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## ► To cite this version:

Laurence Tissot, Véronique Gouraud, Nicolas Poulet, Hervé Capra, Franck Cattané, et al.. Multidecadal trends in brown trout populations in France reveal a decline in adult abundance concomitant with environmental changes. *Canadian Journal of Fisheries and Aquatic Sciences*, 2024, doi/10.1139/cjfas-2024-0209 . hal-04767911

**HAL Id: hal-04767911**

**<https://hal.science/hal-04767911v1>**

Submitted on 5 Nov 2024

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1 **Multidecadal trends in brown trout populations in France reveal a**  
2 **decline in adult abundance concomitant with environmental**  
3 **changes**

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## 26 Abstract

27 Most studies of brown trout (*Salmo trutta*) populations in headwater streams have focused on  
28 the year-to-year variability in recruitment and survival, but only few analyzed long-term trends  
29 in trout densities, under both control and regulated flow conditions. Here, we conducted trend  
30 analyses of brown trout age class densities on 36 stream reaches over the 1990-2020 period,  
31 including reaches located in a bypassed section. We also investigated long-term trends in a  
32 panel of key environmental variables (water temperature, stream flow, current velocity and  
33 habitat suitability). We found that annual water temperatures significantly increased by a  
34 median of +0.21 °C per decade. Analyses of stream flow revealed only a few significant trends,  
35 including a general increase in median values in spring and a general decrease in fall. A  
36 significant general decline in adult trout densities was observed, although disparities between  
37 geographic areas were highlighted. This decline is likely due to multifactorial effects, including  
38 possible interacting factors. Our results highlight the need to maintain and extend long-term  
39 monitoring of trout populations, which should be combined with extensive environmental  
40 monitoring.

41 Keywords: Meta-analysis, long-term surveys, global change, headwaters, *Salmo trutta*

## 42 Introduction

43 Freshwaters are among the most threatened ecosystems and their biodiversity is declining  
44 faster than that of terrestrial or marine environments (Dudgeon 2019, Reid *et al.* 2019). In the  
45 last few decades, 20% of the freshwater fish species described worldwide have been listed as  
46 threatened, endangered or extinct (Magurran 2009). On a European scale, 37% of freshwater  
47 fish species are threatened, and about 17% have declining populations (Freyhof and Brooks  
48 2011). Multiple causes contribute to this decline, including habitat degradation, biological  
49 invasion, water pollution or overfishing (Dudgeon 2019, Mueller *et al.* 2020), all interplaying  
50 with climate change (Moyle *et al.* 2011, Comte *et al.* 2021). Indeed, a high proportion of  
51 freshwater fish species will have their geographic range exposed to climatic extremes in the  
52 future (Barbarossa *et al.* 2021). The predictions indicate a decline in certain freshwater fish  
53 populations in the coming decades (Poulet *et al.* 2011, Wenger *et al.* 2011) and in functional  
54 diversity of stream fish assemblages (Buisson *et al.* 2013).

55 Due to the dendritic nature of hydrographic networks, most of the length of rivers and streams  
56 is located in the upstream part of catchments, which have been identified as ecosystems of  
57 special ecological interest (Meyer *et al.* 2007). In Europe, the brown trout (*Salmo trutta*) is  
58 native and generally the dominant species in headwater streams, and many studies have  
59 highlighted declines in their populations. From 1985 to 1999, the brown trout catches have  
60 decreased by 50% in many Swiss rivers (Burkhardt-Holm *et al.* 2002). The main cause of the  
61 decline appears to be the effect of increasing water temperature combined with the presence  
62 of the proliferative kidney disease (PKD) (Borsuk *et al.* 2006), whose clinical symptoms related  
63 to high mortality occur above 15-16°C (Hari *et al.* 2006, Burkhardt-Holm and Scheurer 2007).  
64 The composition of anadromous salmonids communities in Northern Europe was affected by  
65 gradual climate warming, with a decreasing proportion of Arctic charr and an increasing  
66 proportion of brown trout (Svenning *et al.* 2021). Brown trout populations in Sweden exhibited  
67 contrasting trends, with declines observed in the warmer southern part of the country and

68 increases in the cooler northern streams (Donadi *et al.* 2023). Climate change can also affect  
69 the recruitment of trout species differently depending on the regional context (Maitland and  
70 Latzka 2022). In France, brown trout densities and occurrences have decreased significantly  
71 over the period 1990-2009 (Poulet *et al.* 2011). This observation was recently confirmed by  
72 Santos *et al.* (2022) although disparities between catchments were found, with the main  
73 declines being observed in southwestern and central France. On a European scale, the  
74 causes of the decline of brown trout populations seem to be multiple and to differ between  
75 regions, though a recurrent reference to global warming is to be noted (Pilotto *et al.* 2020).  
76 However, most previous studies on trout population focused on the identification of trout  
77 population dynamics (Alonso *et al.* 2011, Bret *et al.* 2017, Alonso *et al.* 2024) and less on  
78 density trends. Studies on trout density trends have mainly focused on whole population trends  
79 (e.g. Poulet *et al.* 2011, Santos *et al.* 2022) or trends in a specific age class (e.g. young-of-  
80 the-year individuals in Donadi *et al.* 2023), without being able to explore age class-level trends  
81 and the associated drivers that are potentially age class-specific. In addition, the pressure  
82 induced by hydropower plants (Costea *et al.* 2021), mostly located in headwater streams, was  
83 rarely included in previous studies. Our study fills these gaps by combining: (i) a dataset with  
84 long-term monitoring of brown trout populations at age class level and key environmental  
85 drivers, on reaches with and without flow regulation and (ii) a meta-analysis framework to  
86 evaluate the shared trends, considering all reaches together.

87 The objective of this study was to quantify observed trends in the densities of brown trout  
88 populations and in key environmental drivers in four French geographic areas. In line with  
89 recent observations in different European countries, we hypothesized a decline in trout  
90 population densities, associated with concomitant trends in environmental conditions that  
91 could be responsible for this decline. Our dataset consists of 36 stream reaches where  
92 complete fish samplings (i.e. multi-pass electrofishing samplings with fish removal) have been  
93 conducted, of which about half are located in a bypassed section, with a part of the stream  
94 flow diverted by a dam. These sections are subject to a minimum instream flow, which

95 constitutes a pressure on these ecosystems. To our knowledge, trends in brown trout density  
96 have never been compared between bypassed and control sections, and such analysis would  
97 likely provide further insights into the pressure induced by flow reduction in bypassed sections.  
98 In addition, complete fish sampling makes it possible to determine the age class of individuals,  
99 which allows us to investigate trends in the density of each age class separately. To elucidate  
100 the possible environmental drivers of population trends, we investigated long-term seasonal  
101 and annual trends in a panel of environmental variables (water temperature, stream flow,  
102 current velocity and habitat suitability index abbreviated as HSI). In the context of climate  
103 change, for headwater streams, we hypothesized an increase in water temperature and a  
104 decrease in stream flow and current velocity over time. Such trends would lead to an  
105 improvement in HSI for juvenile trout (strong affinity with low current velocity and depth) and  
106 a decrease for adult trout (strong affinity with high current velocity and depth to feed) (Souchon  
107 *et al.* 1989, Ginot *et al.* 1998).

## 108 **Materials and methods**

### 109 ***Description of surveyed reaches***

110 In this study, 36 stream reaches where brown trout was the dominant fish species (i.e. more  
111 than 80% of total fish biomass) were monitored from about 1990 to 2020 (**Figure 1** and **Table**  
112 **S2**). They are located in four geographical areas (the Alps, the Pyrenees, the Massif-Central  
113 and the Brittany-Normandy), distributed across continental France. The surveyed reaches are  
114 headwater streams, typical of the trout zone (Huet 1954) (**Table 1**). They are located in  
115 different geographical contexts: most of them being in mountain ranges (Alps, Pyrenees and  
116 Massif-Central) while some are lowland headwater streams (Brittany-Normandy). Each reach  
117 included one or several sequences of pools, runs, and (or) riffles.

118 Nineteen of the surveyed reaches (53%) are located in a bypassed section (BPS), with part of  
119 the stream flow diverted by a dam, while the others experienced no hydrological modification  
120 (NHM). **Table 2** shows the distribution of the 36 surveyed reaches by type of reach (BPS or  
121 NHM) and by geographical area. In compliance with French regulation, the minimum instream  
122 flow was increased (mostly from about 1/40 to 1/10 of the mean interannual flow) in all  
123 bypassed sections during the study period.

#### 124 ***Fish data***

125 Fish data were acquired thanks to a long-term investment by three French organizations  
126 (Electricité de France, the Office Français de la Biodiversité and the Institut national de  
127 recherche pour l'agriculture, l'alimentation et l'environnement). Reaches were sampled by  
128 wading, using two-pass removal electrofishing sampling, according to the European  
129 Committee for Standardization guidelines (CEN 2003). Sampling was performed without  
130 upstream or downstream blocking nets, in summer or early fall (mostly in September). All  
131 stream-dwelling brown trout (*Salmo trutta*) sampled were measured (total length, to the  
132 nearest 1 mm), and length-frequency histograms allowed distinguishing three age classes  
133 (identifications were made by a few specialists to limit operator bias): young-of-the-year (fish  
134 less than 1 year old; hereinafter referred to as 'YoY'), juveniles (fish between 1 and 2 years  
135 old), and adults (fish older than 2 years old). Fieldwork was conducted with adequate  
136 administrative permits for electrofishing in accordance with French laws and ethical rules.

137 For each survey, brown trout abundance was estimated using the Carle and Strub (1978)  
138 method based on sampled abundances, separately for trout less than 10 cm and for larger  
139 ones in relation with electrofishing efficiency. These abundances were then converted to  
140 densities (i.e. the number of individuals per 100 m<sup>2</sup> sampled), using the total sampled area  
141 (between 477 and 2275 m<sup>2</sup>) calculated as the sampled length × reach width at the interannual  
142 median daily stream flow considered as the structuring flow. Depending on the reach, between  
143 13 and 27 fish surveys were conducted on the 36 stream reaches over the 1994-2020 period

144 (**Figures S1, S2 and S3**, covering an average period ( $\pm$  standard deviation) of  $24.8 \pm 2$  years  
145 (min = 20 years; max = 27 years). Fourteen additional reaches for which sampling began only  
146 in 2005 were also available (**Figure 1, Table S1, Table S2**) and were used for complementary  
147 analyses (**Figure S4**).

