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

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Manuscripts

1   Influence of discharge, hydraulics, water temperature and dispersal on

2   density synchrony in brown trout populations (*Salmo trutta*)

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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

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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

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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. Cattanéo 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., Cattanéo 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 *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.

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.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.

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   Cattanéo 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.

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 [± standard deviation] were:

300   (1) $\log(0+_y) = 1.37\,[\pm0.17] + 0.34\,[\pm0.10].\log(Ad_{y-1})$ $(R^2 = 0.04)$

301   (2) $\log(1+_y) = 0.80\,[\pm0.06] + 0.55\,[\pm0.03].\log(0+_{y-1})$ $(R^2 = 0.54)$

302   (3) $\log(Ad_y) = 0.27\,[\pm0.08] + 0.25\,[\pm0.04].\log(1+_{y-1})$

$$+ 0.57\,[\pm0.03].\log(Ad_{y-1}) \qquad (R^2 = 0.54)$$

303   The global model R² 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 (ρ_{r0+}=0.16, ρ_{r1+}=-0.01,

313 ρ_{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. 3[1]). 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 *r0+* residual density. Synchrony in *r0+* 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 *r0+*. The effect of Euclidean distance

346　　on *r0+* 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 *r0+* (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.

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[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 Cattanéo 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 (ρ_{r0+}=0.16, ρ_{r1+}=-0.01, ρ_{rAd}=0.11),

400   which were generally higher than those obtained by Chevalier et al. (2014) after pooling age-

401   groups (ρ=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 $r0+$ and Euclidean distance was stronger than that between $r0+$ 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 $r0+$ 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, *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

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 Cattanéo 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 (≤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., Cattanéo 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 (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

30

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+**	<u>**r0+**</u>*; r1+; rAd*	
Hydraulics					
fV0.5	Frequency of current velocity > 0.5m.s^{-1}			*r0+*	
fMob	Mobility frequency of the spawning substrate	<u>**r0+**</u>	**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 R² 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).

