)
198 egg development (November 1st to February 29th); (iii) fry emergence (March 1st to April
199 30th); and (iv) the summer growth period (July 1st to September 13th, the median date of the
200 320 trout surveys). The dates for the first three periods (hereafter: ‘spawning’, ‘egg’,
201 ‘emergence’) were estimated for France by a group of fourteen experts from several
202 organizations on the basis of numerous trout monitoring campaigns (Gouraud et al. 2014).
203 The ‘summer’ period was defined to describe low-flow conditions preceding sampling.

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

212 The two daily discharge percentiles described low- and high-flow magnitude. Low-flow
213 magnitude (Q_{90} , defined as daily discharge exceeded 90% of the time during the period, $m^3 \cdot s^{-1}$)

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, $m^3 \cdot s^{-1}$) 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; Cattaneo 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 $0.5 m \cdot s^{-1}$, corresponding to the upper end of the preferred range of current
227 velocity for 0+ (Heggenes 1996; Roussel and Bardonnnet 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 ($T_{water,d} < 4.3^{\circ}C$) and emergence ($T_{water,d} < 7.3^{\circ}C$). 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.

263 *Step 2: Influence of environmental synchrony on trout synchrony*

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

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

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

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

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

287 Dispersal between these reaches was possible only during spates (e.g., drift through the dam).
 288 The second data subset comprised only 22 reaches between which dispersal was impossible
 289 (more than 50km apart or separated by impassable dams in both directions). As there were
 290 various ways of removing reaches, tests on the two subsets were repeated 100 times with
 291 differing random selection of reaches to be removed. Thus, for each significant result of steps
 292 1 and 2, the percentage of cases (in the 100 repetitions) in which the Mantel test remained
 293 valid on the data subsets was quantified.

294 **Results**

295 **Trout data and synchrony in trout times series**

296 Median trout density per reach across surveys varied between 10.3 and 51.3 individuals per
 297 100m². On average, 38% of sampled individuals were 0+, 34% were 1+ and 28% were adult.
 298 Linear regressions indicated a significant relationship between the densities of successive
 299 age-groups ($P < 0.001$; Fig. 2, plain lines). Model coefficients [\pm standard deviation] were:

$$300 \quad (1) \quad \log(0+y) = 1.37 [\pm 0.17] + 0.34 [\pm 0.10]. \log(Ad_{y-1}) \quad (R^2 = 0.04)$$

$$301 \quad (2) \quad \log(1+y) = 0.80 [\pm 0.06] + 0.55 [\pm 0.03]. \log(0+y_{-1}) \quad (R^2 = 0.54)$$

$$302 \quad (3) \quad \log(Ad_y) = 0.27 [\pm 0.08] + 0.25 [\pm 0.04]. \log(1+y_{-1}) \\
 + 0.57 [\pm 0.03]. \log(Ad_{y-1}) \quad (R^2 = 0.54)$$

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

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

312 Median Pearson ρ between all pairs of reaches was close to 0 ($\rho_{r0+}=0.16$, $\rho_{r1+}=-0.01$,
313 $\rho_{rAd}=0.11$), indicating that there was no obvious global synchrony at the spatial scale of the
314 whole dataset.

315 **Step 1: Spatial scales of synchrony**

316 Euclidean distance between pairs of reaches varied between 1.2 and 1,029.0 km, with 39
317 pairs of reaches less than 15 km apart. For the 93 out of 630 pairs of reaches that were not
318 separated by the sea, distance via the river network ranged from 1.2 to 640.0km, (mean:
319 262.0 km), with 25 pairs of reaches less than 15 km apart.

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

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

332 Fig. 3¹). No spatial synchrony was found for only three environmental descriptors: *fTlow*
333 during the egg period, *fMob* during the emergence period and Q_{90} during the summer. Other
334 environmental synchronies were strong (generally >0.5) up to distances around ~ 75 km,
335 except for *fTlow* during emergence (Fig. 3), which showed strong synchronies over longer
336 distances (> 200 km).