## 148 ***Environmental parameters***

### 149 *Water temperature*

150 Daily water temperature was measured in the field using thermographs placed in the sampling  
151 reach (recording every 20 minutes). Missing values were estimated from air temperature over  
152 the previous three days based on reach-specific air-water temperature relationships (see Bret  
153 *et al.* 2016 for a full description of the extrapolation procedure). Comparisons between  
154 extrapolated and observed water temperatures generally showed  $< 1^{\circ}\text{C}$  differences. Water  
155 temperature data were available for 19 of the reaches over the 1990-2015 period (**Figure 1,**  
156 **Table S2**).

### 157 *Stream flow*

158 Daily stream flow was derived from gauging stations (mainly from the French hydrological  
159 monitoring network; [www.hydro.eaufrance.fr](http://www.hydro.eaufrance.fr)). Extrapolations were made for the few periods  
160 affected by gauging station failure, following Bret *et al.* 2016. Stream flow data were available  
161 for 18 of the reaches over the 1990-2017 period. Though they are not located precisely on  
162 each fish surveyed reach (they are mostly less than 20 km of distance from fish surveyed  
163 reach; max distance is 50 km), they are representative of the main characteristics of their  
164 hydrology. For 11 of these reaches, stream flow measurements were available since 1970  
165 and were used for complementary analyses (**Figure S5**).

### 166 *Current velocity*

167 To capture the physical effect of stream flow, we also considered the current velocity. Reach  
168 daily current velocities ( $\text{m}\cdot\text{s}^{-1}$ ) were estimated as the ratio between daily discharge and the

169 corresponding cross-section area (mean depth  $\times$  mean width). Reach-specific depth-  
170 discharge and width-discharge relationships were estimated using hydraulic models (Ginot *et*  
171 *al.* 1998) or detailed hydraulic measurements conducted in the field at different stream flows  
172 (Sabaton and Miquel 1993). Current velocity data were available for 11 of the reaches over  
173 the 1990-2013 period thanks to previous works (Bret 2016, Bret *et al.* 2017).

#### 174 *Habitat Suitability Index*

175 To translate stream flow into habitat suitability for brown trout, we used the Habitat Suitability  
176 Index (HSI). HSI modelling considers physical habitat variables (water depth, current velocity,  
177 and sediment size) to assess the physical quality of a reach to support a target species or life-  
178 stage (Tharme 2003, Dunbar *et al.* 2012). HSI is based on the habitat preference curve of the  
179 target species or life-stage and is a function of the physical habitat variables (Bovee 1982).  
180 HSI varies between 0 (unsuitable) and 1 (most suitable) and provides an estimation of the  
181 suitability of a reach under given hydrological conditions for a target species or age class. In  
182 our case, HSI was calculated separately for juvenile and adult trout at a daily time step. HSI  
183 daily data were obtained using the PHABSIM protocol adapted to French streams (Sabaton  
184 and Miquel 1993, Ginot *et al.* 1998, Lamouroux and Capra 2002) and daily stream flow data.  
185 Similar to current velocity data, HSI data were available for 11 of the reaches over the 1990-  
186 2013 period thanks to previous works (Bret 2016, Bret *et al.* 2017).

187 The year was divided into four seasons of 3 months each, based on the life cycle of the brown  
188 trout:

- 189 - Spring (March-May) corresponds to the post-emergence season, characterized by a  
190 great sensitivity of YoY to high flows (Jensen and Johnsen 1999, Cattaneo *et al.* 2002).
- 191 - Summer (June-August) corresponds to the growing season, a critical period of the year  
192 for all age classes in relation to low flows and high temperatures (Elliott 1994).

- 193 - Fall (September-November) corresponds to the spawning season, during which  
194 stream flow and water temperature can positively (Poff *et al.* 1997, Unfer *et al.* 2011)  
195 or negatively (Montgomery 1996) affect the recruitment of the following year.
- 196 - Winter (December-February) is a season during which the eggs are buried in the gravel  
197 substrate and are relatively protected from environmental fluctuations (Bret *et al.*  
198 2017).

199 For each environmental parameter, annual and seasonal median, 10-percentile and 90-  
200 percentile values were calculated based on daily values. This represented a total of 15 metrics  
201 for each environmental parameter.

## 202 **Statistical analyses**

203 The general temporal trends in the time series of the 75 environmental metrics (i.e. 15 metrics  
204 × 5 environmental parameters - water temperature, stream flow, current velocity, HSI for  
205 juveniles and HSI for adults -) and three brown trout age class densities (i.e. YoY, juveniles  
206 and adults) were assessed using the recently developed meta-analysis framework described  
207 in Maire *et al.* (2019). This method consists in a weighted meta-analysis performed on each  
208 environmental and brown trout metric using Mann-Kendall trend statistics (*S*) computed on  
209 each time series as “effect sizes” (Gurevitch and Hedges 1993, Daufresne and Boët 2007).  
210 This non-parametric method is used to statistically assess if there is a general monotonic  
211 upward or downward trend in the studied variable over time, without this necessarily being  
212 linear. Variances of *S* were corrected for temporal autocorrelation prior to meta-analysis  
213 following Hamed and Rao (1998). To account for spatial autocorrelation, we used a random-  
214 effects model for the meta-analysis, where random effects are allowed to be spatially  
215 correlated according to a Gaussian correlation structure (Cressie 1993, Maire *et al.* 2019, Soto  
216 *et al.* 2023). This procedure produces a variance-covariance matrix based on the pairwise  
217 distances between reaches along the river network (if the reaches are located in different  
218 catchments, a sufficiently high value of 10000 river-km was used). This variance-covariance

219 matrix is finally used as an input variance-covariance matrix of the random effects in the meta-  
220 analyses (see Maire *et al.* (2019) for a comprehensive description of the method).

221 In addition to the general trends at the national scale, we tested whether temporal trends in  
222 brown trout age class densities differed depending on (i) geographic area (i.e. Alps, Brittany-  
223 Normandy, Massif-Central, Pyrenees) and (ii) type of reach (i.e. bypassed section, reach with  
224 no hydrological modification), alternatively adding these parameters as a factor in the meta-  
225 analyses. The difference in trend mean effect sizes between factor modalities was tested using  
226 an omnibus test based on a chi-square distribution (Viechtbauer 2010). These tests could not  
227 be computed on the environmental data due to the smaller number of surveyed reaches.  
228 Complementary analyses were also performed on the 1970-2020 period for stream flow and  
229 on the 2005-2020 period for brown trout age class densities. Analyses were performed using  
230 the R software (R Development Core Team 2022) *metafor* package version 3.0-2 (Viechtbauer  
231 2010) and the R script provided in Maire *et al.* (2019).

232 Although the number of surveyed reaches with all environmental parameters also monitored  
233 was too small to conduct complex and robust analyses to test for relationships between  
234 biological and environmental trends, we explored such relationships using a Principal  
235 Component Analysis (PCA) built on the trend values of all biological and environmental metrics  
236 for which significant trends were found. This multivariate analysis was performed (i) on all  
237 environmental metrics (N = 10 reaches) and (ii) on water temperature and stream flow metrics,  
238 for which a slightly higher number of reaches were available (N = 15 reaches).

## 239 Results

240 In this section, only the key significant and non-significant trends are presented (see **Tables**  
241 **S3**, **S4** and **S5** for a complete list of the statistical outcomes of the meta-analyses conducted).

242 *Trends in water temperature*

243 Trend mean effect size (TMES, unitless as derived from values of the Mann-Kendall trend  
244 statistic [S]) of annual median water temperature at 19 monitoring reaches highlighted  
245 significantly increasing values over the study period (TMES  $\pm$  Standard Error [SE] = 49.9  $\pm$   
246 8.3,  $p$ -value < 0.0001) (**Figure 2.A**). A significant upward trend in 90-percentile values (i.e.  
247 high values) was also found at the annual scale (TMES  $\pm$  SE = 35.5  $\pm$  8.1,  $p$  < 0.0001), while  
248 10-percentile values (i.e. low values) significantly decreased (TMES  $\pm$  SE = -38.6  $\pm$  8.0,  $p$  <  
249 0.0001). These trends reflect overall significant upward trends in spring, summer and fall water  
250 temperature (Median values: TMES  $\pm$  SE = 29.8  $\pm$  6.3,  $p$  < 0.0001) and downward trends in  
251 winter water temperature (median values: TMES  $\pm$  SE = -43.5  $\pm$  6.5,  $p$  < 0.0001). The greatest  
252 trends in water temperature were found in fall with increasing median (TMES  $\pm$  SE = 83.5  $\pm$   
253 8.6;  $p$  < 0.0001) and 90-percentile values (TMES  $\pm$  SE = 73.3  $\pm$  7.6,  $p$  < 0.0001). Median water  
254 temperatures in spring also significantly increased over the study period (TMES  $\pm$  SE = 31.9  
255  $\pm$  8.3,  $p$  = 0.0001).

256 Over the 1990-2015 period, the annual median water temperature increased by +0.21 °C per  
257 decade (median among the 19 surveyed reaches). While median water temperature in winter  
258 decreased by -0.21 °C per decade, it increased by +0.20, +0.16 and +0.51 °C per decade in  
259 spring, summer and fall, respectively.

#### 260 *Trends in stream flow and current velocity*

261 Only a few metrics of stream flow showed significant temporal trends at the scale of the 18  
262 monitoring reaches over the 1990-2017 period (**Figure 2.B**). Fall median stream flow  
263 significantly decreased (TMES  $\pm$  SE = -47.9  $\pm$  10.8,  $p$  < 0.0001), while spring median values  
264 (TMES  $\pm$  SE = 25.0  $\pm$  10.7,  $p$  = 0.019) and winter 10-percentile values (TMES  $\pm$  SE = 27.3  $\pm$   
265 11.1,  $p$  = 0.014) significantly increased.