32

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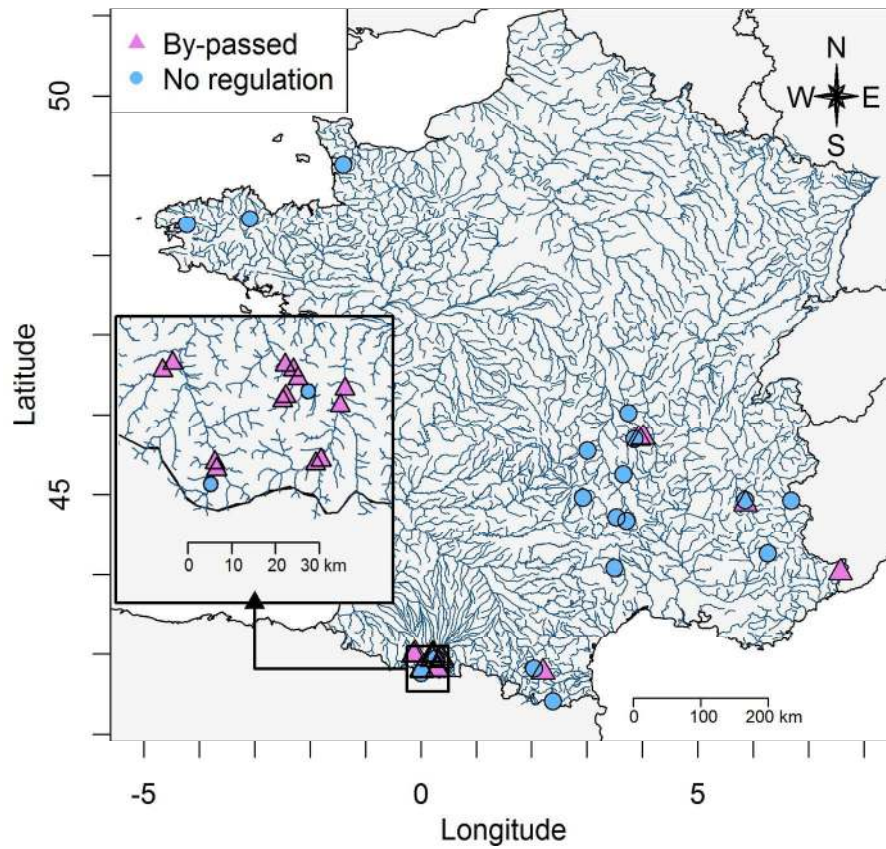
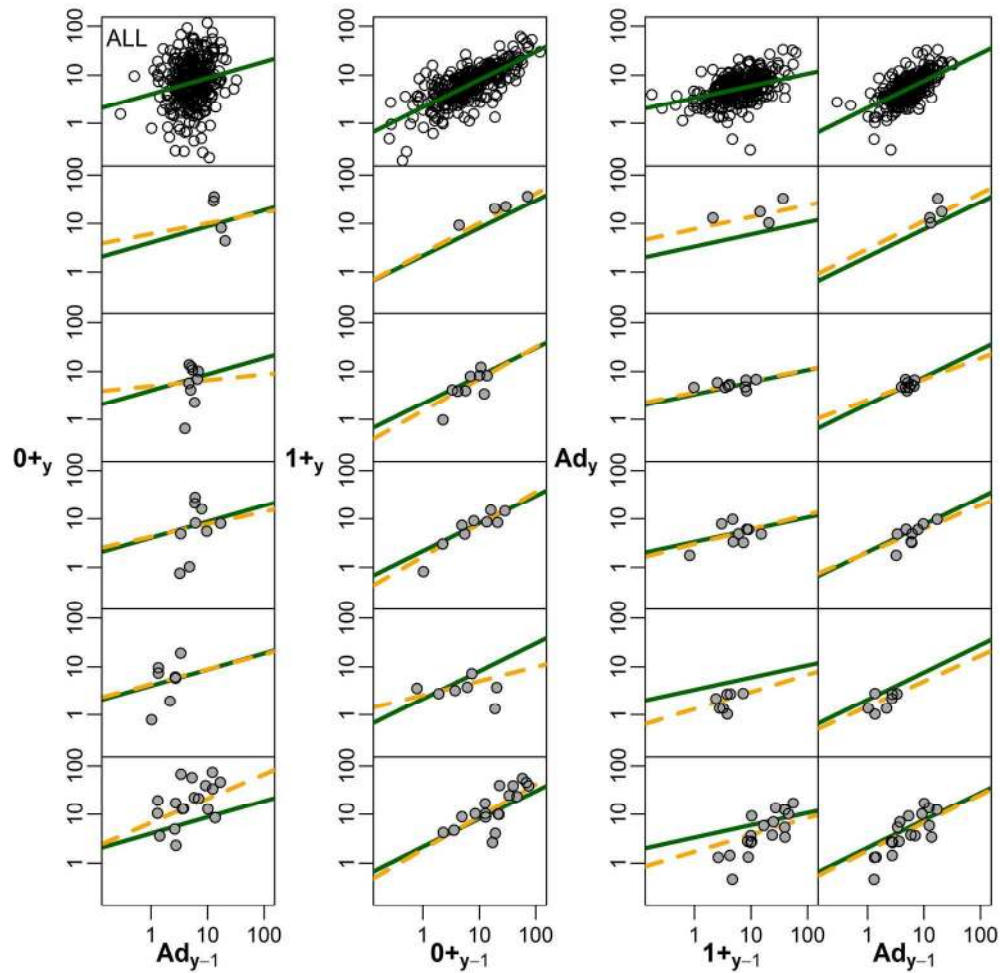Fig. 1. Locations of the 36 reaches (18 in bypassed sections).
169x159mm (300 x 300 DPI)

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.
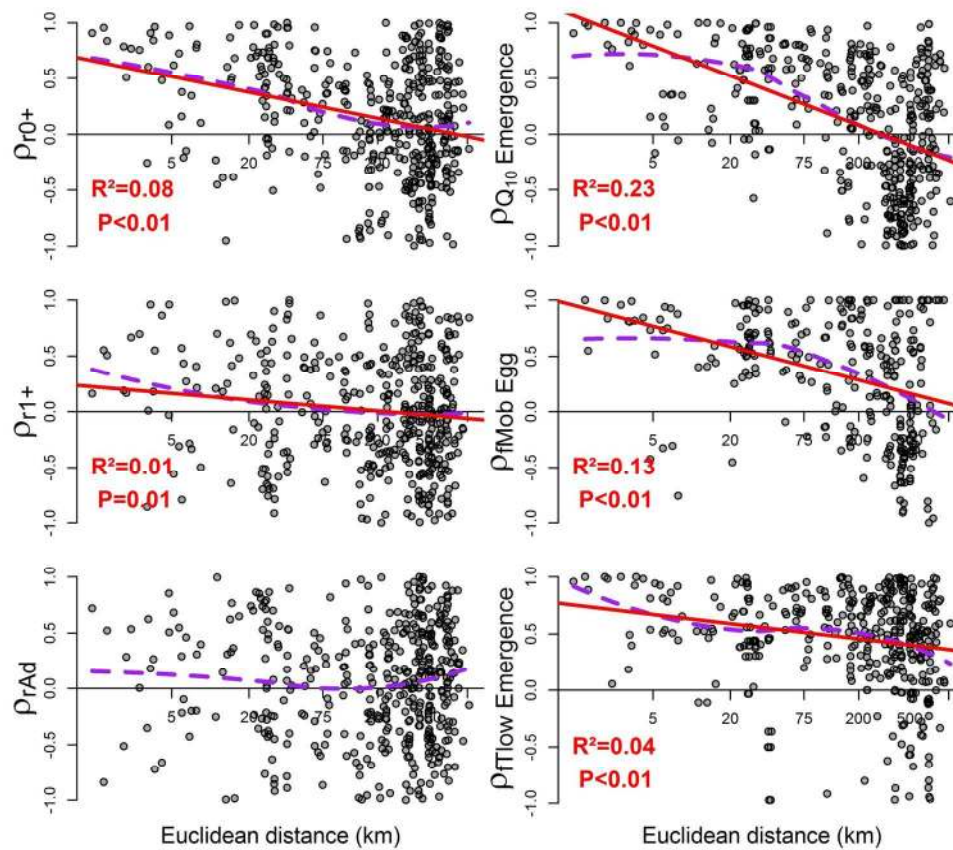179x179mm (300 x 300 DPI)