337 **Step 2: Influence of environmental synchrony on trout synchrony**

338 Mantel tests relating trout synchrony to the environment were significant in 4 out of 14 tests
339 (Table 2; Fig. 5), all concerning r_{0+} residual density. Synchrony in r_{0+} was related to Q_{10}
340 (mainly during emergence and secondarily during the egg period) and *fMob* (mainly during
341 spawning and secondarily during the egg period). Overall Mantel R was lower ($R^2 \leq 0.05$) than
342 for Euclidean distance. Mantel test results partly depended on a substantial number of pairs of
343 reaches in which both physical and biological synchrony were strong (Fig. 5).

344 Partial Mantel tests (Table 3) were made for combinations of Euclidean distance and each of
345 the two main environmental descriptors that influenced r_{0+} . The effect of Euclidean distance
346 on r_{0+} synchrony was significant when the environmental effect was removed, whereas the
347 reverse was not significant ($P \geq 0.06$).

348 Co-plots of time series for trout residual density and the two main significant environmental
349 descriptors in the four groups of synchronous reaches (Fig. 6) showed that Q_{10} during the
350 emergence period was negatively associated with r_{0+} (at least in the three most synchronous
351 groups), whereas there was no clear positive or negative direction of an annual effect of
352 *fMob*. The four groups identified by cluster analysis did not necessarily involve
353 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

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

385 The Mantel tests showed low Mantel R values, but this statistic alone does not reflect the
386 strength of synchrony. Mantel R is expected to be low in data sets collected over large spatial
387 areas and with relatively short time series (see also Cattaneo et al. 2003; Chevalier et al.
388 2014). Pairs of reaches more than 75km apart (Fig. 3) may not be synchronized due to a
389 variety of environmental characteristics not considered here. This inevitably generates noise
390 in the relation between geographic distance and trout synchrony. In the present study, plots
391 relating 0+ synchrony to Euclidean distance or environmental synchrony indicated that 0+
392 synchrony between geographically close reaches was frequently very strong (e.g., trout
393 synchrony ρ was > 0.5 in 75% of pairs of reaches less than 5km apart; Fig. 3). More than the
394 Mantel R value itself, these plots and the P-value of the Mantel tests indicated a strong,
395 biologically significant level of synchrony between geographically close reaches.

396 **Accounting for a global age-group succession model**

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

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

419 The present global model of age-group succession for all reaches was the strongest
420 assumption involved in accounting for serial dependence. This hypothesis was rarely tested
421 explicitly in synchrony studies but is essential to investigating Moran effects. Liebhold et al.
422 (2004) pointed out that the hypothesis probably does not hold in many systems, as spatial
423 variation in population dynamics is frequent. In the present study, comparing the global
424 models with reach-dependent mixed models suggested that a large part of population
425 dynamics was taken into account by the global models. However, the mixed models indicated
426 that variations in population dynamics did occur across reaches (higher explanatory power of

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

434 The slopes of the global models for 1+ and adults were significantly less than 1, indicating an
435 apparent global density-dependence survival for these age-groups, which was rarely
436 previously documented (but see Richard et al. 2013). The present results also suggested a
437 density-dependent regulation on 0+, but we remain cautious about this finding as the global
438 0+ model showed very low explanatory power ($R^2=4\%$). Density-dependence mechanisms on
439 0+ have often been discussed in the literature, being difficult to identify (e.g., Elliott 1984;
440 Nicola et al. 2008; Lobón-Cerviá 2013), mainly due to their high annual variability
441 influenced by environmental conditions.

