Interpretation of interannual variability in long-term aquatic ecological surveys

Cauvy-Fraunié Sophie ^{1,*}, Trenkel Verena ², Daufresne Martin ³, Maire Anthony ⁴, Capra Hervé ⁵,
Olivier Jean-Michel ⁶, Lobry Jérémy ⁷, Cazelles Bernard ⁸, Lamouroux Nicolas ⁵

¹ Irstea Centre de Lyon-Villeurbanne, 89723, 5 rue la doua, Villeurbanne, France

² IFREMER - Centre de Nantes, 70611, Nantes, Pays de la Loire, France

³ Irstea Centre d'Aix-en-Provence, 84233, Aix-en-Provence, Provence-Alpes-Côte d'Azur, France

⁴ EDF R and D Site de Chatou, 151443, Chatou, Île-de-France, France

⁵ Irstea Centre de Lyon-Villeurbanne, 89723, Villeurbanne, Rhône-Alpes, France

⁶ Université Claude Bernard Lyon 1 Faculté des Sciences et Technologies, 200932, LEHNA, Villeurbanne, France

⁷ Irstea Centre de Bordeaux, 84269, Cestas, Aquitaine, France

⁸ ENS, 26909, Paris, Île-de-France, France

* Corresponding author : Sophie Cauvy-Fraunié, email address : sophie.cauvy-fraunie@irstea.fr

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

Introduction

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

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

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

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

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

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

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

Methods

Data description

Trout populations in small streams

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

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

Fish populations in a large river

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

Fish and invertebrate populations in an estuary

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

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

Marine fish and invertebrate populations on continental shelf

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

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

Data analyses

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

Symbolic transformation

To describe the rhythm of continuous time series, we discretized them into a sequence of a finite number of symbols (Cazelles 2004). As our objective was to identify the main drivers of interannual variability in ecological time series, we used a simple discretization based on three 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'.

Mutual information

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 1995). The mutual information I_{S1S2} between the symbolic sequences $S1$ and $S2$ is defined as:

$$I_{S1S2} = H_{S1} + H_{S2} - H_{S1S2}$$

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:

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

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

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

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

Statistical significance level

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

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

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

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

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

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

Description of hypotheses

Trout populations in small streams

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

Fish populations in a large river

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

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

Fish and invertebrate populations in an estuary

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

Marine fish and invertebrate populations on continental shelf

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

Results

Trout populations in small streams

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

Fish populations in a large river

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

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

Fish and invertebrate populations in an estuary

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

Marine fish and invertebrate populations on continental shelf

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

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

Discussion

A relatively low number of significant associations

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

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

Interannual variability in aquatic ecological observations due to uncertainty in density estimates

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

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

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

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

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

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

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

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

Methodological limitations

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

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

Conclusion

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

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

Improved analyses of the drivers of short-term population dynamics would require more 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
565 overlooked.

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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
Stream	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.	-	
River	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.	+	
Estuary	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)	-	
Marine	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

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

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

Figure legends:

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

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