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Interpretation of interannual variability in long-term aquatic ecological surveys

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Abstract :

Long-term ecological surveys (LTES) often exhibit strong variability among sampling dates. The use and interpretation of such interannual variability is challenging due to the combination of multiple processes involved and sampling uncertainty. Here, we analysed the interannual variability in ~30 years of 150 species-density (fish and invertebrate) and environmental-observation time series in four aquatic-systems (stream, river, estuary, and marine continental shelf) with different sampling efforts to identify the information provided by this variability. We tested, using two empirical methods, whether we could observe simultaneous fluctuation between detrended time series corresponding to widely acknowledged assumptions about aquatic population dynamics: spatial effects, cohort effects, and environmental effects. We found a low number of significant results (36, 9, 0% for spatial, cohort, and environmental effects), suggesting that sampling uncertainty overrode the effects of biological processes. Our study does not question the relevance of LTES for detecting important trends, but clearly indicated that the statistical power to interpret interannual variations in aquatic-species densities is low, especially in large systems where the degree of sampling effort is always limited.

Keywords : long-term ecological surveys (LTES), aquatic species (stream -river-estuary- marine), interannual variability, symbolic analyses, sampling efficiency

36 **Introduction**

37 Long-term ecological surveys (LTES) are essential to examine the dynamics of ecosystems
38 and identify the processes involved (Hobbie et al. 2003; Magurran et al. 2010; Kuebbing et al.
39 2018). Indeed, LTES are key to assess ecological responses (gradual or abrupt) to slow
40 continuous environmental changes (e.g. climatic change; Sommer 2012) and sudden infrequent
41 disturbance events (e.g., hurricanes, fires; Scheffer et al. 2001). This is particularly relevant in
42 the Anthropocene, in which all ecosystems are threatened by a combination of multiple stressors
43 such as climatic shifts, over-exploitation of resources, pollution, habitat degradation, and
44 invasion by exotic species (Dudgeon et al. 2006; Halpern et al. 2008; Tilman et al. 2017;
45 Belliard et al. 2018). In this context, LTES are of particular interest for quantifying the
46 ecological impacts of current environmental changes and for reliably predicting future impacts
47 (Kuebbing et al. 2018). LTES are thus crucial to provide the knowledge necessary for
48 developing appropriate management tools to mitigate the impacts of anthropogenic pressures
49 on ecosystems (Geheber and Piller 2012; Robertson et al. 2012) and to evaluate the
50 effectiveness of restoration measures (Morandi et al. 2014). Nevertheless, their establishment
51 and maintenance remains highly challenging, partly due to their cost in a context of reduced
52 long-term funding (Lindenmayer 2017), but also due to a bias against the publication of long-
53 term research results in favour of short-term “newsy” articles (Kuebbing et al. 2018), and a
54 focus on funding equipment rather than funding long-term research contracts (Lindenmayer
55 2018).

56 Beyond revealing ecological trends or abrupt shifts and associated drivers, most long-term
57 ecological time-series exhibit strong variability among sampling dates (Knapp and Smith 2001;
58 Kratz et al. 2003). Understanding this variability is essential to identify the processes governing
59 population and community dynamics (Lepš et al. 2019). However, the use and interpretation of
60 such temporal (usually annual) variability is challenging due do the combination of multiple

61 processes involved and sampling uncertainty. This temporal variability might be related to
62 temporal variability in environmental conditions (e.g., interannual variations in phytoplankton
63 linked to nutrient concentration; Salmaso 2005; 2010), change in biomass of trophic-related
64 species (e.g., amphipod oscillation linked to diatom biovolume; Johnson and Wiederholm
65 1992). Variability could be also linked to variation in data collection (changes in sampling
66 techniques, samplers, sampling timing, sampling area; Trenkel et al. 2004), and sampling
67 inefficiency, i.e. when the study organisms being sampled do not reflect characteristics of the
68 whole population of interest (Peterson et al. 2004; Trenkel and Cotter 2009). Sampling
69 inefficiency depends on sampling techniques, design, and effort but also on the study
70 organisms' dispersal capacity and their distribution area compared to the finite study area
71 (Koenig et al. 1996). To analyse and interpret temporal variability in LTES, two approaches
72 could be considered: an empirical approach based only on observational data or a numerical
73 simulation including specific hypotheses concerning population dynamics. When the
74 underlying processes of population dynamics are well identified and sampling noise is reduced,
75 numerical simulation can allow testing alternative hypotheses about the ecological processes
76 driving temporal variability and the effects of sampling uncertainty (Bret et al. 2017; Rivot et
77 al. 2004). However, in the case of LTES influenced by multiple processes and with unknown
78 sampling noise, such as LTES in large aquatic systems (e.g., river, estuary or marine continental
79 shelf), an empirical approach is more suitable and may help identify the most relevant
80 ecological processes involved.

81 In this study, we used an empirical approach to identify and interpret the information
82 provided by the interannual variability in a unique data set grouping four independent LTES of
83 aquatic species in France: 1) trout populations in small streams, 2) fish populations in a large
84 river, 3) fish and invertebrate populations in an estuary, and 4) fish and invertebrate marine
85 populations on the continental shelf (Fig. 1). These four LTES include relatively long-term (~

86 30 years) annual observations of both multiannual aquatic species density with annual
87 reproduction cycles (with an identification of age classes) and environmental measurements at
88 various reaches Moreover, the datasets were characterized by various degrees of sampling
89 effort, defined here as the percentage of the study area sampled (sampled area divided by the
90 total study area): low for the three large aquatic systems (river, estuary and marine continental
91 shelf) and high for streams. Previous analyses of these LTES revealed trends and abrupt shifts
92 in community composition and certain aquatic species related to environmental changes. For
93 example, Daufresne et al. 2015 showed a positive effect of restored flows on the proportion of
94 midstream fish in the large river; Chaalali et al. (2013) showed negative effect of water
95 warming on shrimp reproduction in the estuary; and Poulard and Blanchard 2005 reported a
96 positive effect of sea temperature increase on subtropical species (Table 1). Here, we did not
97 examine trends but rather focused on understanding interannual variability and potential
98 drivers.