442 **Environmental drivers of 0+ synchrony**

443 The correlation between r_{0+} and Euclidean distance was stronger than that between r_{0+} and
444 environmental synchrony, although the dataset included geographically close reaches with
445 differing characteristics due to dams. Thus, close reaches are likely to be synchronous, even
446 if they are separated by dams and have different flow regimes. Moreover, partial tests
447 revealed that environmental variables did not explain r_{0+} synchrony when the effect of
448 Euclidean distance was removed. Therefore, Euclidean proximity probably accounted for a
449 combined effect of several environmental variables including those studied here (e.g., high
450 flow during emergence, or substrate mobility during spawning) and others not included in
451 analysis.

452 Nevertheless, r_{0+} 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; Cattaneo 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 Cattaneo et al. (2002), could have been tested. Finally,
476 averaged physical conditions within a given reach could have been translated into hydraulic

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

480 **Influence of density-dependent dispersal on 0+ synchrony**

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

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

502 Synchrony in 1+ and adults

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

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

526 of global environmental change, further synchrony analyses are needed to better quantify the
527 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 (km ²)	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).

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

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 \times 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 r^2	% tests still significant on first subset	% tests still significant on second subset
$\text{Log}(\text{Euclid dist})$	Q_{10} Emergence	<0.01	0.06	100	35
Q_{10} Emergence	$\text{Log}(\text{Euclid dist})$	0.20			
$\text{Log}(\text{Euclid dist})$	$f\text{Mob}_{\text{Spawning}}$	<0.01	0.07	100	11
$f\text{Mob}_{\text{Spawning}}$	$\text{Log}(\text{Euclid dist})$	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).

722 **Figures**

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

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

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

736 **Fig. 4.** Synchrony of $r0+$ related to geographic distance (Euclidean or network distance), as in Figure
737 3 but restricted to 93 pairs of reaches for which a network distance could be computed.

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

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

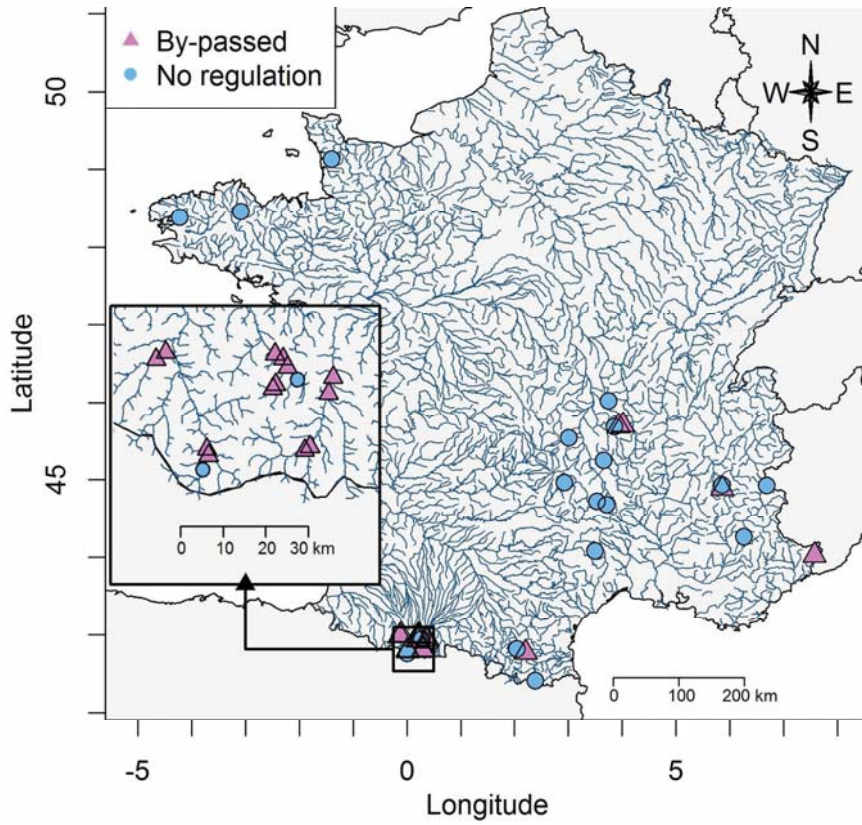


Fig. 1. Locations of the 36 reaches (18 in bypassed sections).
169x159mm (300 x 300 DPI)

