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HIGHLIGHTED STUDENT RESEARCH

Measurements of spatial population synchrony: influence of time series transformations

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Abstract Two mechanisms have been proposed to explain spatial population synchrony: dispersal among populations, and the spatial correlation of density-independent factors (the "Moran effect"). To identify which of these two mechanisms is driving spatial population synchrony, time series transformations (TSTs) of abundance data have been used to remove the signature of one mechanism, and highlight the effect of the other. However, several issues with TSTs remain, and to date no consensus has emerged about how population time series should be handled in synchrony studies. Here, by using 3131 time series involving 34 fish species found in French rivers, we computed several metrics commonly used in synchrony studies to determine whether a large-scale climatic factor (temperature) influenced fish population dynamics at the regional scale, and to test the effect of three commonly used TSTs (detrending, prewhitening and a combination of both) on these metrics. We also tested whether the influence of TSTs on time series and population synchrony levels was related to the features of the time series using both empirical and simulated time series. For several species, and regardless of the TST used, we evidenced a Moran effect on freshwater fish populations. However, these results were globally biased downward by TSTs which reduced our ability to detect significant signals. Depending on the species and the features of the time series, we found that TSTs could lead to contradictory results, regardless of the metric considered. Finally, we suggest guidelines on how population time series should be processed in synchrony studies.

Keywords Raw data · Prewhitening · Detrending · Fish · Moran effect

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Highlighted student research: This paper represents an outstanding contribution to the field of spatial population synchrony. Using empirical and simulated data sets, we highlighted the influence of time series transformation (TSTs) on several measures classically used in synchrony studies to identify the determinants of spatial population synchrony (i.e., large-scale climatic factors such as climate or local factors such as dispersion of individuals between localities). Our results highlight how TSTs influence both synchrony measurements and the conclusions regarding the determinants of population synchrony. Based on these results, we provide guidelines about how time series should be handled in synchrony studies. These guidelines are expected to improve our general understanding of the drivers influencing spatial population synchrony.

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Introduction

Population densities in different locations often fluctuate synchronously over time (Buonaccorsi et al. 2001). This

phenomenon, known as spatial population synchrony, is common in animal populations ranging from parasites (Cattadori et al. 2005) to insects (Sutcliffe et al. 1996), fish (Grenouillet et al. 2001), amphibians (Trenham et al. 2003), and birds (Koenig and Knops 1998) to mammals (Moran 1953). Two mechanisms have been identified as the principal drivers of spatial synchrony (Liebhold et al. 2004): dispersal among spatially structured populations (Ranta et al. 1995), and the spatially correlated effects of density-independent factors that synchronize populations with the same linear density-dependent structure, a process known as the "Moran effect" (Moran 1953).

Depending on the main mechanism driving population synchrony, the fate of the metapopulations involved may vary (Hanski and Woiwod 1993). If synchrony is caused by dispersal, then a population that suffers severe decline can be rescued by adjacent populations, ensuring persistence of the metapopulation. In contrast, if synchrony is caused by environmental factors, then all populations could suffer a severe decline simultaneously, which could lead to metapopulation extinction. It is generally thought that large-scale synchrony is caused by environmental factors, whereas local synchrony is mainly driven by dispersal (Ranta et al. 1998). However it has been shown that dispersal between neighboring populations could interact with local demographic processes to generate patterns of spatial synchrony over very large distances (Gouhier et al. 2010). Moreover, it is likely that these mechanisms are not mutually exclusive, and in fact operate jointly in many systems, with varying relative importance (Ranta et al. 1999).