99 We thus examined the shape of the time series after removing the long-term trend (Lepš et al.
100 2019) and compared the shapes among time series to identify whether we could detect similarity
101 in shape among time series; i.e. simultaneous year-to-year fluctuations. For the four LTES,
102 characterized by a range of sampling efforts, we tested whether we could observe simultaneous
103 fluctuations between time series corresponding to widely acknowledged assumptions about
104 aquatic population dynamics: 1) *spatial effects*, spatial correlation between densities of
105 individuals (especially for fish juveniles) between pairs of neighbouring reaches, i.e. reaches
106 with similar environmental conditions and close enough to allow dispersal between them 2)
107 *cohort effects*, temporal correlation between the densities of juveniles and the densities of older
108 individuals with a one-year time lag (only for fish) and 3) *environmental effects*, correlation
109 between aquatic species (or guild) densities and the main environmental drivers (identified in
110 previous studies). For *spatial effect*, we expected a positive association between the interannual

111 variability of aquatic-species densities from neighbouring reaches; time series should fluctuate
112 simultaneously, rising and falling together. For *cohort effects*, we expected a positive
113 association between the interannual variability of fish density of juveniles at year t and older
114 individuals at year $t+1$; time series of fish densities of juveniles and older individuals should
115 fluctuate together in the same direction with a one-year time lag. For *environmental effects*, we
116 expected a positive association between the interannual variability of environmental and
117 ecological time series when the sign of the relationship between species (or guild) densities and
118 environmental parameters was positive, and negative otherwise; time series should fluctuate
119 together in the same direction when the sign of the relationship was positive, and
120 antagonistically (one rising and the other falling at the same time) otherwise. For this, we
121 applied two empirical methods: a residual Pearson correlation analysis and a symbolic analysis
122 based on Information Theory.

123 **Methods**

124 *Data description*

125 *Trout populations in small streams*

126 This dataset included 5-18 years of brown trout (*Salmo trutta*) time series sampled between
127 1990 and 2014 in 42 stream reaches distributed across 23 streams in France (Fig. 1). At each
128 stream reach (~ 100 m²), trout density (number of individuals per m²) was estimated by counting
129 all individuals sampled using a two-pass removal electrofishing technique, without block nets
130 (Fig. 1). Each year, the whole reach ($\sim 100\%$ of the study reach) was electrofished in September
131 by various operators following the European Committee for Standardization guidelines (CEN
132 2003; Bret et al. 2015). Based on their size, trout individuals were separated in the field into
133 three age classes: young-of-the-year (age-0), one-year-old fish (age-1), and 2 years and older
134 (age-2⁺). This dataset also included daily water temperature and flow velocity time series for
135 each stream reach (see Bret et al. 2015 for more details on the environmental data). *Spatial*

136 *effect* was examined between the closest stream reaches (< 5 km apart) not disconnected by
137 dams.

138

139 *Fish populations in a large river*

140 This dataset included 18-34 years of freshwater fish time series sampled between 1979 and
141 2015 in six river reaches situated along the Rhône River (Fig. 1). At each river reach (~1 km²),
142 fish density (number of individuals per m²) was estimated based on electrofishing using either
143 point abundance sampling (between 20 and 200 sampling points with an average area of 7m²
144 or 32m² depending on the study reach) or continuous sampling along the banks during 30 min
145 (Fig. 1). Each year, around 0.1% of the study reach was sampled in fall by various academic
146 teams (see Daufresne et al. 2015; Lamouroux et al. 2015 for more details on the dataset). Based
147 on their size, fish individuals (for each species) were separated in the field into two age classes:
148 young-of-the-year (age-0), and one year and older (age-1⁺). Among the 41 species sampled
149 within the six river reaches, we removed species that occurred in less than 30% of all samples
150 (reaches and years combined), thereby preserving 16 species. For the analysis of both *spatial*
151 *effect* and *cohort effect*, we only considered, for each river reach, species occurring in more than
152 30% of all sampling dates (see Table S1 for the resulting number of studied species per
153 analysis). *Spatial effect was analysed for the closest* river reaches (< 35 km apart) with similar
154 environment and not disconnected by dams. For the analysis of *environmental effects*, the 16
155 selected species were grouped into three guilds, according to their habitat preferences following
156 Daufresne et al. (2015), among which we examined lithophilic, midstream (species preferring
157 deep and fast water), and southern guilds. This dataset also included daily water temperature
158 and discharge time series for each river reach (see Daufresne et al. 2015; Maire et al. 21019 for
159 more details on the environmental data).

160

161 *Fish and invertebrate populations in an estuary*

162 This dataset included 24-30 years of estuarine-species time series sampled between 1979
163 and 2014 in four estuary reaches situated along the Gironde estuary (Fig. 1). At each estuary
164 reach (~5 km²), estuarine fish and invertebrate density (number of individuals per m³) were
165 estimated based on point abundance sampling (three sampling points along one transect;
166 Pasquaud et al. 2012). At the three sampling points (one close to each bank and one on the
167 middle axis of the estuary), surface and bottom samples were taken simultaneously using,
168 respectively, two 4.0 x 1.0 m rectangular frame nets, fitted at either side of the boat, and a 2.0
169 x 1.2 m frame trawl, kept at 0.2 m above the bottom by skates. Sampling lasted around 7 min
170 and was performed during daytime, between the mid-discharge and the slack period of high
171 tide, with the gear being towed against the current (Fig. 1). Each year, around 0.01% of the
172 study reach was sampled every month by academic teams (see Lobry et al. 2006 for more details
173 on the dataset). For each species, we calculated a mean autumn density by averaging the
174 densities of the September, October, and November samples. Based on their size, fish
175 individuals (for each species) were separated in the field into two age classes: young-of-the-
176 year (age-0), and one year and older (age-1⁺). Among the 59 species sampled within the four
177 estuary reaches, we removed species that occurred in less than 30% of all samples (reaches and
178 years combined), thereby preserving 16 species. For the analysis of both *spatial* and *cohort*
179 *effects*, we only considered, for each estuary reach, species occurring in more than 30% of all
180 sampling dates (see Table S1 for the resulting number of studied estuarine species per analyses).
181 *Spatial effect* was examined between each pair of the four estuary reaches (< 20km apart). For
182 the analysis of *environmental effects*, the 16 selected species were grouped into four guilds,
183 according to their habitat preference following Lobry et al. (2006), among which we examined
184 freshwater and marine guilds. This dataset also included daily water temperature, salinity, and