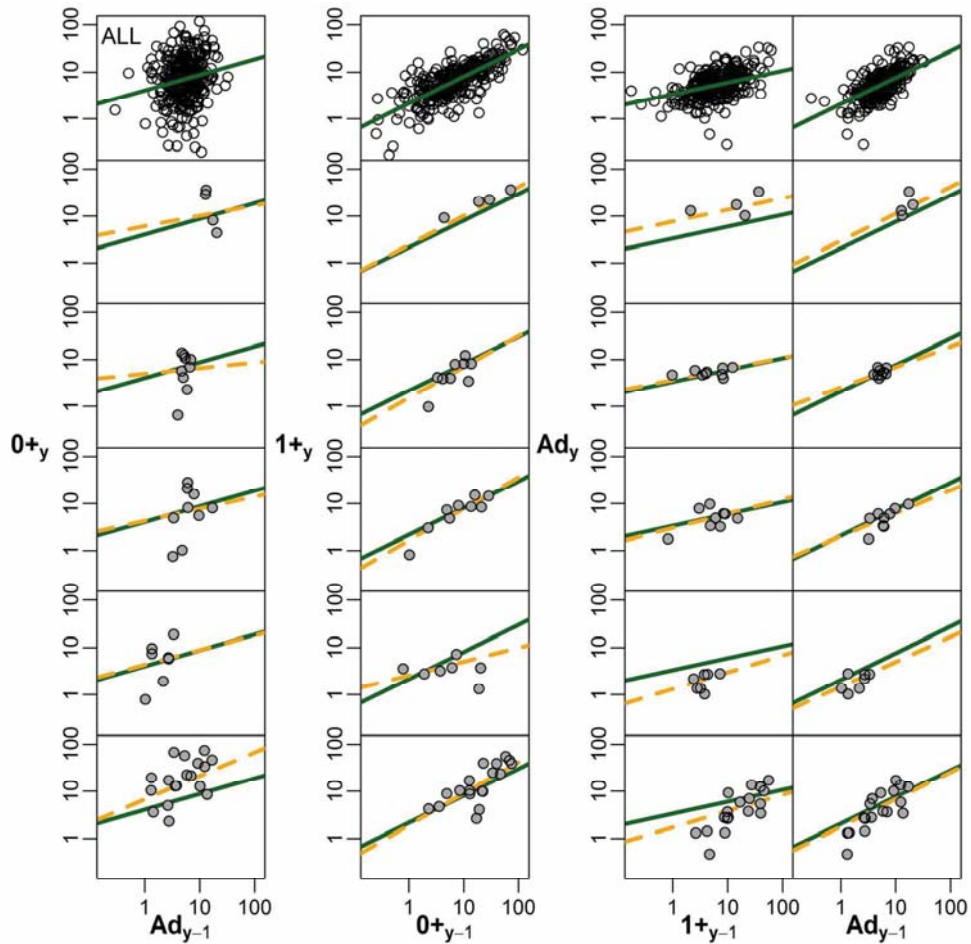


Fig. 2. Relationships between raw densities of successive age-groups. Recruitment is linked to the adult density of the previous year (1st column) and 1+ are linked to previous density of 0+ (2nd column). Adult densities are linked to previous density of 1+ and adults (3rd and 4th columns); they are 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)