266 Although current velocity is closely linked to stream flow, we found some differences in their  
267 temporal trends. The trends in current velocity assessed at the 11 monitoring reaches where  
268 these data were available showed significant decreasing median (TMES  $\pm$  SE = -26.4  $\pm$  11.7,

269  $p = 0.024$ ) and 90-percentile values (TMES  $\pm$  SE =  $-29.6 \pm 11.6$ ,  $p = 0.011$ ) at the annual scale  
270 (**Figure 2.C**). Summer median current velocity also significantly decreased over the study  
271 period (TMES  $\pm$  SE =  $-24.6 \pm 11.6$ ,  $p = 0.034$ ). Similar to the trends in stream flow, median  
272 current velocity significantly decreased in fall (TMES  $\pm$  SE =  $-55.6 \pm 11.6$ ,  $p < 0.0001$ ) and 10-  
273 percentile values significantly increased in winter (TMES  $\pm$  SE =  $25.4 \pm 11.7$ ,  $p = 0.030$ ) over  
274 the same period.

275 Similar analyses were conducted on stream flow recorded at 11 monitoring reaches over the  
276 1970-2017 period. In contrast to the 1990-2017 period, 13 of the 15 metrics tested showed  
277 significantly decreasing trends, with the largest reductions in stream flow occurring in summer  
278 and spring (**Figure S5; Table S4**).

#### 279 *Trends in Habitat Suitability Index*

280 Habitat suitability for juvenile brown trout assessed at 11 monitoring reaches showed  
281 significant improvement at the annual scale over the study period (median values: TMES  $\pm$   
282 SE =  $24.4 \pm 11.7$ ,  $p = 0.037$ ; 10-percentile values: TMES  $\pm$  SE =  $29.4 \pm 11.7$ ,  $p = 0.012$ )  
283 (**Figure 2.D**). Median habitat suitability for juvenile trout also significantly increased in summer  
284 (TMES  $\pm$  SE =  $25.4 \pm 11.6$ ,  $p = 0.012$ ) and fall (TMES  $\pm$  SE =  $48.1 \pm 11.6$ ,  $p < 0.0001$ ), while  
285 90-percentile values significantly decreased in winter (TMES  $\pm$  SE =  $-25.2 \pm 11.8$ ,  $p = 0.033$ ).

286 All metrics of habitat suitability for adult brown trout showed no significant trend over the study  
287 period ( $p$ -values  $> 0.05$ ), except for significantly increasing median (TMES  $\pm$  SE =  $35.1 \pm 12.6$ ,  
288  $p = 0.005$ ) and 10-percentile values (TMES  $\pm$  SE =  $36.3 \pm 12.6$ ,  $p = 0.004$ ) in winter (**Figure**  
289 **2.D**).

#### 290 *Trends in trout densities*

291 A total of 752 year-reach  $\times$  3 brown trout age classes (YOY, juvenile, adult) over the 1994-  
292 2020 period were considered in the analyses. We found no significant general trends in YoY  
293 (TMES  $\pm$  SE =  $-1.9 \pm 6.4$ ,  $p = 0.77$ ; **Figure 2.E; Table S4**) and juvenile trout densities (TMES  
294  $\pm$  SE =  $-6.8 \pm 9.3$ ,  $p = 0.47$ ; **Figure 2.F; Table S4**) at the national scale over the 1994-2020

295 period. In contrast, adult densities decreased significantly over the same period (TMES  $\pm$  SE  
296 =  $-32.2 \pm 11.2$ ,  $p = 0.004$ ; **Figure 2.G**; **Table S4**). Over the 36 surveyed reaches, the densities  
297 of adult trout have decreased by a median of  $-24.6\%$  between the first 5 and last 5 years of  
298 each survey (**Figure 3**). We found that trends in YoY densities did not differ significantly  
299 between geographic areas (Chi-square test,  $\chi^2 = 0.41$ ,  $p = 0.94$ ). In contrast, trends were  
300 significantly different between geographic areas for juvenile ( $\chi^2 = 9.22$ ,  $p = 0.027$ ) and adult  
301 densities ( $\chi^2 = 12.73$ ,  $p = 0.005$ ). For juvenile densities, the difference in trends between  
302 geographic areas is attributable to a marked decreasing trend in the Pyrenees, contrasting  
303 with the trends in the other areas. For adult densities, marked decreasing trends were found  
304 in the Pyrenees and in the Massif-Central, while trends in the Alps and in Brittany-Normandy  
305 were more contrasted between reaches. Finally, we found that trends were not significantly  
306 different between the reaches located in a bypassed section and those with no hydrological  
307 modification for YoY ( $\chi^2 = 0.07$ ,  $p = 0.79$ ), juvenile ( $\chi^2 = 2.67$ ,  $p = 0.10$ ) and adult densities ( $\chi^2$   
308 =  $1.63$ ,  $p = 0.21$ ).

309 The analyses conducted on brown trout age class densities surveyed at 50 reaches over the  
310 2005-2020 period (**Tables S1, S2, S5**) showed significantly decreasing general trends in  
311 juvenile (TMES  $\pm$  SE =  $-6.7 \pm 3.0$ ,  $p = 0.025$ ; **Figure S4.A**) and adult trout densities (TMES  $\pm$   
312 SE =  $-15.6 \pm 3.6$ ,  $p < 0.0001$ ; **Figure S4.B**) at the national scale, while the general trend was  
313 not significant for YoY densities (TMES  $\pm$  SE =  $-5.3 \pm 3.0$ ,  $p = 0.077$ ; **Figure S4.C**). Over the  
314 2005-2020 period, the only significant difference in trends between geographic areas or type  
315 of reach was found for YoY densities between geographic areas ( $\chi^2 = 7.99$ ,  $p = 0.046$ ), with a  
316 marked decreasing trend in the Massif-Central.

317 According to the PCA built on the trend values of the biological and environmental parameters  
318 for which significant trends were found, trends in adult trout densities appeared to be positively  
319 related to trends in stream flow and current velocity in winter (10-percentile values), in fall  
320 (median values) and annual metrics of current velocity (median and 90-percentile values) and  
321 negatively related to trends in median stream flow in spring (**Figure S6**). The relationships

322 between trends in adult trout densities and all other environmental metrics, especially water  
323 temperature, were found to be orthogonal.

## 324 Discussion

### 325 *Long-term environmental trends*

326 The meta-analysis carried out for each environmental metric showed significant trends for  
327 water temperature, stream flow, current velocity and habitat conditions, which depend on the  
328 period of the year considered. We found that annual median and the metric of high water  
329 temperatures (i.e. 90-percentile values) significantly increased while the metric of low water  
330 temperatures (i.e. 10-percentile values) significantly decreased. The meta-analyses  
331 highlighted the shared nature of this result across reaches and geographic areas, implying  
332 that global drivers are probably involved. Indeed, climate change is underway in European  
333 mountain areas, where substantial increases in air temperature are observed (Brunetti *et al.*  
334 2009, Maris *et al.* 2009). In the headwaters studied, annual water temperatures have  
335 increased by a median of +0.21 °C per decade. Spring, summer and fall water temperatures  
336 also showed general significant increases. The warming of the surveyed reaches was not as  
337 fast as that observed on larger mountain rivers in Austria (Niedrist 2023) or large French rivers  
338 (Maire *et al.* 2019), but was twice as fast as previous observations reported for headwater  
339 streams in the northwestern United States (Isaak *et al.* 2016). The slower warming of  
340 headwater streams compared to larger rivers could be linked to strong local temperature  
341 gradients (e.g., proximity to persistent snowfields, forest canopies, groundwater influxes)  
342 associated with topographic controls (Isaak *et al.* 2016) and a greater thermal influence of  
343 snow and glacier melt (Michel *et al.* 2020). We found significant decreasing trends in water  
344 temperatures in winter and, to our knowledge, no other study has reported seasonal declining  
345 trends in water temperature for any kind of stream or river. Some studies reported a

346 substantially slower warming in winter compared to other seasons (Kędra 2020,  
347 Seyedhashemi *et al.* 2022), but no decreasing trends. Such a decrease in winter stream  
348 temperatures seems counterintuitive in the context of global warming. Still, they could be  
349 explained by the fact that the months chosen to describe the winter season (December to  
350 February) were fixed for the entire study period, while earlier snow and glacier melt was  
351 observed over the same period (Han *et al.* 2024) . This may have led to a progressively earlier  
352 inflow of cold water into snow- and glacier-fed headwater streams, resulting in a decreasing  
353 trend in winter stream temperature in our analyses. This hypothesis is consistent with the  
354 increase of median water temperature in spring.

355 Analyses of stream flow revealed only a few significant trends over the 1990-2017 period,  
356 including a general increase in median values in spring and a general decrease in fall. In  
357 contrast, stronger and more significant decreasing trends in stream flow were found over the  
358 1970-2017 period for all seasons. This highlights the historical context of stream flow reduction  
359 in which the main study period 1990-2020 falls. Similar long-term decreases in mean annual  
360 flow have been reported for headwater streams (e.g. Lorenzo-Lacruz *et al.* 2012 for the 1945-  
361 2005 period, Buendia *et al.* 2016 for the 1965-2009 period), while, in line with our findings, no  
362 significant trends are generally found for more recent periods (Mostowik *et al.* 2019 for the  
363 1986-2015 period). A high variability of trends between periods of the year and between  
364 regions or basins is documented, in relation to differences in air temperature, precipitation and  
365 land cover (Buendia *et al.* 2016, Mostowik *et al.* 2019). A tipping point in the trend of annual  
366 stream flow in a Pyrenean river was identified in the 1980s by Buendia *et al.* (2016). Regarding  
367 low flows, Vlach *et al.* (2021) observed that the seasonality of drought events changed  
368 markedly after 1992 in the Ore Mountains (Central Europe), with the most severe droughts  
369 concentrated between August and October. These observations, combined with ours, support  
370 the spatial complexity of river flow trends observed on a global scale (Gudmundsson *et al.*  
371 2021), which is further accentuated when drilling down to seasonal patterns. Our results also

372 emphasize the influence of the depth of the study period on stream flow trends, which must  
373 be kept in mind in general when investigating long-term environmental trends.

374 Trends in current velocity were greater and more significant than those found for stream flow.  
375 Such a difference is due to the translation of stream flow into current velocity, which depends  
376 on reach morphology. This result emphasizes the value and greater sensitivity of direct  
377 environmental descriptors compared to proxies (Picard *et al.* 2022). The decreasing trend  
378 observed for current velocity led to an increase in HSI for juvenile trout because of their affinity  
379 with low current velocity (Bovee 1978, Heggenes *et al.* 1999).