185 discharge time series for each estuary reach (see Béguer et al. 2012 for more details on the
186 environmental data).

187

188 *Marine fish and invertebrate populations on continental shelf*

189 This dataset included 26 years of marine-species time series sampled between 1987 and
190 2014 on the eastern continental shelf of the Bay of Biscay (Fig. 1). The study area extended
191 from 47°53'12.01"N - 5°38'35.99"O to 43°41'15.00"N - 1°13'14.99"O, covering around 75, 574
192 km² between 15 and 600m depth. Fish and invertebrate density (number of individuals per km²)
193 and biomass (kg per km²) were estimated based on a stratified groundfish survey, using a 36/47
194 GOV trawl with a 20 mm mesh codend liner. Each year, between 56 and 154 hauls spread over
195 the study area (30 min samples at a towing speed of 4 knots), i.e. around 0.007% of the study
196 area, were collected in November by Ifremer (see Poulard and Trenkel 2007 for more details
197 on the dataset; EVHOE survey, Fig. 1). We computed density and biomass time series of the
198 entire Bay of Biscay by averaging across all hauls. Among the 296 marine species sampled
199 including both fish and invertebrates, we conserved only 32 species, i.e. the species occurring
200 at more than 30% of all sampling dates. For the analysis of *environmental effects*, the marine
201 selected species were separated into three functional groups according to their biogeographical
202 affinity (temperature preference) following Quéro (1984), among which we examined boreal
203 and subtropical groups. This dataset also included daily sea surface temperature and annual
204 fishing pressure time series, estimated using commercial catch data obtained from the data base
205 held by the International Council for the Exploration of the Sea ([http://www.ices.dk/marine-](http://www.ices.dk/marine-data/dataset-collections/Pages/Fish-catch-and-stock-assessment.aspx)
206 [data/dataset-collections/Pages/Fish-catch-and-stock-assessment.aspx](http://www.ices.dk/marine-data/dataset-collections/Pages/Fish-catch-and-stock-assessment.aspx)). For the analysis of
207 *spatial effect*, as the environmental fluctuations were relatively homogeneous within the Bay
208 of Biscay and most studied marine species exhibit large scale dispersal, we split the Bay of
209 Biscay into two zones (northern and southern) separated perpendicularly to the coast to display

210 similar bathymetric features (Poulard and Blanchard 2015). For both zones, we computed
211 marine species density time series by averaging the densities recorded in all hauls from each
212 zone (equivalent to reach in the three other LTES). Note that zone limits varied among species
213 according to their spatial distribution to maintain a similar number of occurrences in each zone
214 (see Fig. S1 for the zone delimitation by species).

215

216 ***Data analyses***

217 We used two different methods to examine the existence of *environmental effects*, *cohort*
218 *effects*, and *spatial effects* in the detrended time series. The first method (described below)
219 consisted in describing the rhythm of each time series using symbolic transformation (Fig. 2 a)
220 and techniques from *Information Theory*, and quantifying the association between the rhythms
221 of the different time series, i.e. the degree to which time series tended to oscillate together,
222 rising and falling with the same frequency (Cazelles 2004; Descamps et al. 2010). Previous
223 studies already tested the application of this method on ecological data, compared their results
224 with cross-correlation techniques, and concluded this method improved the detection of weak
225 relationships between time series, even short ones and in the presence of noise (Cazelles 2003;
226 2004). We compared the results of this method with a second more conventional approach,
227 which consisted in fitting a *LOESS* model to each time series and then calculating the Pearson
228 correlation among detrended *LOESS* residuals (linear model, Fig. 2 b).

229

230 *Symbolic transformation*

231 To describe the rhythm of continuous time series, we discretized them into a sequence of a
232 finite number of symbols (Cazelles 2004). As our objective was to identify the main drivers of
233 interannual variability in ecological time series, we used a simple discretization based on three
234 symbols (“Flat”, “Increase”, and “Decrease”) reflecting changes between consecutive values

(Fig. 2 a). Therefore, continuous time series X of length n were transformed into discrete sequences S of length $n-1$. First, for each species, guild or environmental parameter, we computed the series Δ of length $n-1$ defined as $\Delta_t = X_t - X_{t-1}$, and computed two thresholds I (for increase) and D (for decrease) calculated as the standard deviation of positive values of Δ , and the standard deviation of negative values of Δ , respectively.

Then, given a time series X , and the corresponding thresholds I and D :

if $X_{t-1} < X_t$ and $X_t - X_{t-1} > I$, S_t was coded ‘Increase’

if $X_{t-1} > X_t$ and $|X_t - X_{t-1}| > D$, S_t was coded ‘Decrease’

if $|X_t - X_{t-1}| < D$ or $|X_t - X_{t-1}| < I$, S_t was coded ‘Flat’.