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 R² and p-values are given. The environmental variables showing the strongest relation to geographic distance (with highest R²) are shown for each environmental group (Table 2).
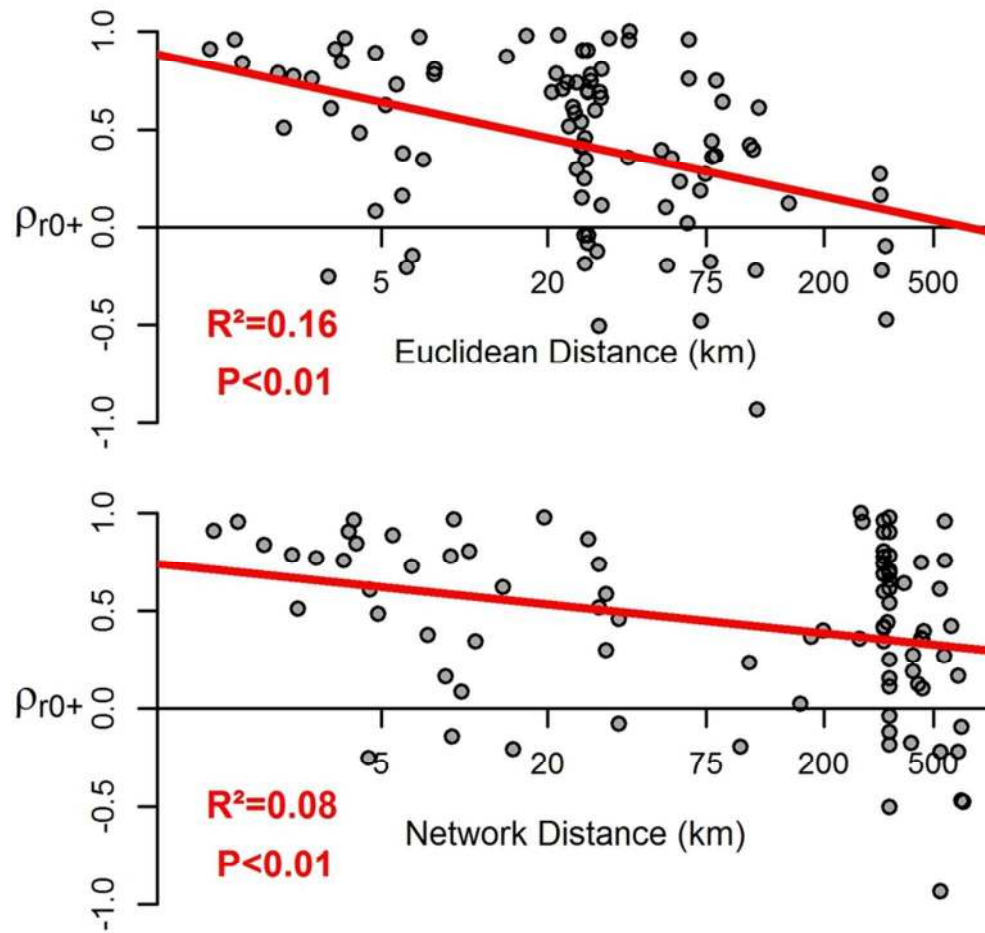159x142mm (300 x 300 DPI)