### 380 *Long-term trends in brown trout age class densities*

381 The primary finding regarding trends in brown trout populations was a significant general  
382 decline in adult densities, although disparities between geographic areas were found. A clear  
383 decline in adult densities was observed in the Pyrenees, where the majority of the surveyed  
384 reaches are located, as well as in the Massif-Central. The trends were more contrasting  
385 between reaches in the Alps and in Brittany-Normandy. The decline in adult densities was  
386 also observed more markedly on the 2005-2020 period, without significant difference  
387 between geographic areas. This decline is consistent with previous studies of brown trout  
388 population trends in France (Poulet *et al.* 2011, Santos *et al.* 2022), which were conducted  
389 over a larger number of reaches but over a shorter period.

390 Our dataset is substantial in terms of temporal depth and spatial coverage on a national scale,  
391 with 36 reaches sampled over a 26-year period, spanning the main French mountain ranges  
392 and some coastal streams. However, it remains limited to allow the identification of robust  
393 regional trends due to relatively few replicates in each geographical area (**Table 2**). Therefore,  
394 results in Brittany-Normandy (3 reaches) and in the Alps (5 reaches) should be interpreted  
395 with caution. The two other geographical areas, which comprise most of the surveyed reaches,  
396 are those where our analyses showed declines in adult densities, thus supporting a plausible

397 nationwide decline in adult brown trout densities. In addition, it is also possible that the spatial  
398 differences found in adult trout density trends between geographical area are the result of  
399 differences in flow and water temperatures trends (Dayon *et al.* 2018) or of regional  
400 characteristics (e.g. lowland vs. mid- or high-altitude streams, forested vs. cultivated areas)  
401 (Pilotto *et al.* 2020).

402 No significant trends were observed for densities of younger age classes (YoY and juveniles)  
403 over the period 1994-2020. This result is in line with a previous study on a partially shared  
404 dataset that highlighted the great natural interannual variability of these age classes, which  
405 usually prevents the detection of any relationship between adult densities and the recruitment  
406 of the following year (Bret *et al.* 2017, Cauvy-Fraunié *et al.* 2020). This high variability on YoY  
407 densities makes it difficult to detect significant long-term trends. The reproductive success and  
408 level of recruitment (reflected here by YoY densities) are closely related to hydrology during  
409 spawning in fall and during the post-emergence period in spring (Jensen and Johnsen 1999,  
410 Cattaneo *et al.* 2002, Lobón-Cerviá 2004, Tissot *et al.* 2016), suggesting a greater influence  
411 of specific events (e.g. floods) compared to long-term drivers (e.g. climate). Yet, studies have  
412 identified significant trends in YoY brown trout densities on a large scale (e.g. Donadi *et al.*  
413 2023 in Sweden), which were moreover spatially contrasted between southern and northern  
414 areas. This suggests that the identification of trends in young age class densities is achievable,  
415 and that our finding of non-significant trends is potentially a valid indication of the absence of  
416 long-term trends in brown trout recruitment in the study reaches. In contrast, we found a  
417 declining trend in the densities of juvenile trout over a shorter period 2005-2020 for an  
418 extended dataset (50 surveyed reaches), mirroring that observed for adult trout over the longer  
419 term.

420 Although the decrease in juvenile and adult densities seems more pronounced in reaches  
421 located in bypassed sections (BPS) compared to reaches without hydrological modifications  
422 (NHM), these differences were not significant. First, even if the dataset is almost balanced  
423 between BPS and NHM, the BPS/NHM ratio is unbalanced by geographical area (15 among

424 the 19 BPS are in the Pyrenees, see **Table 2**). Second, all the BPS reaches surveyed in this  
425 study have experienced a regulatory increase of their minimum instream flow during the study  
426 period (in 1998 or 2014 for most BPS reaches) that could limit the differences between NHM  
427 and BPS reaches. Moreover, brown trout populations are structured by both biotic (density-  
428 dependent processes, prey availability) and abiotic factors, some of which are directly linked  
429 to stream flow (depth, current velocity) while others are not (shelter availability, water  
430 temperature, sediment size, water quality) (Milner *et al.* 2003, Bret *et al.* 2017, Alonso *et al.*  
431 2024). The effect of instream flow on brown trout populations remains sometimes difficult to  
432 determine, being a function of a complex set of factors, which can be very limiting for some  
433 BPS reaches, but not systematically (Baran *et al.* 1995, Bilotta *et al.* 2016).

#### 434 *Potential causes of the decline in adult brown trout densities*

435 The trend meta-analyses we conducted did not quantify the role of studied factors, nor the  
436 relative share of their effect on brown trout density trends. As a first and complementary  
437 approach, the multivariate analyses performed on the significant biological and environmental  
438 trends available concomitantly, for a limited number of surveyed reaches, showed that the  
439 reaches with the strongest downward trends in adult trout densities seem to have experienced  
440 the strongest trends in median stream flow in spring and the smallest trends in low winter  
441 values and median fall values of stream flow and current velocity. However, the small fraction  
442 of surveyed reaches for which all the environmental parameters were monitored over the study  
443 period makes these basic relationships hard to generalize and should be considered as a  
444 preliminary approach, the best we can achieve with this dataset. Nevertheless, the increase  
445 of median flow in spring could have contributed to increase trout mortality, particularly YoY,  
446 that would impact on the older age classes in subsequent years. Specific events may also  
447 have played a major role in these trends. In particular, a strong rainfall episode occurred in  
448 July 2013 in the Pyrenees and caused a 100-year flood that affected part of the surveyed  
449 reaches, with a high mortality rate observed on fish communities (Rocaspana *et al.* 2019).

450 YoY densities drastically decreased in 2013 (visible on **Figure S1** for the reaches in the  
451 Pyrenees) and the effect on older age classes is still discernible years later. This event could  
452 partly explain the strong decreasing trend in adult trout densities found in the Pyrenees.  
453 Furthermore, the historical significant decreasing trends in stream flow over the 1970-2017  
454 period may have contributed to brown trout population trends observed on a shorter, more  
455 recent time scale, for example by having led to altered demographic processes as early as  
456 the beginning of the study period. Of the other environmental parameters we were able to  
457 study, increasing water temperatures in spring, summer and fall, even if they remained in the  
458 thermal range of the species, may have led to greater competition between adult trout (results  
459 on a partially shared dataset, Bret *et al.* 2017). This is particularly the case during periods of  
460 limiting habitat availability, which occurs in fall with the decrease in stream flow that may have  
461 limited the access to deep habitats suitable for adult trout.

462 Biotic processes may also be involved in the decline of adult trout densities. Increased  
463 predation on trout is a plausible hypothesis as effect of predation on salmonids population  
464 were already observed (Falkegård *et al.* 2023). The American mink (*Neovison vison*) is  
465 present in the eastern and western parts of the Pyrenees and the geographic range of the  
466 Eurasian otter (*Lutra lutra*) is clearly expanding in France and particularly in the Pyrenees  
467 (Museum National d'Histoire Naturelle and Office Français de la Biodiversité 2022). These two  
468 mammals are known to feed on brown trout (Vehanen *et al.* 2022, Sortland *et al.* 2023),  
469 especially the otter (Melero *et al.* 2008, Harper *et al.* 2020). The expansion of the otter in  
470 southwestern France from the early 90s matches the beginning of our study period. Other  
471 potential predators of brown trout have also shown expanding trends and density increases  
472 (e.g. great cormorant, *Phalacrocorax carbo*) (Källo *et al.* 2019, Källo *et al.* 2023). It is therefore  
473 possible that the increase in predation pressure has contributed to the observed trends in  
474 brown trout densities, particularly in the Pyrenees. Such an effect suggests that the decline  
475 observed would be rather a transitory effect until densities reach a level consistent with the  
476 presence of otters than a “never ending” decline of trout populations. In addition, we cannot

477 exclude an effect of fish parasites or diseases on the decline in adult trout densities in relation  
478 to warming (Macnab and Barber 2012, Bailey *et al.* 2017), although no such events on adult  
479 trout has been reported on the study reaches. Finally, an effect of fish stocking on brown trout  
480 densities could not be excluded. Although no quantitative information is extensively available  
481 in France, trout stocking has decreased in recent years, as observed in other countries (Hunt  
482 and Jones 2018). It is therefore possible that there is a link between the observed decrease  
483 in brown trout densities and the reduction in fish stocking, even though most studies agree on  
484 the weak effect of stocking on salmonid densities (Baer and Brinker 2010, Young 2013,  
485 McMillan *et al.* 2023), in relation to the carrying capacity of the stream (Ayllón *et al.* 2012).

486 The decline in adult trout densities is thus likely due to multifactorial drivers, including water  
487 temperature and flow. Other factors seem to drive the decline, as predation or possible  
488 interacting factors especially with water temperature (Waldner *et al.* 2020, Casas-Mulet *et al.*  
489 2021). Our results highlight the need to extend long-term monitoring of trout populations, which  
490 should be combined with extensive environmental monitoring if we aim to identify the drivers  
491 of the observed biological trends (Magurran *et al.* 2010). Future analyses could focus on the  
492 characterization of the potential geographical differences. This would allow appropriate and  
493 efficient management measures to be taken to improve living conditions for brown trout  
494 populations (Willis and Birks 2006, Dieterman *et al.* 2020). Our study also highlights that  
495 analysis of seasonal environmental trends is relevant to identify their potential effects on brown  
496 trout density trends throughout the life cycle of the species.

## 497 **Acknowledgments**

498 We thank the numerous people (working at OFB, Electricité de France, INRAE, ECOGEA,  
499 angling associations, and other consulting firms) who contributed to electrofishing and habitat  
500 measurements. We also thank the organizations that provided environmental data (OFB,  
501 DREAL).

## 502 **Competing interests statement**

503 We declare no conflict of interests.

## 504 **Author contribution statement**

505 Conceptualisation: AM, LT, VG. Developing methods: AM, LT, VG. Data analysis: AM, LT.

506 Preparation of figures and tables: AM, LT. Conducting the research, data interpretation,

507 writing: AM, FC, HC, LT, NP, VG.