244

245 *Mutual information*

246 To quantify the degree of association between two time series, we calculated the mutual information between the corresponding symbolic sequences (Pompe 1993; Prichard and Theiler 247 1995). The mutual information I_{S1S2} between the symbolic sequences $S1$ and $S2$ is defined as:

$$249 \quad I_{S1S2} = H_{S1} + H_{S2} - H_{S1S2}$$

250 where H_{S1} and H_{S2} are the entropy of the symbolic sequences $S1$ and $S2$, and H_{S1S2} is their joint entropy. The entropy of a symbolic sequence S is defined as:

$$252 \quad H_S = - \sum_{i=1}^k P(S_i) \log (P(S_i))$$

253 where $P(S_i)$ is the probability of observing the symbol $S_i \in$ (“Increase”, “Decrease”, “Flat”),
254 estimated as the proportion of the symbol in the sequence, and k is the number of different
255 symbols in the sequence ($k = 3$ in our case). The joint entropy H_{S1S2} between two symbolic
256 sequences $S1$ and $S2$ is defined as:

$$257 \quad H_{S1S2} = - \sum_{i=1}^k \sum_{j=1}^k P(S1_i, S2_j) \log (P(S1_i, S2_j))$$

258 where $P(S1_i, S2_j)$ is the probability of observing simultaneously the symbols $S1_i$ and $S2_j$,
 259 estimated as the proportion of pairs $(S1_i, S2_j)$ observed in the sequence.

260

261 *Statistical significance level*

262 To quantify the statistical significance of this measure of common information between
 263 two time series, we compared the observed mutual information with those obtained with $n =$
 264 1000 couples of randomly-generated time series (Cazelles 2004). These randomly-generated
 265 time series were built under the null hypothesis of no association between two observed time
 266 series. The randomly-generated time series Z were obtained by resampling the observed time
 267 series based on a Markov process scheme that preserved the short-term temporal correlations
 268 of the series (Cazelles et al. 2014). The randomly-generated time series were thus computed in
 269 the following way (Cazelles and Stone 2003; Descamps et al. 2010):

- 270 1. A frequency histogram with n_b equal-sized intervals was created from the values of the
 271 observed time series X to estimate its distribution ($n_b = 3$ for time series < 30 years);
- 272 2. A transition matrix describing the time evolution of the series was created based on the
 273 frequencies of the data contained within each interval. The transition matrix gives the
 274 probability of moving from values that are within interval b_i at time t to values that are within
 275 interval b_j at time $t+1$;
- 276 3. An initial value Z_0 was randomly selected from the observed time series X ;
- 277 4. To determine Z_{t+1} , we randomly selected the interval b_j to which Z_{t+1} belonged based on the
 278 interval b_i of Z_t , and the probabilities from the transition matrix. The value of Z_{t+1} was then
 279 randomly selected among all the elements of interval b_j ;
- 280 5. The previous step was iterated to obtain a randomly-generated time series Z of the same
 281 length as the observed time series X .

282 We then transformed the 1000 randomly-generated time series Z into 1000 randomly-
283 generated symbolic sequences, and computed the distribution of the 1000 randomly-generated
284 mutual information values under the Null hypothesis of independence. We then compared the
285 mutual information of the observed time series (I_{obs}) with the 95th percentiles of the distribution
286 of the 1000 randomly-generated mutual information (I_{sur}). We determined a p-value for the
287 association using a procedure based on ranks; i.e. p-value was defined as 1 minus the proportion
288 of randomly-generated mutual information values exceeded by the observed mutual
289 information value (the rank of I_{obs} relative to all randomly-generated mutual information
290 values). All analyses were performed in R using the package *synchrony* and *infotheo*.

291 Mutual information allowed quantifying the degree of association between two time series,
292 but without any assumption regarding the sign of the relationship between the two time series.
293 Thus, for significant associations, we verified that joint probabilities contributing to the mutual
294 information corresponded to our ecological hypotheses. Similarly, we verified whether the
295 signs of the linear models between residuals corresponded to our ecological hypotheses (see the
296 hypotheses section and Table 1).

297 For comparative purposes, all ecological time series were standardized by dividing all
298 values by the respective mean prior to symbolic transformation. For each dataset, our
299 hypotheses were generic across all reaches for both *environmental* and *cohort effects*, and across
300 all pairs of neighbouring reaches for *spatial effects*. For example, for a given species, a *cohort*
301 *effect* should occur at all reaches. To increase the statistical power of our tests for shorter time
302 series, we concatenated, separately for each dataset, the time series of all reaches (for the
303 *Stream*, *River* and *Estuary* datasets) to test both *cohort* and *environmental effects*; and we
304 concatenated the symbolic sequences of all pairs of neighbouring reaches for the *Stream* and
305 *River* datasets to test *spatial effect* (see the description of hypotheses for details). Note that
306 randomly-generated time series were independently computed for each reach, independently

307 transformed into randomly-generated symbolic sequences, and concatenated afterwards. For
308 both *spatial* and *environmental effects*, association between time series was tested with no time
309 lag, except for one hypothesis for the *Marine* dataset (see the hypotheses description and Table
310 1). In our analyses, significance thresholds were not corrected for multiple tests. Instead, we
311 considered the number of positive tests as evidence for the validity of the tested hypothesis. In
312 results, we provided $I_{obs} - I_{sur}$ and the associated P-value for the symbolic analysis and R^2 and
313 the P-value for the residual approach.

314 ***Description of hypotheses***

315 *Trout populations in small streams*

316 We tested *spatial*, *cohort*, and *environmental effects* for the trout populations. For the
317 *spatial effect*, we concatenated the time series of age-0 trout density of all pairs of neighbouring
318 reaches. For *cohort* and *environmental effects*, we concatenated all (42 reaches) time series of
319 trout density (for both age-0 and age-1) and environmental conditions. For *environmental effect*,
320 we expected annual median of mean-daily water-temperature and age-0 trout-density time
321 series to fluctuate simultaneously in the same direction, while annual median of mean-daily
322 water-temperature and age-1 trout-density time series, and flow velocity during emergence
323 period and age-0 trout-density time series should fluctuate antagonistically (Table 1).