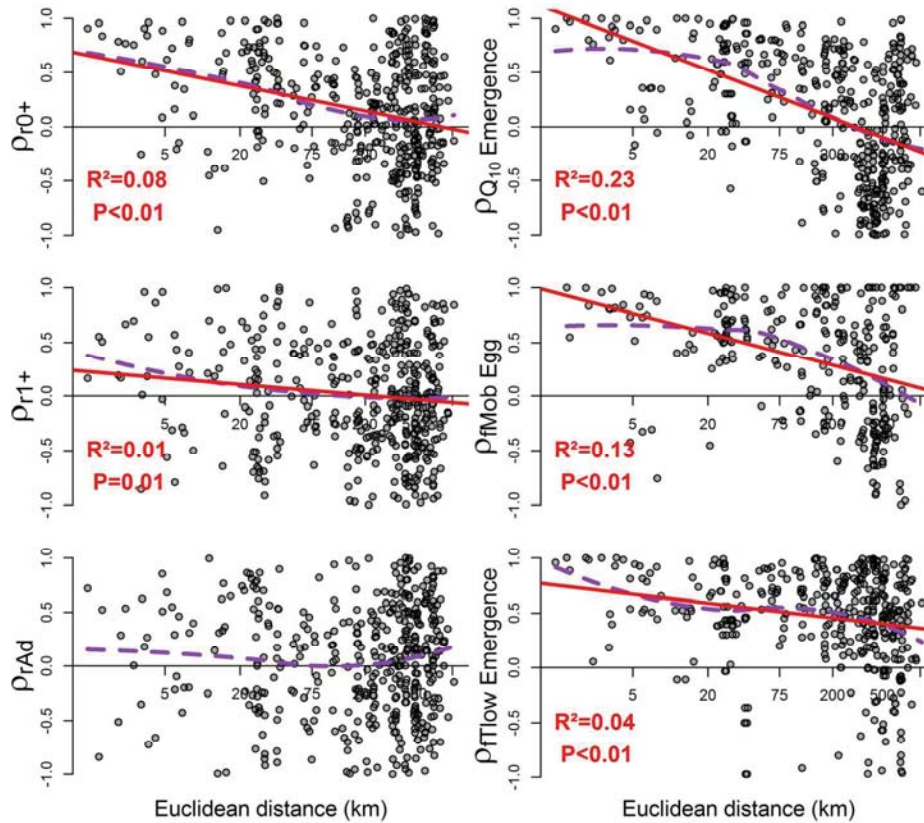


Fig. 3. Trout synchrony (1st column) or environmental synchrony (2nd column) related to geographic distance. Linear relationships (full lines) correspond to the Mantel tests. Local polynomial fittings (dashed lines) present the smoothed spatial evolution of synchronies. For significant Mantel tests, 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)