## 508 **Funding statement**

509 The authors declare no specific funding for this work.

## 510 **Data availability statement**

511 Data used to perform the trend analyses are available from Figshare:

512 <https://dx.doi.org/10.6084/m9.figshare.27186471>

## 513 **References**

514 Alonso, C., D. García de Jalón, J. Álvarez and J. Gortázar (2011). "A large-scale approach  
515 can help detect general processes driving the dynamics of brown trout populations in  
516 extensive areas." Ecology of Freshwater Fish **20**(3): 449-460.

517 Alonso, C., M. M. Jauregui, J. Ardaiz, A. Campos, J. Elso, J. Gortázar, P. M. Leunda, P.  
518 Matute, M. A. Moreno and D. G. de Jalón (2024). Components of Brown Trout Age-Class  
519 Density Dynamics. Advances in the Ecology of Stream-Dwelling Salmonids. J. Lobon-  
520 Cervia, P. Budy and R. Gresswell. Cham, Springer International Publishing: 415-440.

- 521 Ayllón, D., A. Almodóvar, G. G. Nicola, I. Parra and B. Elvira (2012). "Modelling carrying  
522 capacity dynamics for the conservation and management of territorial salmonids." Fisheries  
523 Research **134–136**(0): 95-103.
- 524 Baer, J. and A. Brinker (2010). "The response of a brown trout stocks and perception of  
525 anglers to cessation of brown trout stocking." Fisheries Management and Ecology **17**(2):  
526 157-164.
- 527 Bailey, C., H. Segner, A. Casanova-Nakayama and T. Wahli (2017). "Who needs the  
528 hotspot? The effect of temperature on the fish host immune response to *Tetracapsuloides*  
529 *bryosalmonae* the causative agent of proliferative kidney disease." Fish & Shellfish  
530 Immunology **63**: 424-437.
- 531 Baran, P., M. Delacoste, F. Dauba, J. M. Lascaux, A. Belaud and S. Lek (1995). "Effects of  
532 reduced flow on brown trout (*Salmo trutta* L.) populations downstream dams in French  
533 Pyrenées." Regulated rivers **10**(2-4): 347-361.
- 534 Barbarossa, V., J. Bosmans, N. Wanders, H. King, M. F. P. Bierkens, M. A. J. Huijbregts and  
535 A. M. Schipper (2021). "Threats of global warming to the world's freshwater fishes." Nature  
536 Communications **12**(1): 1701.
- 537 Bilotta, G. S., N. G. Burnside, J. C. Gray and H. G. Orr (2016). "The Effects of Run-of-River  
538 Hydroelectric Power Schemes on Fish Community Composition in Temperate Streams and  
539 Rivers." PLOS ONE **11**(5): e0154271.
- 540 Borsuk, M. E., P. Reichert, A. Peter, E. Schager and P. Burkhardt-Holm (2006). "Assessing  
541 the decline of brown trout (*Salmo trutta*) in Swiss rivers using a Bayesian probability  
542 network." Ecological Modelling **192**(1-2): 224-244.
- 543 Bovee, K. D. (1978). Probability of Use Criteria for The Family Salmonidae. Washington  
544 D.C., Fish and Wildlife Service: 53 p.
- 545 Bovee, K. D. (1982). A guide to stream habitat analysis using the Instream Flow Incremental  
546 Methodology. Instream Flow Information Paper n°12, FWS/OBS 82/86. U.S.D.S. Fort  
547 Collins, Colorado, Fish and Wildlife Service, Office of Biological Services: 248.
- 548 Bret, V. (2016). Dynamique spatio-temporelle des populations de truites en milieu naturel et  
549 au voisinage des ouvrages hydroélectriques, Thèse Université Claude Bernard Lyon 1.
- 550 Bret, V., H. Capra, V. Gouraud, N. Lamouroux, J. Piffady, L. Tissot and E. Rivot (2017).  
551 "Understanding inter-reach variation in brown trout (*Salmo trutta*) mortality rates using a  
552 hierarchical Bayesian state-space model." Canadian journal of fisheries and Aquatic  
553 Sciences **74**: 1612-1627.
- 554 Brunetti, M., G. Lentini, M. Maugeri, T. Nanni, I. Auer, R. Böhm and W. Schöner (2009).  
555 "Climate variability and change in the Greater Alpine Region over the last two centuries  
556 based on multi-variable analysis." International Journal of Climatology **29**(15): 2197-2225.

- 557 Buendia, C., R. J. Batalla, S. Sabater, A. Palau and R. Marcé (2016). "Runoff Trends Driven  
558 by Climate and Afforestation in a Pyrenean Basin." Land Degradation & Development **27**(3):  
559 823-838.
- 560 Buisson, L., G. Grenouillet, S. Villéger, J. Canal and P. Laffaille (2013). "Toward a loss of  
561 functional diversity in stream fish assemblages under climate change." Global Change  
562 Biology **19**(2): 387-400.
- 563 Burkhardt-Holm, P., A. Peter and H. Segner (2002). "Decline of fish catch in Switzerland."  
564 Aquatic Sciences **64**(1): 36-54.
- 565 Burkhardt-Holm, P. and K. Scheurer (2007). "Application of the weight-of-evidence approach  
566 to assess the decline of brown trout (*Salmo trutta*) in Swiss rivers." Aquatic Sciences **69** 51–  
567 70.
- 568 Carle, R. T. and M. R. Strub (1978). "A new method for estimating population size from  
569 removal data." Biometrics **34**(4): 621-630.
- 570 Casas-Mulet, R., E. Matthews, J. Geist, I. Durance and J. Cable (2021). "Negative effects of  
571 parasite exposure and variable thermal stress on brown trout (*Salmo trutta*) under future  
572 climatic and hydropower production scenarios." Climate Change Ecology **2**: 100039.
- 573 Cattaneo, F., N. Lamouroux, P. Breil and H. Capra (2002). "The influence of hydrological  
574 and biotic processes on brown trout (*Salmo trutta*) population dynamics." Canadian Journal  
575 of Fisheries and Aquatic Sciences **59**: 12-22.
- 576 Cauvy-Fraunié, S., V. M. Trenkel, M. Daufresne, A. Maire, H. Capra, J. M. Olivier, J. Lobry,  
577 B. Cazelles and N. Lamouroux (2020). "Interpretation of interannual variability in long-term  
578 aquatic ecological surveys." Canadian Journal of Fisheries and Aquatic Sciences **77**(5): 894-  
579 903.
- 580 CEN (2003). Water quality – sampling of fish with electricity. European Standard. EN 14011.
- 581 Comte, L., J. D. Olden, P. A. Tedesco, A. Ruhi and X. Giam (2021). "Climate and land-use  
582 changes interact to drive long-term reorganization of riverine fish communities globally."  
583 Proceedings of the National Academy of Sciences **118**(27): e2011639118.
- 584 Costea, G., M. T. Pusch, D. Bănăduc, D. Cosmoiu and A. Curtean-Bănăduc (2021). "A  
585 review of hydropower plants in Romania: Distribution, current knowledge, and their effects  
586 on fish in headwater streams." Renewable and Sustainable Energy Reviews **145**: 111003.
- 587 Cressie, N. (1993). Statistics for spatial data, John Wiley & Sons, New York, USA.
- 588 Daufresne, M. and P. Boët (2007). "Climate change impacts on structure and diversity of fish  
589 communities in rivers." Global Change Biology **13**(12): 2467-2478.
- 590 Dayon, G., J. Boé, É. Martin and J. Gailhard (2018). "Impacts of climate change on the  
591 hydrological cycle over France and associated uncertainties." Comptes Rendus Geoscience  
592 **350**(4): 141-153.

- 593 Dieterman, D. J., R. J. H. Hoxmeier, J. Roloff and D. F. Staples (2020). "Use of long-term  
594 (40+ year) trend data to evaluate management actions on brown trout, *Salmo trutta*,  
595 populations in groundwater-fed streams." Fisheries Management and Ecology **27**(6): 551-  
596 566.
- 597 Donadi, S., J. Näslund, L. Sandin, B. Sers, A. Vasemägi and E. Degerman (2023).  
598 "Contrasting long-term trends in juvenile abundance of a widespread cold-water salmonid  
599 along a latitudinal gradient: effects of climate, stream size and migration strategy."  
600 Ecography **2023**(5): e06522.
- 601 Dudgeon, D. (2019). "Multiple threats imperil freshwater biodiversity in the Anthropocene."  
602 Current Biology **29**(19): R960-R967.
- 603 Dunbar, M. J., K. Alfredsen and A. Harby (2012). "Hydraulic-habitat modelling for setting  
604 environmental river flow needs for salmonids." Fisheries Management and Ecology **19**(6):  
605 500-517.
- 606 Elliott, J. M. (1994). Quantitative ecology and the brown trout, Oxford University Press,  
607 Oxford, United-Kingdom.
- 608 Falkegård, M., R. J. Lennox, E. B. Thorstad, S. Einum, P. Fiske, Ø. A. Garmo, A. Garseth,  
609 H. Skoglund, M. F. Solberg, K. R. Utne, K. W. Vollset, L. A. Vøllestad, V. Wennevik and T.  
610 Forseth (2023). "Predation of Atlantic salmon across ontogenetic stages and impacts on  
611 populations." Canadian Journal of Fisheries and Aquatic Sciences **in press**.
- 612 Freyhof, J. and E. Brooks (2011). European Red List of Freshwater Fishes, Luxembourg:  
613 Publications Office of the European Union.
- 614 Ginot, V., Y. Souchon, H. Capra, P. Breil and S. Valentin (1998). Logiciel EVHA 2.0.  
615 Evaluation de l'habitat physique des poissons en rivière, Cemagref BEA/LHQ et Ministère de  
616 l'Aménagement du Territoire et de l'Environnement: 130.
- 617 Gudmundsson, L., J. Boulange, H. X. Do, S. N. Gosling, M. G. Grillakis, A. G. Koutroulis, M.  
618 Leonard, J. Liu, H. Müller Schmied, L. Papadimitriou, Y. Pokhrel, S. I. Seneviratne, Y. Satoh,  
619 W. Thiery, S. Westra, X. Zhang and F. Zhao (2021). "Globally observed trends in mean and  
620 extreme river flow attributed to climate change." Science **371**(6534): 1159-1162.
- 621 Gurevitch, J. and L. V. Hedges (1993). Meta-analysis: Combining the results of independent  
622 experiments. Design and Analysis of Ecological Experiments, G. J. e. Scheiner S. New  
623 York, USA: 378–398.
- 624 Hamed, K. H. and A. R. Rao (1998). "A modified Mann-Kendall trend test for autocorrelated  
625 data." Journal of Hydrology **204**(1-4): 182-196.
- 626 Han, J., Z. Liu, R. Woods, T. R. McVicar, D. Yang, T. Wang, Y. Hou, Y. Guo, C. Li and Y.  
627 Yang (2024). "Streamflow seasonality in a snow-dwindling world." Nature **629**(8014): 1075-  
628 1081.