324 *Fish populations in a large river*

325 We tested *spatial*, *cohort*, and *environmental effects* for various fish populations. For the
326 *spatial effect*, we concatenated the time series of age-0 fish density for six species (Table S1)
327 of all pairs of neighbouring reaches. For *cohort effect*, we concatenated all (six reaches) time
328 series of age-0 and age-1⁺ fish density for 16 species (Table S1). For *environmental effect*, we
329 concatenated all time series of age-0 fish, age-0 lithophilic-fish, southern-fish, midstream-fish
330 densities, and environmental conditions. We expected the time series of the number of days
331 with high flows during cyprinid reproductive period to fluctuate antagonistically with age-0

332 fish and age-0 lithophilic-fish densities (Table 1). We expected southern-fish densities to
333 fluctuate simultaneously with time series of annual maximum of mean daily water temperature
334 and time series of mean water temperature during reproductive and growth periods. Finally, we
335 expected midstream-fish densities and annual low-flow hydraulic conditions time series to
336 fluctuate simultaneously.

337 *Fish and invertebrate populations in an estuary*

338 We tested *spatial*, *cohort*, and *environmental effects* for both fish and invertebrate
339 populations. For the *spatial effect*, we examined the fluctuation of density time series among
340 each pair of estuary reaches for 13 species (Table S1). For *cohort effect*, we concatenated all
341 (four reaches) time series of age-0 and age-1⁺ fish density for four species (Table S1). For
342 *environmental effect*, we concatenated all time series of environmental conditions, and expected
343 mean annual salinity time series to fluctuate simultaneously with marine-species densities, and
344 antagonistically with freshwater-species and *Palaemon longirostris* densities (Table 1). We also
345 expected mean annual salinity time series to fluctuate simultaneously with *Argyrosomus regius*,
346 *Engraulis encrasicolus*, and *Dicentrarchus labrax* densities, and antagonistically with
347 *Palaemon longiros* densities and the percentage of shrimp ovigerous female.

348 *Marine fish and invertebrate populations on continental shelf*

349 For this dataset, we could only test the *spatial* and *environmental effects* for the marine
350 populations. For the *spatial effect*, we examined the fluctuation of density time series between
351 the northern and the southern zones for 32 species (Table S1, Fig. S1). For *environmental effect*,
352 we expected mean annual sea surface temperature time series to fluctuate simultaneously with
353 subtropical-species and antagonistically with boreal-species densities (Table 1). We also
354 expected a simultaneous fluctuation between the annual commercial catch and scientific survey
355 biomass. Finally, we expected an antagonist fluctuation between the annual commercial catch
356 biomass at year t and the scientific survey biomass at year $t+1$.

357

358 **Results**359 *Trout populations in small streams*

360 Using the residual Pearson correlation approach and the symbolic analysis, we found
 361 significant *spatial effect* between interannual variation of age-0 trout densities of neighbouring
 362 reaches (Table 2). Indeed, using the symbolic analysis, we found a significant association
 363 between variations in age-0 trout time series; i.e. more than what could be expected by chance
 364 ($I_{obs} - I_{sur} = 0.30$, $P < 0.001$, $n = 35$), with joint probabilities contributing to the mutual
 365 information corresponding to our hypothesis (age-0 trout density in neighbouring reaches
 366 oscillated together, rising and falling simultaneously). Similarly, using the residual analysis, we
 367 found a positive significant relationship between residuals of age-0 in neighbouring reaches (R^2
 368 $= 0.48$, $P < 0.001$). We also found a significant *cohort effect* (association between variation in
 369 age-0 trout density at year t and age-1 trout density at year $t+1$) using both methods ($I_{obs} - I_{sur}$
 370 $= 0.2$, $P < 0.001$, $n = 394$, using the symbolic analysis with the joint probabilities contributing
 371 to the mutual information for analogous symbols; and $R^2 = 0.44$, $P < 0.001$ using the residual
 372 analysis). However, we found no significant *environmental effects* as interannual variations in
 373 environmental drivers were not linked with interannual variations of trout densities ($I_{obs} - I_{sur} <$
 374 0 for the symbolic analysis, and $R^2 < 0.025$ for the residual analysis, $n = [405-521]$ for three
 375 environmental drivers, see table 1).

376

377 *Fish populations in a large river*

378 Among the five tests of *spatial effect* performed for the dominant species (*Alburnus*
 379 *alburnus*, *Squalius cephalus*, *Rutilus rutilus*, *Gobio gobio*, and *Chondrostoma nasus*), we found
 380 a significant relationship between temporal variations of age-0 densities of neighbouring
 381 reaches only for gudgeon (*Gobio gobio*) based on both the mutual information approach ($I_{obs} -$

382 $I_{sur} = 0.029$, $P = 0.023$, $n = 32$) and the residuals approach ($R^2 = 0.22$, $P = 0.04$, Table 2). For
 383 the 16 tested species, we only found a significant *cohort effect* for pumpkinseed (*Lepomis*
 384 *gibbosus*) based on both the mutual information approach ($I_{obs} - I_{sur} = 0.011$, $P = 0.038$, $n = 104$)
 385 and the residuals approach ($R^2 = 0.36$, $P < 0.001$). The results for the *environmental effects*
 386 hypotheses showed no significant associations between variations in environmental drivers and
 387 variations in guild densities with either method ($I_{obs} - I_{sur} < 0$, $P > 0.05$, $n=1130$ for the symbolic
 388 analysis; $R^2 < 0.2$ for the residual analysis).