Despite an abundant literature on population synchrony, very few studies (e.g., Grenfell et al. 1998; Tedesco and Hugueny 2004) have clearly identified which mechanism is involved in particular populations. This has been done experimentally (Benton et al. 2001) or by studying systems where the influence of one of the mechanisms could be discarded, as for instance with populations located in different islands between which dispersion is impossible (Grenfell et al. 1998). However, such systems are rare and experimental settings are not appropriate for studying large organisms (e.g., mammals) over long time periods. Consequently, the most common approach to identify which mechanism prevails in population synchrony has been to use time series transformations (TSTs) of abundance data using statistical methods. The idea in such a procedure is to eliminate the signature of one mechanism to highlight the effect of the other (Bjørnstad et al. 1999). For instance, eliminating temporal autocorrelation (by a prewhitening procedure) in population time series makes it possible to focus on density-independent mechanisms, such as environmental noise (Hanski and Woiwod 1993). Likewise, eliminating long-term trends (by a detrending procedure) makes it possible to focus on local processes (e.g., dispersal) rather than global ones, such as long-term climate change (Koenig 1999). However, removing trends in time series can reduce the power to detect real relationships (Pyper and Peterman 1998) and, in some cases, detrending can increase the autocorrelation in a data set. For instance, if observations in time series are independent, detrending creates a dependency among data points (Brown et al. 2011). Furthermore, the presence of temporal autocorrelation and/or long-term trends in a time series could indicate the presence of low-frequency (i.e., slowly changing) variability (Pyper et al. 1999). Yet, if low-frequency sources are also sources of real covariation between time series, then their removal (by a detrending or a prewhitening procedure) can greatly reduce our ability to detect that covariation (increase of type II error rate). As far as we are aware, the effects of various TSTs on synchrony measurements remain to be compared.

Here we looked at time series of the abundance data for 34 fish species in 592 French rivers in four different ways: as raw data, as detrended data, as prewhitened data, and as a combination of both TSTs (prewhitening and detrending). We then computed various statistics, frequently used in synchrony analyses, to find out whether a large-scale climatic factor (temperature) had any influence on fish population dynamics in these four time series. We then compared the results obtained using each of the TSTs to those obtained using the raw data in order to identify the effect of each transformation on the different measures used. Finally, using empirical and simulated time series, we tested whether the influence of TSTs on time series and population synchrony levels vary depending on the features of the original time series (i.e., length, strength and evidence of both density dependence and long-term trend).

Our expectations were as follows. First, by eliminating the signature of one mechanism, TSTs should reduce our overall ability to detect significant synchrony, but could be used to identify drivers of population synchrony by comparing the results obtained using raw data (Bjørnstad et al. 1999). However, we supposed that TSTs could lead to false outcomes by removing part of the signal of interest. Second, TSTs were expected to have different influences on the results depending on the features of the raw time series. For instance, for time series that do not display long-term trends (or density dependence), detrending (or prewhitening) should have little influence on the time series and therefore on the results.

Materials and methods

Fish and temperature data sets

Fish population abundances were provided by the French National Agency for Water and the Aquatic Environment

(Onema). These annual data were obtained between 1982 and 2010 by electrofishing during periods of low flow (for further details see Poulet et al. 2011). At each sampling occasion, fish were identified to species level, counted, and released. From this data set we conserved only the species for which at least nine population time series including at least 8 years of non-null captures were available. This resulted in the selection of 34 fish species (Table 1). We chose to have at least nine population time series, because we wanted to have: (1) populations that were representative of the different conditions experienced by the species in its geographic range, and (2) enough populations to compute a reliable estimate of species synchrony levels. For the number of years within the time series, we chose the same number as that used in a study involving a previous version of our database (Poulet et al. 2011). We therefore used a data set consisting of 609 sites located throughout France (Fig. 1a) with 8–25 years of sampling (mean 12.5 years; SD 3.6 years), corresponding to a total of 7015 sampling occasions. The method used neither required the same exact years to be covered for the different sites nor the years to be consecutive, but all times series that had more