- 629 Hari, R. E., D. M. Livingstone, R. Siber, P. Burkhardt-Holm and H. Guttinger (2006).  
630 "Consequences of climatic change for water temperature and brown trout populations in  
631 Alpine rivers and streams." Global Change Biology **12**(1): 10-26.
- 632 Harper, L. R., H. Watson, R. Donnelly, R. Hampshire, C. Sayer, T. Breithaupt and B.  
633 Hänfling (2020). "Using DNA metabarcoding to investigate diet and niche partitioning in the  
634 native European otter (*Lutra lutra*) and invasive American mink (*Neovison vison*)." Metabarcoding and Metagenomics **4**.
- 636 Heggenes, J., J. L. Baglinière and R. A. Cunjak (1999). "Spatial niche variability for young  
637 atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) in heterogeneous streams."  
638 Ecology of Freshwater Fish **8**: 1-21.
- 639 Huet, M. (1954). "Biologie, profils en long et en travers des eaux courantes." Bulletin français  
640 de pisciculture **175**: 41-53.
- 641 Hunt, T. L. and P. Jones (2018). "Informing the Great Fish Stocking Debate: An Australian  
642 Case Study." Reviews in Fisheries Science & Aquaculture **26**(3): 275-308.
- 643 Isaak, D. J., M. K. Young, C. H. Luce, S. W. Hostetler, S. J. Wenger, E. E. Peterson, J. M.  
644 Ver Hoef, M. C. Groce, D. L. Horan and D. E. Nagel (2016). "Slow climate velocities of  
645 mountain streams portend their role as refugia for cold-water biodiversity." Proceedings of  
646 the National Academy of Sciences **113**(16): 4374-4379.
- 647 Jensen, A. J. and B. O. Johnsen (1999). "The functional relationship between peak spring  
648 floods and survival and growth of juvenile Atlantic Salmon (*Salmo salar*) and Brown Trout  
649 (*Salmo trutta*)." Functional Ecology **13**(6): 778-785.
- 650 Källo, K., H. Baktoft, N. Jepsen and K. Aarestrup (2019). "Great cormorant (*Phalacrocorax*  
651 *carbo sinensis*) predation on juvenile down-migrating trout (*Salmo trutta*) in a lowland  
652 stream." ICES Journal of Marine Science **77**(2): 721-729.
- 653 Källo, K., K. Birnie-Gauvin, N. Jepsen and K. Aarestrup (2023). "Great cormorant  
654 (*Phalacrocorax carbo sinensis*) predation on adult anadromous brown trout (*Salmo trutta*)." Ecology of Freshwater Fish **32**(2): 488-495.
- 656 Kędra, M. (2020). "Regional Response to Global Warming: Water Temperature Trends in  
657 Semi-Natural Mountain River Systems." Water **12**(1): 283.
- 658 Lamouroux, N. and H. Capra (2002). "Simple predictions of instream habitat model outputs  
659 for target fish populations." Freshwater Biology **47**: 1543–1556.
- 660 Lobón-Cerviá, J. (2004). "Discharge-dependent covariation patterns in the population  
661 dynamics of brown trout (*Salmo trutta*) within a Cantabrian river drainage." Canadian Journal  
662 of Fisheries and Aquatic Sciences **61**(10): 1929-1939.
- 663 Lorenzo-Lacruz, J., S. M. Vicente-Serrano, J. I. López-Moreno, E. Morán-Tejeda and J.  
664 Zabalza (2012). "Recent trends in Iberian streamflows (1945–2005)." Journal of Hydrology  
665 **414-415**: 463-475.

- 666 Macnab, V. and I. Barber (2012). "Some (worms) like it hot: fish parasites grow faster in  
667 warmer water, and alter host thermal preferences." Global Change Biology **18**(5): 1540-  
668 1548.
- 669 Magurran, A. E. (2009). "Threats to Freshwater Fish." Science **325**: 1215-1216.
- 670 Magurran, A. E., S. R. Baillie, S. T. Buckland, J. M. Dick, D. A. Elston, E. M. Scott, R. I.  
671 Smith, P. J. Somerfield and A. D. Watt (2010). "Long-term datasets in biodiversity research  
672 and monitoring: assessing change in ecological communities through time." Trends in  
673 Ecology and Evolution **25**(10): 574-582.
- 674 Maire, A., E. Thierry, W. Viechtbauer and M. Daufresne (2019). "Poleward shift in large-river  
675 fish communities detected with a novel meta-analysis framework." Freshwater Biology **64**(6):  
676 1143-1156.
- 677 Maitland, B. M. and A. W. Latzka (2022). "Shifting climate conditions affect recruitment in  
678 Midwestern stream trout, but depend on seasonal and spatial context." Ecosphere **13**(12):  
679 e4308.
- 680 Maris, M., G. Giraud, Y. Durand, J.-P. Navarre and L. Mérindol (2009). Results of 50 years  
681 of climate reanalysis in the French Pyrenees (1958-2008) using the SAFRAN and CROCUS  
682 models. International Snow Science Workshop Davos
- 683 McMillan, J. R., B. Morrison, N. Chambers, G. Ruggerone, L. Bernatchez, J. Stanford and H.  
684 Neville (2023). "A global synthesis of peer-reviewed research on the effects of hatchery  
685 salmonids on wild salmonids." Fisheries Management and Ecology **30**(5): 446-463.
- 686 Melero, Y., S. Palazón, L. Bonesi and J. Gosálbez (2008). "Feeding habits of three  
687 sympatric mammals in NE Spain: the American mink, the spotted genet, and the Eurasian  
688 otter." Acta Theriologica **53**(3): 263-273.
- 689 Meyer, J. L., D. L. Strayer, J. B. Wallace, S. L. Eggert, G. S. Helfman and N. E. Leonard  
690 (2007). "The Contribution of Headwater Streams to Biodiversity in River Networks." JAWRA  
691 Journal of the American Water Resources Association **43**(1): 86-103.
- 692 Michel, A., T. Brauchli, M. Lehning, B. Schaeffli and H. Huwald (2020). "Stream temperature  
693 and discharge evolution in Switzerland over the last 50 years: annual and seasonal  
694 behaviour." Hydrology and Earth System Sciences **24**(1): 115-142.
- 695 Milner, N. J., J. M. Elliott, J. D. Armstrong, R. Gardiner, J. S. Welton and M. Ladle (2003).  
696 "The natural control of salmon and trout populations in streams." Fisheries Research **62**(2):  
697 111-125.
- 698 Montgomery, D. (1996). "Stream-bed scour, egg burial depths, and the influence of salmonid  
699 spawning on bed surface mobility and embryo survival." Canadian journal of fisheries and  
700 aquatic sciences **53**(5): 1061-1070.
- 701 Mostowik, K., J. Siwek, M. Kisiel, K. Kowalik, M. Krzysik, J. Plenzler and B. Rzonca (2019).  
702 "Runoff trends in a changing climate in the Eastern Carpathians (Bieszczady Mountains,  
703 Poland)." CATENA **182**: 104174.

- 704 Moyle, P. B., J. V. E. Katz and R. M. Quiñones (2011). "Rapid decline of California's native  
705 inland fishes: A status assessment." Biological Conservation **144**(10): 2414-2423.
- 706 Mueller, M., A. M. Bierschenk, B. M. Bierschenk, J. Pander and J. Geist (2020). "Effects of  
707 multiple stressors on the distribution of fish communities in 203 headwater streams of Rhine,  
708 Elbe and Danube." Science of The Total Environment **703**: 134523.
- 709 Museum National d'Histoire Naturelle and Office Français de la Biodiversité (2022). Fiche de  
710 *Lutra lutra* (Linnaeus, 1758). Inventaire national du patrimoine naturel (INPN).
- 711 Niedrist, G. H. (2023). "Substantial warming of Central European mountain rivers under  
712 climate change." Regional Environmental Change **23**(1): 43.
- 713 Picard, C., M. Flourey, H. Seyedhashemi, M. Morel, H. Pella, N. Lamouroux, L. Buisson, F.  
714 Moatar and A. Maire (2022). "Direct habitat descriptors improve the understanding of the  
715 organization of fish and macroinvertebrate communities across a large catchment." PLOS  
716 ONE **17**(9): e0274167.
- 717 Pilotto, F., I. Kühn, R. Adrian, R. Alber, A. Alignier, C. Andrews, J. Bäck, L. Barbaro, D.  
718 Beaumont, N. Beenaerts, S. Benham, D. S. Boukal, V. Bretagnolle, E. Camatti, R. Canullo,  
719 P. G. Cardoso, B. J. Ens, G. Everaert, V. Evtimova, H. Feuchtmayr, R. García-González, D.  
720 Gómez García, U. Grandin, J. M. Gutowski, L. Hadar, L. Halada, M. Halassy, H. Hummel,  
721 K.-L. Huttunen, B. Jaroszewicz, T. C. Jensen, H. Kalivoda, I. K. Schmidt, I. Kröncke, R.  
722 Leinonen, F. Martinho, H. Meesenburg, J. Meyer, S. Minerbi, D. Monteith, B. P. Nikolov, D.  
723 Oro, D. Ozoliņš, B. M. Padedda, D. Pallett, M. Pansera, M. Â. Pardal, B. Petriccione, T.  
724 Pipan, J. Pöyry, S. M. Schäfer, M. Schaub, S. C. Schneider, A. Skuja, K. Soetaert, G.  
725 Springé, R. Stanchev, J. A. Stockan, S. Stoll, L. Sundqvist, A. Thimonier, G. Van Hoey, G.  
726 Van Ryckegem, M. E. Visser, S. Vorhauser and P. Haase (2020). "Meta-analysis of  
727 multidecadal biodiversity trends in Europe." Nature Communications **11**(1): 3486.
- 728 Poff, N. L., J. D. Allan, M. B. Bain, J. R. Karr, K. L. Prestegard, B. D. Richter, R. E. Sparks  
729 and J. C. Stromberg (1997). "The natural flow regime - A paradigm for river conservation and  
730 restoration." Bioscience **47**(11): 769-784
- 731 Poulet, N., L. Beaulaton and S. Dembski (2011). "Time trends in fish populations in  
732 metropolitan France: insights from national monitoring data." Journal of fish biology **79**(6):  
733 1436-1452.
- 734 R Development Core Team (2022). R: A language and environment for statistical computing.  
735 Vienna, Austria.
- 736 Reid, A. J., A. K. Carlson, I. F. Creed, E. J. Eliason, P. A. Gell, P. T. J. Johnson, K. A. Kidd,  
737 T. J. MacCormack, J. D. Olden, S. J. Ormerod, J. P. Smol, W. W. Taylor, K. Tockner, J. C.  
738 Vermaire, D. Dudgeon and S. J. Cooke (2019). "Emerging threats and persistent  
739 conservation challenges for freshwater biodiversity." Biological Reviews **94**(3): 849-873.
- 740 Rocaspana, R., E. Aparicio, Q. Rovira, E. Cruset, J. Caner, F. Lucati, T. Buchaca, I. Afonso  
741 and M. Ventura (2019). Conservation status of the Pyrenean sculpin (*Cottus hispaniolensis*)  
742 in the Aran Valley. <http://hdl.handle.net/10261/226823>.