389

390 *Fish and invertebrate populations in an estuary*

391 Among the 78 tests performed (13 selected species among 6 pairs of reaches), we found 28
 392 significant *spatial effects* for interannual variations of age-0 densities of neighbouring reaches
 393 based on the mutual information approach ($I_{obs} - I_{sur} > 0$, $P < 0.05$, $n = [24-30]$, Table 2). Note
 394 that we obtained 35 significant associations, but for seven tests, the joint probabilities
 395 contributing to the mutual information did not correspond to our hypothesis of positive
 396 associations. In particular, results showed significant *spatial effects* among most pairs of
 397 reaches for *Alosa alosa*, *Alosa fallax*, *Anguilla anguilla*, and *Sprattus sprattus*. With the residual
 398 approach, we obtained 56 significant positive relationships ($R^2 > 0.2$, $P < 0.05$), among which
 399 35 with $R^2 > 0.4$. We found no significant *cohort effect* at time lag 1 ($I_{obs} - I_{sur} < 0$, $P > 0.05$, n
 400 $= 98$ for the symbolic analysis; $R^2 < 0.2$, $P > 0.05$ for the residual analysis) and no *environmental*
 401 *effects* ($I_{obs} - I_{sur} < 0$, $P > 0.05$, $n = [72-96]$ for the symbolic analysis; $R^2 < 0.2$, $P > 0.05$ for the
 402 residual analysis).

403

404 *Marine fish and invertebrate populations on continental shelf*

405 Among the 32 dominant species, we found 12 significant *spatial effects* ($I_{obs} - I_{sur} > 0$, $P <$
 406 0.05 , $n = 26$ for the symbolic analysis, Table 2). For four other species, the association was

407 significant but the joint probabilities contributing to the mutual information did not correspond
408 to our hypothesis. Using the residual method, we found significant positive correlations
409 between the residuals of both zones with R^2 value higher than 0.2 for 18 species, and higher
410 than 0.4 for 10 species. We found no significant correlation between interannual variations in
411 sea surface temperature and interannual variations in subtropical or boreal guild densities using
412 both approaches. Among the 17 dominant commercially exploited species, we found no
413 significant association between interannual variations in commercial catches and interannual
414 variations scientific survey biomass at time lag 0. In contrast, we found a significant negative
415 relationship between the residuals of both commercial catches and scientific biomass at lag 1
416 for *Capros aper* ($R^2 = 0.22$, $P = 0.027$ for the residual analysis).

417

418 Discussion

419 *A relatively low number of significant associations*

420 In this study, we analysed more than 150 aquatic-ecological time series from four
421 independent datasets to examine the information provided by the short term (interannual)
422 temporal variability in long-term aquatic ecological time series. Overall, we identified few
423 significant associations between the interannual variability of the different time series, both
424 environmental and ecological, and thus did not find all expected patterns resulting from
425 population dynamics. For all datasets and using two analytical methods, we found no significant
426 association between the short-term variations in environmental parameters and those of species
427 or guilds densities, although we tested environmental parameters that have been previously
428 identified as long-term drivers of aquatic population dynamics (e.g., Bret et al. 2015; Daufresne
429 et al. 2015; Maire et al. 2019). Similarly, we found only few significant tests for *cohort effects*
430 that is an association between the interannual variations in densities of juveniles and older
431 individuals at a one-year lag: only 2 of the 21 tests performed (9%) were significant, while

432 cohort tracking has been commonly observed in fish populations (e.g., Cattaneo et al. 2002;
433 Lobón-Cerviá et al. 2012; Bret et al. 2015). Nevertheless, for *spatial effects*, among the 116
434 tests performed, 36% were significant based on the symbolic approach (39% based on the
435 residuals approach). The higher number of significant tests for *spatial effect* seems consistent
436 as the densities of individuals sampled in neighbouring sites, with similar environmental
437 conditions and located close enough to allow dispersal between them, should oscillate
438 simultaneously.

439

440 *Interannual variability in aquatic ecological observations due to uncertainty in density*
441 *estimates*

442 We hypothesize that the overall low number of significant results was mainly linked to
443 uncertainty in density estimates due to high sampling inefficiency and variable bias between
444 sampling dates; i.e. variable proportion of the population sampled on each survey. More
445 generally, because the entire population is rarely sampled in ecological studies, the proportion
446 of the population captured (the catchability or capture probability) strongly depends on
447 sampling effort, i.e. the area (or volume) sampled compared to the area (or volume) over which
448 the population is distributed (Hilborn and Walters 2013). This might explain why we found
449 significant *spatial effects* and *cohort effects* for the *Stream* dataset for which the whole reach
450 was sampled, while little for the other datasets for which less than 0.1% of the study area was
451 sampled.

452 In addition, catchability can also vary over time and space although it is often assumed to
453 be constant (Korman and Yard 2017). Variation in catchability depends on the temporal and
454 spatial variation in the efficiency of the sampling gear used to capture individuals, and how
455 sampling points are distributed relative to the distribution of individuals (Trenkel and Cotter
456 2009). Aquatic populations are usually distributed unevenly over different habitats within the

457 study area (Ahmadi-Nedushan et al. 2006; Mérioux et al. 2009), and the spatial distribution of
458 habitats varies over time according to environmental conditions (Korman and Campana 2009;
459 Dunbar et al. 2012; Capra et al. 2017). Thus, catchability could also be affected by the
460 environmental conditions prior and during the surveys. For example, previous studies showed
461 that spatial distribution of aquatic organisms was influenced by high wind velocity and
462 associated marine currents in the ocean (Poulard and Trenkel 2007), high turbidity in rivers as
463 the associated reduction in predation risk modified fish behaviour (Dodrill et al. 2016; Ward et
464 al. 2016) or changes in flow and associated modifications in the proportion and spatial
465 distribution of habitats (Girard et al. 2014). These environmental conditions could have also
466 affected the sampling capacity; e.g., high wind velocity modifies ship motion and trawl
467 geometry (Poulard and Trenkel 2007), and high discharge increases the size of the study area
468 (or volume), and consequently reduces sampling effort.