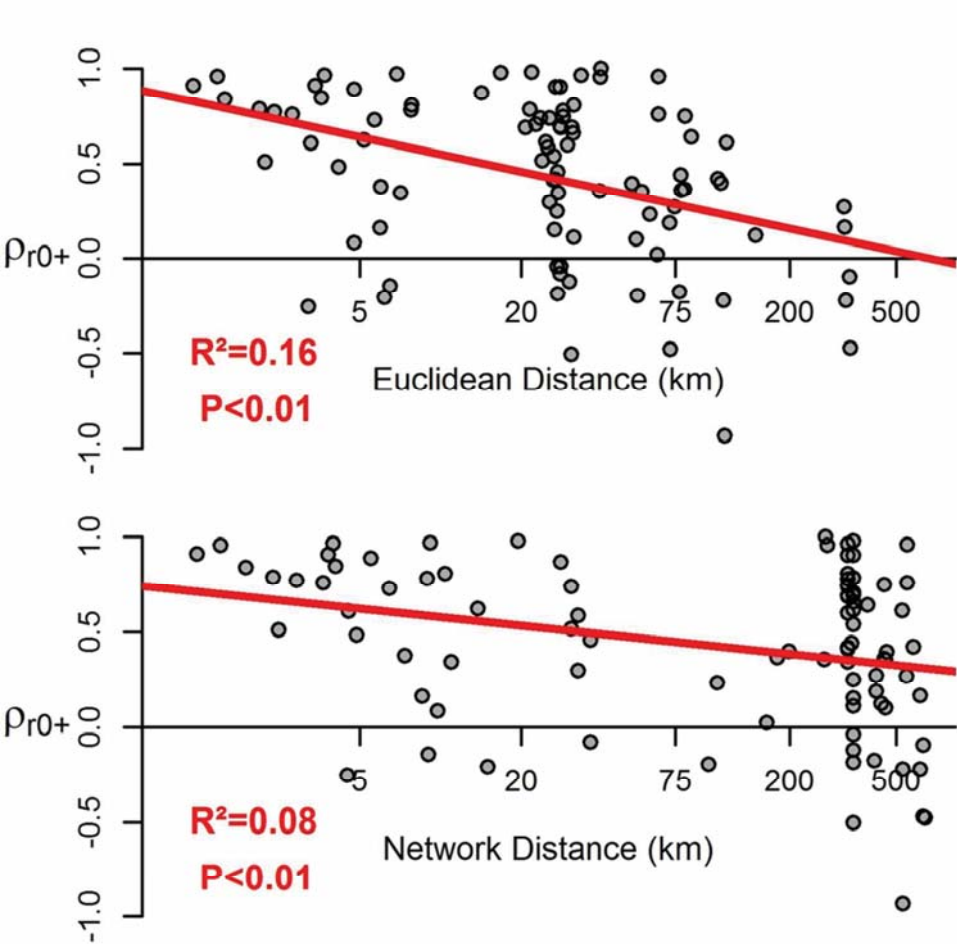


Fig. 4. Synchrony of r_{0+} related to geographic distance (Euclidean or network distance), as in Figure 3 but restricted to 93 pairs of reaches for which a network distance could be computed.
79x79mm (300 x 300 DPI)

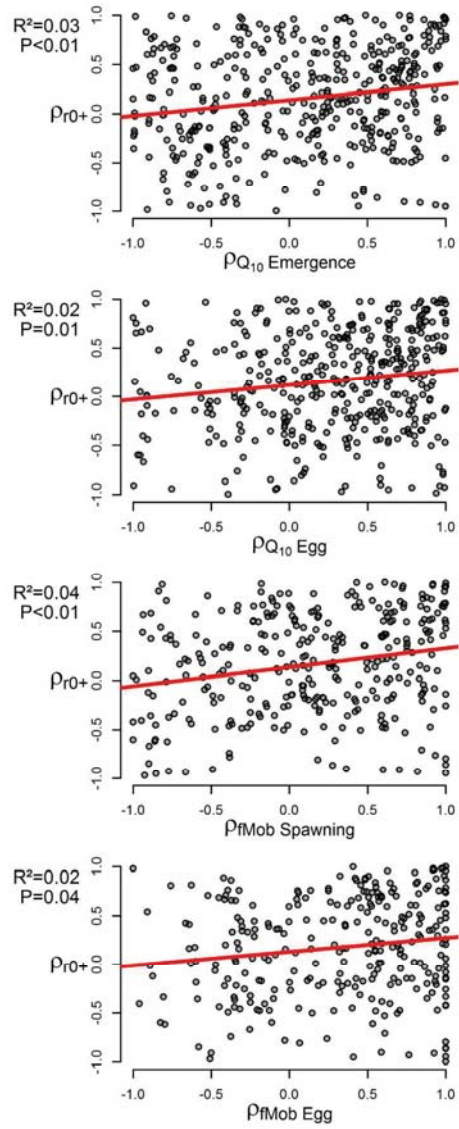


Fig. 5. Significant relationships (on Mantel tests) between the synchrony of r_{0+} and the synchrony of environmental descriptors.
199x500mm (300 x 300 DPI)