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.
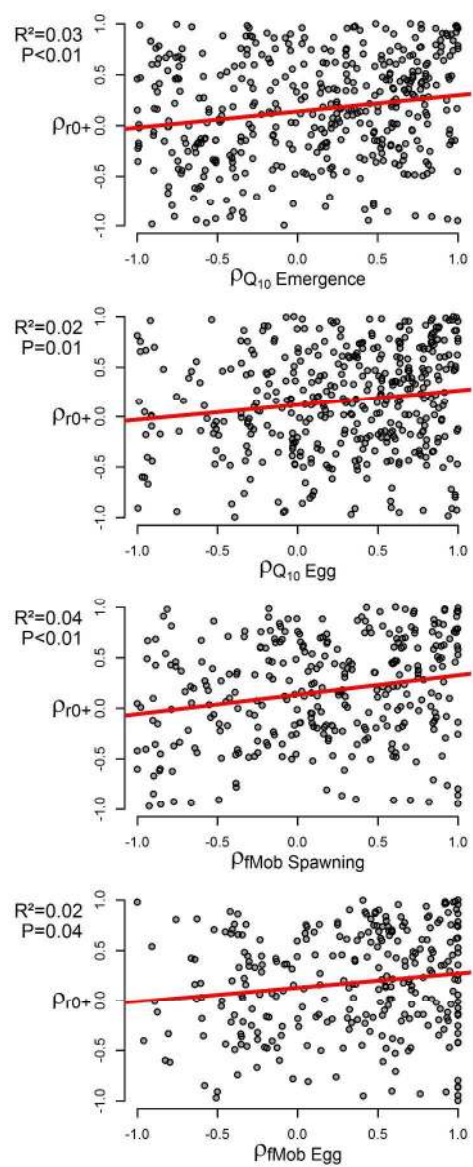79x79mm (300 x 300 DPI)

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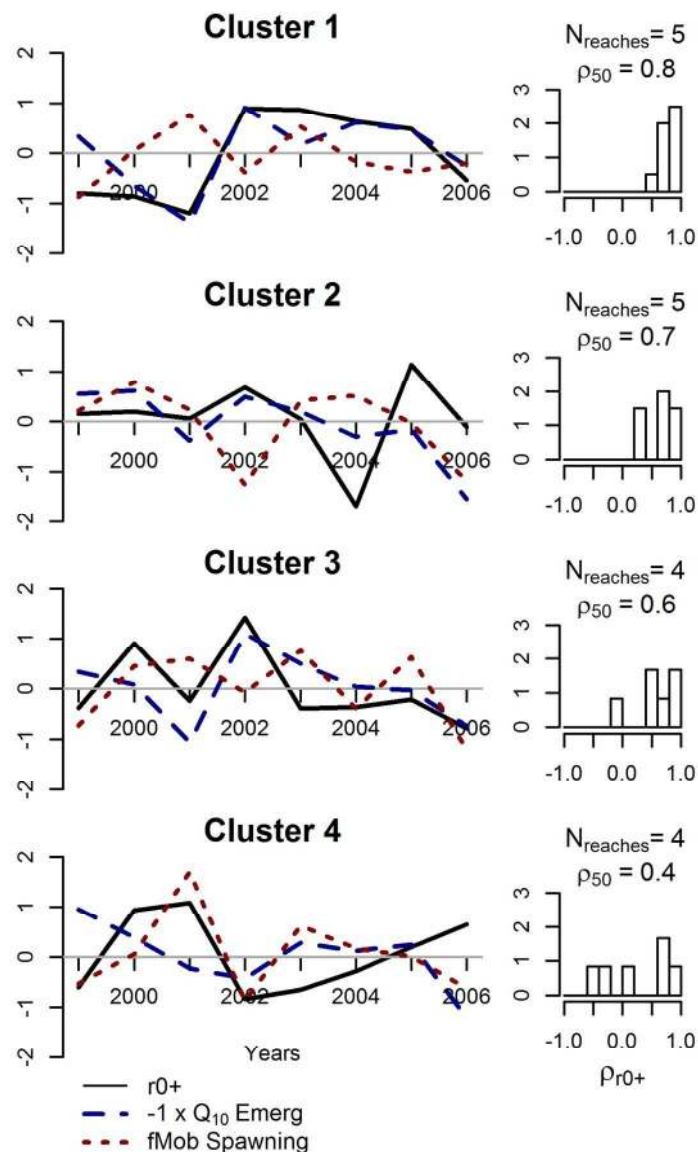199x500mm (300 x 300 DPI)

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 pr0+ 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 ($m^3.s^{-1}$) 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 ($m.s^{-1}$) were estimated as the ratio between daily discharge and

12   the corresponding cross-section area (average depth × 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   (A1) $T_{water,d} = \mu + \dfrac{(A\text{-}\mu)}{(1+\exp\left[\Gamma.\left(B\text{-}(0.5 \times T_{air,d}+0.3 \times T_{air,d\text{-}1}+0.2 \times T_{air,d\text{-}2})\right)\right])}$

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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