469 Moreover, catchability strongly depends on species traits and dispersal capacity (Trenkel
470 and Cotter 2009). In particular, many aquatic species are gregarious (e.g., especially cyprinid
471 species as *Alburnus alburnus*, *Chondrostoma nasus*; Vaudor et al. 2011), thereby not evenly
472 distributed over the study area (spatial aggregation). Spatial distribution and behaviour of
473 aquatic species can also vary with age and size; e.g. larger fish individuals are often distributed
474 at greater depths and further from the shore compared to smaller individuals (Vehanen et al.
475 1999; Woillez et al. 2007). This variation of catchability with age and size might explain the
476 low number of significant *cohort effect* detected. The efficiency of a sampling design (gear,
477 timing, spatial distribution of effort) to capture individuals also varies with organism sizes and
478 ages (Borgstroem and Skaala 1993; Korman et al. 2009). For example, the EVHOE survey
479 (*Marine* dataset) was designed for catching young (small) organisms and hence was less reliable
480 for estimating the density of larger individuals (Trenkel and Cotter 2009). This might explain

481 why we found almost no significant association between scientific and commercial catch
482 biomass as commercial fishing mainly targeted larger fish.

483

484 *Complex interacting processes prevent the understanding of population dynamics at the*
485 *annual time scale, even using 30-years of annual surveys*

486 In addition to the uncertainty in density estimates, there are additional explanations for the
487 overall low number of significant results. First, the lack of significant *environmental effects*
488 might be because the environmental drivers selected for this study were not appropriate to
489 explain the observed interannual variations although relevant for long-term trends, e.g.,
490 significant increase in southern fish density with global warming (Daufresne et al. 2015), and
491 decrease in shrimp density with estuary salinization (Béguer et al. 2012). Moreover, the
492 mechanisms driving interannual variations were probably more complex than those driving
493 long-term trends and might involve a combination of interacting environmental parameters
494 (e.g., substrate quality and clogging, temperature rapid variations, short-term flow variations)
495 at different phases of the life cycle, in particular during the first developmental stages of larvae
496 (Schiemer et al. 2003) and recruitment of juvenile fish (Myers 1998; Grenouillet et al. 2001)
497 but also during the period of reproduction and incubation (Korman et al. 2011). Second, the
498 lack of consistency between the densities of juveniles and older individuals the following year
499 might be due to high levels of dispersion, and/or high levels of mortality, linked to unknown or
500 unmeasured environmental drivers, biotic interactions between and within species (predation,
501 competition, facilitation) or endogenous regulatory processes such as density-dependent
502 regulation (Grenouillet et al. 2001; Daufresne and Renault 2006; Lobón-Cerviá 2013). The lack
503 of significant *cohort effects* could also be due to an inappropriate assignment of age classes.
504 For both *River* and *Estuary* datasets, and for long-lived fish, the age class age-1⁺ aggregated
505 various cohorts, potentially affected by different environmental conditions. Third, non-

506 significant *spatial effect* tests could be also due to the definition of neighbouring reaches,
507 probably not similar and/or close enough to host the same population. Indeed, for the *Estuary*
508 dataset, we found more significant results among the closest stations (< 5 km), than among the
509 most distant ones (>20 km). Similarly, Bret et al. (2015) found a decrease in *spatial effect*
510 among age-0 trout densities with increasing distance between streams.

511

512 *Methodological limitations*

513 We could also question the relevance of symbolic analyses to assess the relationships
514 between the interannual variability in environmental and ecological time series, as well as the
515 relevance of the selected rules at the different steps of the analysis (i.e. symbolic transformation
516 and statistical significance level). However, we repeated our analyses using different number
517 of symbols (from 3 to 5), different threshold values (I and D, see methods), different
518 transformation rules (coding peaks and troughs instead of increases and decreases, Cazelles et
519 al. 2004; or coding low, medium, and high density values); and using different procedures for
520 randomly-generated time series computation (e.g. preserving or not temporal dependencies; see
521 Theiler et al. 1991). These complementary analyses led to similar conclusions (results not
522 shown). Consistently, we obtained comparable results with the symbolic and residuals
523 approaches, suggesting that our results are largely independent of the analytical method of our
524 empirical approach. Besides, numerical simulations of aquatic-species density time series based
525 on known ecological patterns, associated with tests of the statistical power of our two analytic
526 methods to detect association between interannual variability of the different time series, could
527 be an alternative approach. However, such numerical simulations are not straightforward, as
528 illustrated for the *River* dataset by Vaudor et al. (2015), but rather require to make strong and
529 questionable assumptions about numerous ecological patterns and processes (e.g., dispersal
530 ability of the different species, strength and direction of environmental effects, and density-

531 dependent growth) and species distribution within study reaches to consider sampling
532 uncertainty (see above). Therefore, although analysis of statistical power based on numerical
533 simulations would complement our empirical approach, such analyses would be challenging
534 and complex and are out of the scope of this paper.

535

536 **Conclusion**

537 Our study clearly indicates that the statistical power to identify and interpret significant
538 interannual variations in aquatic species densities is low, especially in large systems where a
539 complete sampling of populations is unrealistic and sampling effort is limited. Although the
540 significant *spatial effects* observed in our study suggests that interannual variations contains
541 some valuable information of similarities in population dynamics, whose environmental drivers
542 are probably multiple and not clearly identified yet; our results point out that moderate and/or
543 isolated annual ecological changes cannot be revealed by the analysis of interannual variations
544 in such LTES.

545 Our study is focused on interannual variations and does not question the relevance of
546 LTES for detecting important trends or shifts as demonstrated in previous studies. However,
547 interannual variability linked to sampling inefficiency lowers the statistical power to identify
548 trends in large systems, supporting that long time series are required for detecting trends (Hatch
549 2003; Nicholson and Jennings 2004). Consistently, Vaudor et al. (2015) showed, when studying
550 the effects of major flow restoration measures with the *River* dataset, that the probability of
551 detecting moderate changes (50-200 %) in population density after a restoration event averaged
552 16%, compared to 61% for large changes (500-1000 %), and that the number of surveys well
553 balanced before and after restoration increased this probability.