- 743 Sabaton, C. and J. Miquel (1993). "La méthode des micro-habitats : un outil d'aide au choix  
744 d'un débit réservé à l'aval des ouvrages hydroélectriques. Expérience d'Electricité de  
745 France." Hydroécologie appliquée **5**(1): 127-163
- 746 Santos, R., G. Astruc, N. Poulet and A. Besnard (2022). "Spatially structured freshwater fish  
747 population dynamics at the River Basin District scale: Implication for environmental  
748 management and fish conservation." Journal of Environmental Management **317**: 115180.
- 749 Seyedhashemi, H., J. P. Vidal, J. S. Diamond, D. Thiéry, C. Monteil, F. Hendrickx, A. Maire  
750 and F. Moatar (2022). "Regional, multi-decadal analysis on the Loire River basin reveals that  
751 stream temperature increases faster than air temperature." Hydrology and Earth System  
752 Sciences **26**(9): 2583-2603.
- 753 Sortland, L. K., R. J. Lennox, G. Velle, K. W. Vollset and M. Kambestad (2023). "Impacts of  
754 predation by Eurasian otters on Atlantic salmon in two Norwegian rivers." Freshwater  
755 Biology **68**(7): 1176-1193.
- 756 Soto, I., R. N. Cuthbert, D. A. Ahmed, A. Kouba, S. Domisch, J. R. G. Marquez, A. Beidas,  
757 G. Amatulli, J. Kiesel, L. Q. Shen, M. Florencio, H. Lima, E. Briski, F. Altermatt, G.  
758 Archambaud-Suard, P. Borza, Z. Csabai, T. Datry, M. Floury, M. Forcellini, J.-F. Fruget, P.  
759 Leitner, M.-H. Lizée, A. Maire, A. Ricciardi, R. B. Schäfer, R. Stubbington, G. H. Van der  
760 Lee, G. Várbió, R. C. M. Verdonschot, P. Haase and P. J. Haubrock (2023). "Tracking a  
761 killer shrimp: *Dikerogammarus villosus* invasion dynamics across Europe." Diversity and  
762 Distributions **29**(1): 157-172.
- 763 Souchon, Y., F. Trocherie, E. Fragnoud and C. Lacombe (1989). "Les modèles numériques  
764 des microhabitats des poissons : application et nouveaux développements." Revue des  
765 Sciences de l'Eau **2**(4): 807-830.
- 766 Svenning, M.-A., M. Falkegård, J. B. Dempson, M. Power, B.-J. Bårdsen, G. Guðbergsson  
767 and P. Fauchald (2021). "Temporal changes in the relative abundance of anadromous Arctic  
768 charr, brown trout, and Atlantic salmon in northern Europe: Do they reflect changing  
769 climates?" Freshwater Biology **67**(1): 64-77.
- 770 Tharme, R. E. (2003). "A global perspective on environmental flow assessment: emerging  
771 trends in the development and application of environmental flow methodologies for rivers."  
772 River Research and Applications **19**: 397-441.
- 773 Tissot, L., V. Bret, H. Capra, P. Baran and V. Gouraud (2016). "Main potential drivers of trout  
774 population dynamics in bypassed stream sections." Ecology of Freshwater Fish **26**(3): 336-  
775 346.
- 776 Unfer, G., C. Hauer and E. Lautsch (2011). "The influence of hydrology on the recruitment of  
777 brown trout in an Alpine river, the Ybbs River, Austria." Ecology of Freshwater Fish **20**(3):  
778 438-448.
- 779 Vehanen, T., A. Huusko, E. Bergman, Å. Enefalk, P. Louhi and T. Sutela (2022). "American  
780 mink (*Neovison vison*) preying on hatchery and wild brown trout (*Salmo trutta*) juveniles in  
781 semi-natural streams." Freshwater Biology **67**(3): 433-444.

- 782 Viechtbauer, W. (2010). Conducting Meta-Analyses in R with the metafor Package. **36**: 48.
- 783 Vlach, V., M. Matouskova and O. Ledvinka (2021). "Impacts of regional climate change on  
784 hydrological drought characteristics in headwaters of the Ore Mountains." River Research  
785 and Applications **37**(7): 919-930.
- 786 Waldner, K., T. Bechter, S. Auer, F. Borgwardt, M. El-Matbouli and G. Unfer (2020). "A  
787 brown trout (*Salmo trutta*) population faces devastating consequences due to proliferative  
788 kidney disease and temperature increase: A case study from Austria." Ecology of  
789 Freshwater Fish **29**(3): 465-476.
- 790 Wenger, S. J., D. J. Isaak, C. H. Luce, H. M. Neville, K. D. Fausch, J. B. Dunham, D. C.  
791 Dauwalter, M. K. Young, M. M. Elsner and B. E. Rieman (2011). "Flow regime, temperature,  
792 and biotic interactions drive differential declines of trout species under climate change."  
793 Proceedings of the National Academy of Sciences **108**(34): 14175-14180.
- 794 Willis, K. J. and H. J. B. Birks (2006). "What Is Natural? The Need for a Long-Term  
795 Perspective in Biodiversity Conservation." Science **314**(5803): 1261-1265.
- 796 Young, K. A. (2013). "The balancing act of captive breeding programmes: salmon stocking  
797 and angler catch statistics." Fisheries Management and Ecology **20**(5): 434-444.  
798
- 799

800 **Tables**801 **Table 1:** Description of the main physical characteristics of the 36 surveyed reaches.

<b>Physical characteristic</b>	<b>Min.</b>	<b>Mean</b>	<b>Max</b>
Width at median flow (m)	3	8	16
Reach slope (%)	0.3	3.1	13.2
Elevation (m)	15	772	1320
Distance from source (km)	3.0	18.4	49.0
Upstream drainage area (km <sup>2</sup> )	9	147	605
Annual mean flow (m <sup>3</sup> .s <sup>-1</sup> )	0.2	4.1	16.5
Median daily current velocity (m.s <sup>-1</sup> )	0.13	0.40	0.86
Median daily water temperature (°C)	6.7	8.9	11.2

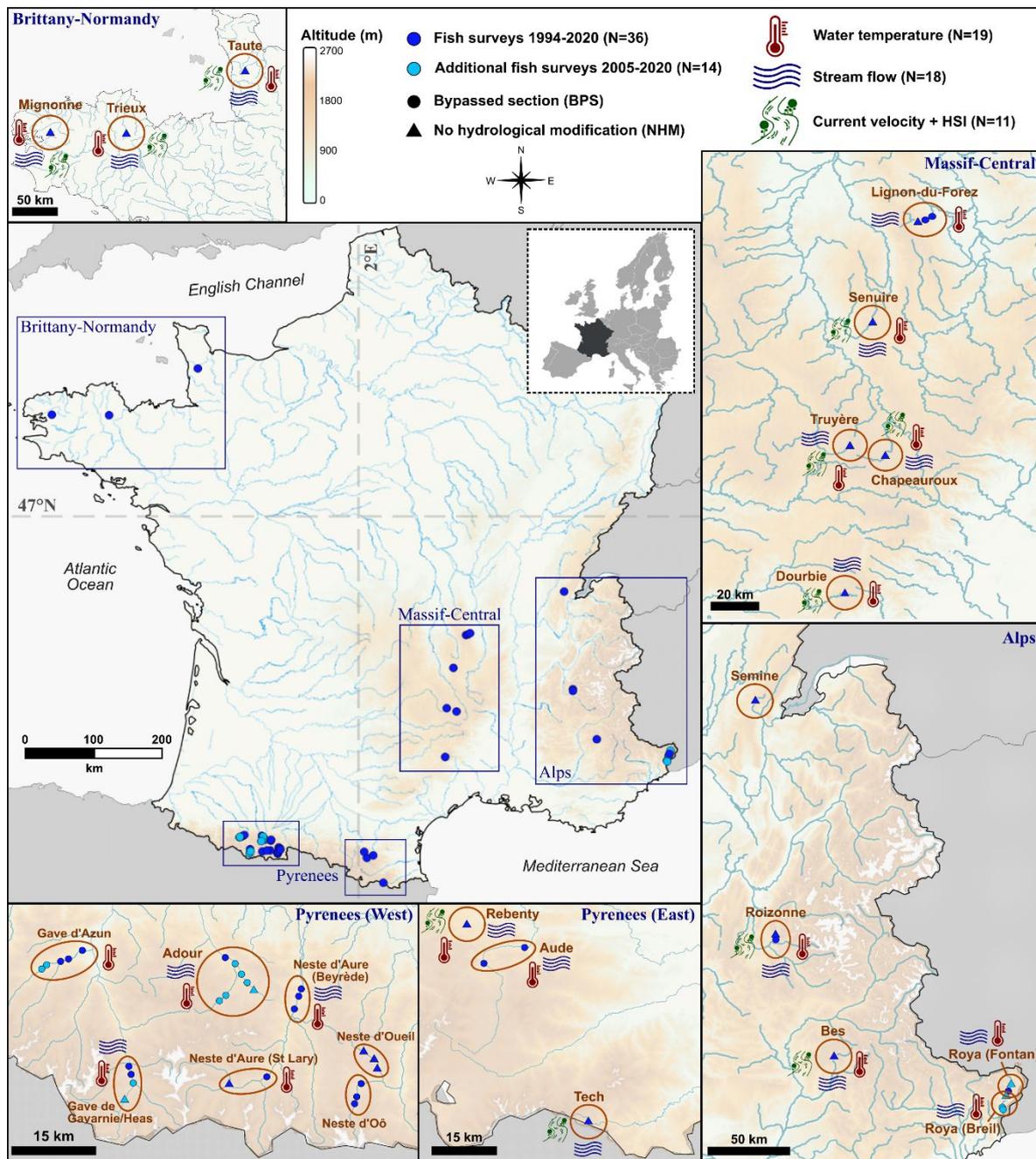
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803 **Table 2:** Distribution of the 36 surveyed reaches by type of reach (BPS or NHM) and by  
804 geographical area. BPS: bypassed section, NHM: no hydrological modification.