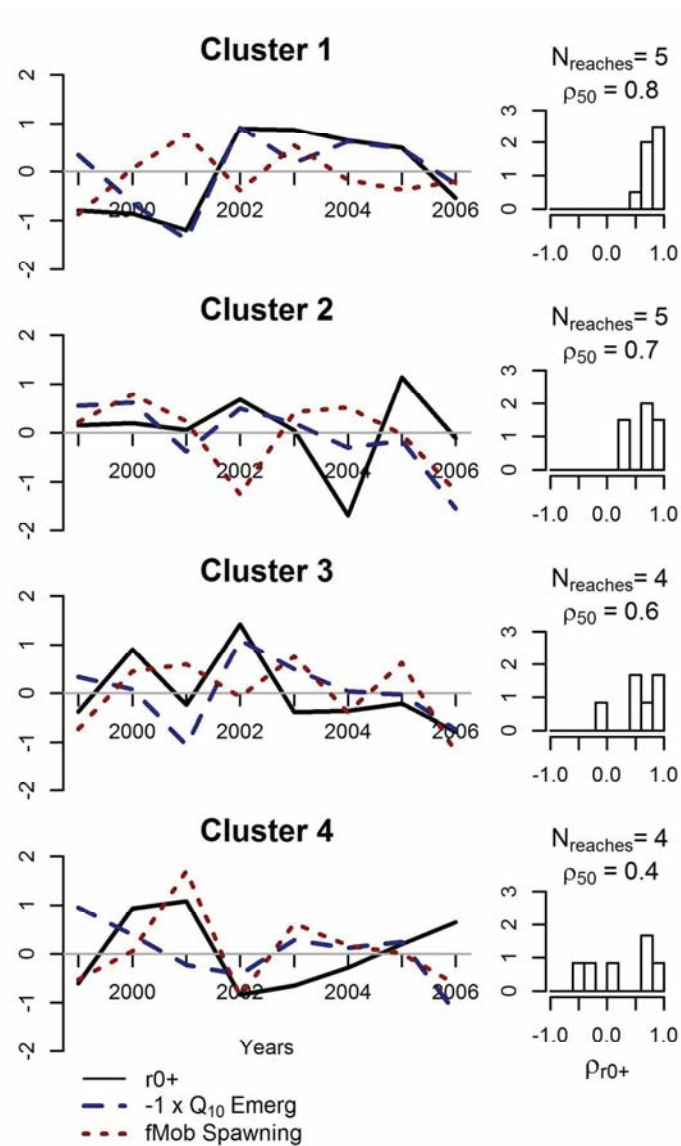


Fig. 6. Time series of r_{0+} trout residual densities and environmental descriptors illustrating the most significant Mantel tests. Series were standardized by reach and grouped according to the results of a cluster analysis on trout synchrony. The cluster analysis was performed on the 18 (out of 36) 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 $p_{r_{0+}}$ between all pairs of reaches within the groups.

129x211mm (300 x 300 DPI)

1 **Appendix A: Daily data series**

2 **A.1 Discharge**

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

10 **A.2 Hydraulic conditions: flow velocity and substrate mobility**

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

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

28 **A.3 Water temperature time series**

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

31 *Twenty-two reaches with available water temperature measurements*

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

$$37 \quad (A1) \quad T_{water,d} = \mu + \frac{(A-\mu)}{(1+\exp[\Gamma \cdot (B-(0.5 \times T_{air,d} + 0.3 \times T_{air,d-1} + 0.2 \times T_{air,d-2}))])}$$

38 T_{air} was recorded at meteorological stations close to our reaches (median Euclidean distance:
 39 6.8 km, maximum: 31.1 km). Parameters corresponded to minimal (μ) and maximal (A) water
 40 temperature and air temperature at inflection point (B) or were linked to the slope at
 41 inflection point (Γ). Each reach model was fitted using least-squares criteria (“nls” function
 42 of R 3.1.1 software; R Core Team 2014).

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

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

52 *Five reaches close to another reach with water temperature data*

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

57 *Nine reaches without water temperature data*

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

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

69 **Appendix : References**

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