554 Improved analyses of the drivers of short-term population dynamics would require more
555 exhaustive and specific monitoring methods, involving intensive sampling at a finer temporal

556 scale. Alternative approaches would be to combine LTES with intensive continuous sampling
557 during specific periods corresponding to particular life stages (e.g., fish recruitment), or
558 measure population dynamic through individual tracking using telemetry devices or mark-
559 recapture techniques to estimate the probability of detection of species, thereby assessing the
560 observation error of the LTES for a given population (Capra et al. 2018; Radinger et al. 2019).
561 Finally, developing and improving population dynamic models, also using LTES (and
562 combining spatial replications of LTES; Clark et al. 2015) to test the relevance of simulations,
563 should also be encouraged; however, the requirement of continuous sampling and/or specific
564 experiments under controlled conditions to calibrate the model drivers should not be
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777 (*Merluccius merluccius*) in the Bay of Biscay. *ICES Journal of Marine Science* **64**(3):
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779 **Table 1:** Summary of the hypotheses for *environmental effects*. This table summarize the relationship (including the sign) between
780 aquatic species (or guild) and environmental parameters observed in previous studies examining the same datasets.

Datasets	Environmental parameters	Ecological data	Expected sign of the relationship	References
<i>Stream</i>	Annual median of mean daily water temperature	age-0 trout d.	+	Bret et al. 2015
	Annual median of mean daily water temperature	age-1 trout d.	-	
	Flow velocity during emergence period (March-April)	age-0 trout d.	-	
<i>River</i>	Nbr. of days with high flows during cyprinid reproductive period (March-June)	age-0 fish d.	-	Daufresne et al. 2015 Lamouroux et al. 2015
	Nbr. of days with high flows during cyprinid reproductive period (March-June)	age-0 lithophilic-fish d.	-	
	Annual maximum of mean daily water temperature	southern-fish d.	+	
	Mean water temperature during reproductive and growth periods (April-August)	southern-fish d.	+	
	Annual low-flow hydraulic conditions	midstream-fish d.	+	
<i>Estuary</i>	Mean annual salinity	marine-species d.	+	Béguer et al. 2012 Pasquaud et al. 2012
	Mean annual salinity	freshwater-species d.	-	
	Mean annual temperature	<i>Argyrosomus regius</i> d.	+	
	Mean annual temperature	<i>Engraulis encrasicolus</i> d.	+	
	Mean annual temperature	<i>Dicentrarchus labrax</i> d.	+	
	Mean annual temperature	<i>Palaemon longirostris</i> d.	-	
	Mean annual salinity	<i>Palaemon longirostris</i> d.	-	
	Mean spring temperature	Shrimp reproduction (% ovigerous female)	-	
<i>Marine</i>	Mean annual sea surface temperature	subtropical-species d.	+	Poulard and Blanchard 2005
	Mean annual sea surface temperature	boreal-species d.	-	
	Annual commercial catch b. (year t)	scientific survey b. (year t)	+	
	Annual commercial catch b. (year t)	scientific survey b. (year t+1)	-	

781 d. = density, b. = biomass; nbr. = number

782 **Table 2:** Summary of our results: number of significant associations per number of test performed
 783 for each hypothesis and dataset. We considered a significant synchrony, for the symbolic analysis,
 784 when the observed mutual information was higher than the 95th percentiles of the distribution of
 785 the 1000 surrogate mutual information ($I_{\text{obs}} - I_{\text{sur}} > 0$), and the joint probabilities contributing to the
 786 mutual formation corresponded to our hypothesis. For the residual analysis, we considered a
 787 significant synchrony when the correlation between residuals was significant ($P < 0.05$) with R^2
 788 > 0.4 , and the sign of the relationship corresponded to our hypothesis.

789

Datasets	<i>Spatial effects</i>			<i>Cohort effects</i>			<i>Environmental effects</i>		
	<i>Symbolic</i>	<i>Residual</i>		<i>Symbolic</i>	<i>Residual</i>		<i>Symbolic</i>	<i>Residual</i>	
		$R^2 > 0.4$	$R^2 > 0.2$		$R^2 > 0.4$	$R^2 > 0.2$		$R^2 > 0.4$	$R^2 > 0.2$
<i>Stream</i>	1/1	1/1	1/1	1/1	1/1	1/1	0/3	0/3	0/3
<i>River</i>	1/5	0/5	1/5	1/16	0/16	1/16	0/5	0/5	0/5
<i>Estuary</i>	28/78	35/78	56/78	0/4	0/4	0/4	0/8	0/8	0/8
<i>Marine</i>	12/32	10/32	18/32	-	-	-	0/36	0/36	1/36

790

791 **Figure legends:**

792 Figure 1: Site localisation and sampling methods of the four datasets: 1) Trout populations in small
793 streams (in green), 2) Fish populations in a large river (in red), 3) Fish and invertebrate populations
794 in an estuary (in purple), and 4) Marine fish and invertebrate populations on continental shelf (in
795 orange). The theoretical hydrographical network (RHT, Pella et al. 2012) was used to represented
796 the French stream network (Strahler order >2).

797
798 Figure 2: Illustration of the first step of both approaches used to evaluate the synchrony between
799 time series: a) the symbolic transformation, and b) the residual computation. In both panels, open
800 dots represent a standardized fish density time series. In panel a, the continuous time series is
801 transformed into a discrete sequence of three symbols (F for “Flat”, I for “Increase”, and D for
802 “Decrease”). This step precedes the mutual information calculation between two symbolic
803 sequences. In panel b, residuals of a LOESS model are extracted. This step precedes the linear
804 model among residuals from two time series.