	<b>BPS</b>	<b>NHM</b>	<b>TOTAL</b>
<b>Alps</b>	2	3	<b>5</b>
<b>Pyrenees</b>	15	6	<b>21</b>
<b>Massif-Central</b>	2	5	<b>7</b>
<b>Brittany-Normandy</b>	0	3	<b>3</b>
<b>TOTAL</b>	<b>19</b>	<b>17</b>	<b>36</b>

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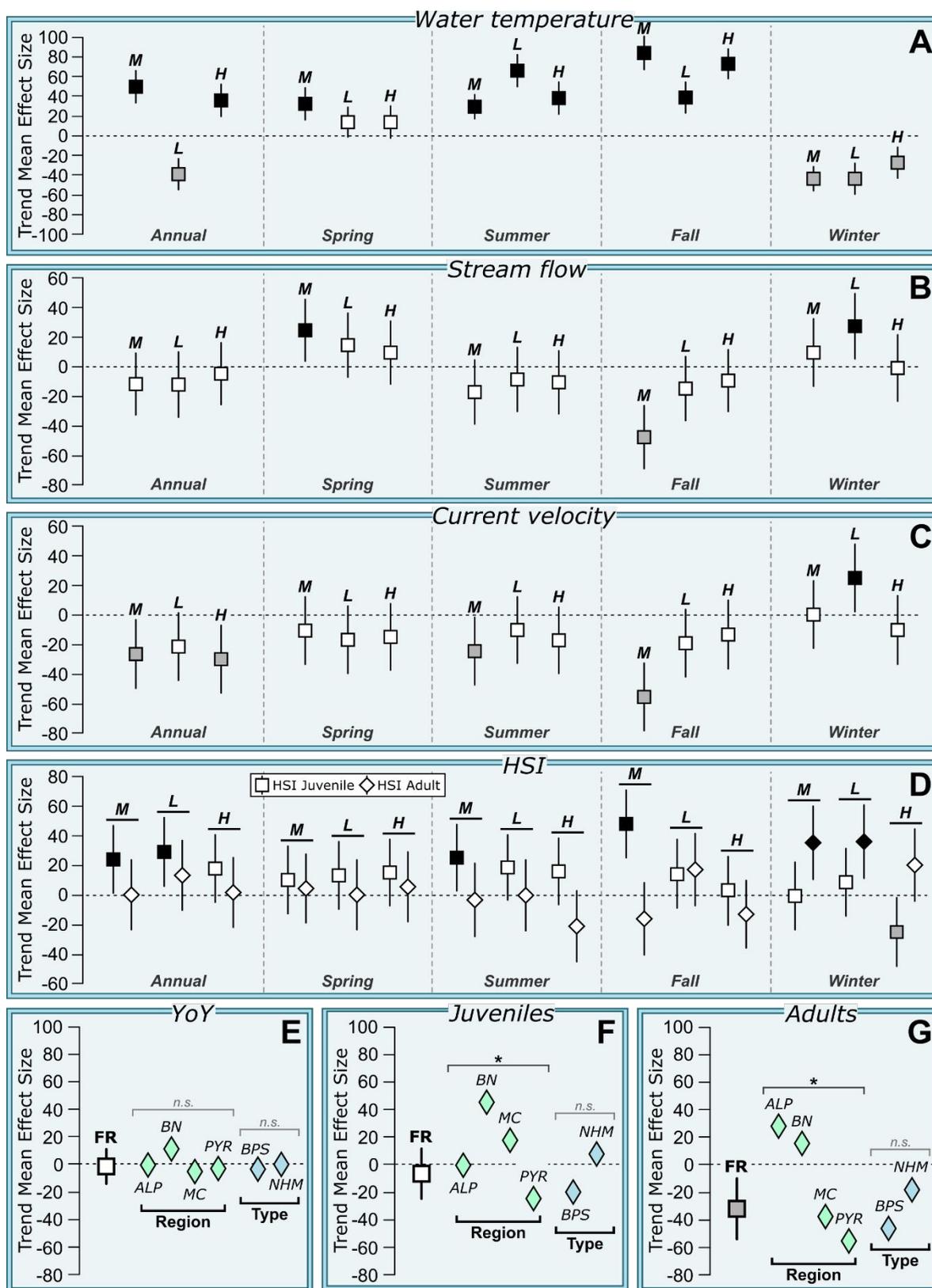
807 **Figures**

808

809 **Figure 1.** Location of surveyed reaches and associated available data. Background map -  
 810 sources: IGN BD ALTI®, IGN BD CARTHAGE®. Inserted map - source: Natural Earth.  
 811 Coordinate system: WGS84.

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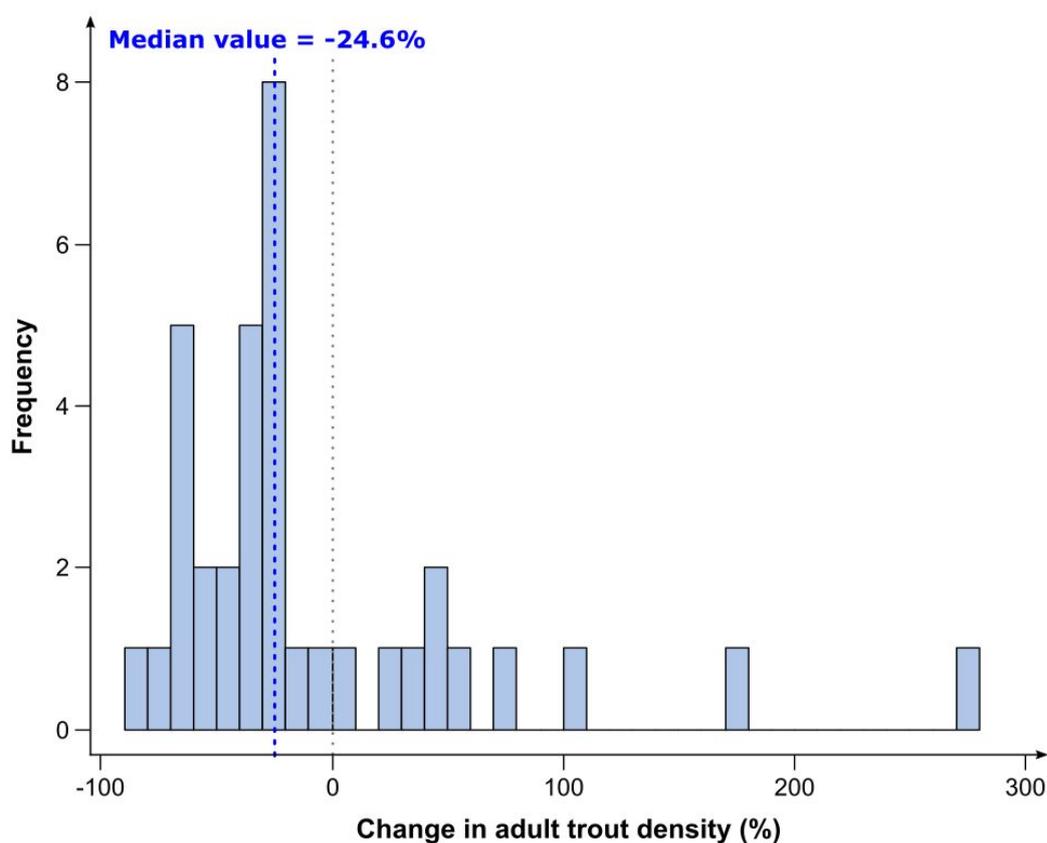
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815 **Figure 2.** Results of the meta-analyses conducted on the trends in metrics of (A) water  
 816 temperature, (B) stream flow, (C) current velocity, (D) HSI for juvenile (squares) and adult  
 817 (diamonds) trout, and (E) brown trout densities per age class over the 1990-2020 period. For  
 818 environmental parameters (panels A-D), the trends in the different metrics are shown (M:  
 819 median values, L: low-percentile 10 values, H: high-percentile 90 values) at the annual scale  
 820 and for each season (spring: March-May, summer: June-August, fall: September-November,  
 821 winter: December-February). For trends in trout densities per age class (panel E-G), the  
 822 general trends at the national scale are shown (FR), and their decomposition according to  
 823 each modality of the parameters tested is depicted with diamonds (geographical area in light  
 824 green and type of hydrological modification in light blue). ALP: Alps, BN: Brittany-Normandy,  
 825 MC: Massif-Central, PYR: Pyrenees, BPS: bypassed section, NHM: no hydrological  
 826 modification. For any general trend mean effect size, if the confidence interval does not  
 827 intersect the 0 value (horizontal dashed lines), the trend is significant (upward trend: black  
 828 symbols; downward trend: grey symbols) and otherwise non-significant (white symbols).



829

830 **Figure 3.** Histogram of changes in adult trout density between the first 5 and last 5 years of  
831 each survey. The median value calculated over the 36 surveyed reaches is represented by  
832 the blue vertical dotted line.

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