Table 1 Data for the 34 French fish species studied

Species name	*n*	*npairs*	GRS (km^2)	LS[a] (years)	Mean distance (km)
Abramis brama	24	204	260,713	14.5	396
Alburnoides bipunctatus	53	794	273,135	6	308
Alburnus alburnus	107	2480	453,288	6	371
Ameiurus melas	17	64	138,562	9	247
Anguilla anguilla	205	12,173	604,842	17	413
Barbatula barbatula	245	21,344	550,434	7	377
Barbus barbus	129	4813	407,407	14	366
Blicca bjoerkna	26	126	273,271	10	279
Carassius sp.	12	46	195,257	10	326
Chondrostoma nasus	26	268	146,168	13.5	222
Cottus gobio	25	160	118,620	5	259
Cottus perifretum	167	10,586	358,455	6	310
Cyprinus carpio	11	54	176,032	15.5	270
Esox lucius	61	1073	402,545	13	312
Gasterosteus gymnurus	17	89	233,558	3	336
Gobio gobio	219	14,353	403,731	5	338
Gobio lozanoi	9	36	3732	5	59
Gobio occitaniae	73	1848	103,693	5	188
Gymnocephalus cernua	25	214	257,607	8.5	390
Lampetra planeri	67	2043	364,842	7	330
Lepomis gibbosus	161	6180	437,089	8	325
Leuciscus burdigalensis	40	597	225,996	10	285
Leuciscus leuciscus	60	961	244,492	10	221
Perca fluviatilis	83	1720	382,141	14	327
Phoxinus phoxinus	247	22,170	535,689	6.5	362
Pungitius laevis	17	105	104,217	4	248
Rhodeus amarus	31	174	163,084	5	286
Rutilis rutilis	261	17,860	554,946	12	371
Salmo salar	22	153	224,366	8	300
Salmo trutta	285	29,691	634,835	6.5	433
Scardinius erythrophthalmus	27	87	300,342	8	413
Squalius cephalus	311	27,854	532,186	8	368
Telestes souffia	25	220	90,361	10	183
Tinca tinca	43	445	412,592	12	382

n Number of time series, *npairs* number of cross-correlation coefficients, *GRS* species' geographic range size (km^2), *LS* species' life span (years), *mean distance* mean pairwise distance between sites (km)

[a] For some species the LS is the mean of different values found in the literature

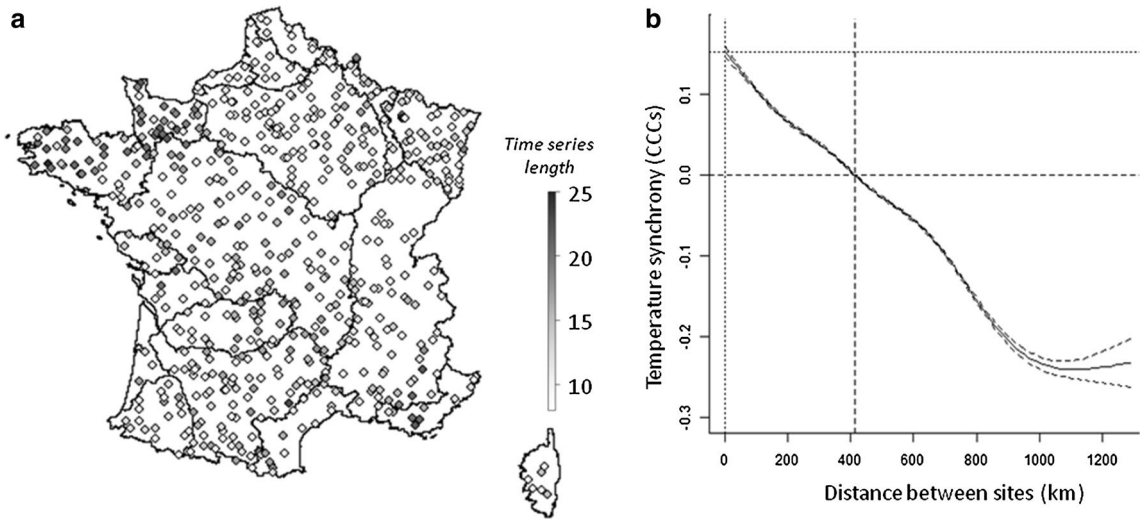

Fig. 1 **a** Study area showing the distribution of the sampling sites. *Gray scale* indicates the number of years available for each site, *light gray* indicates sites for which we have the fewest years, *dark gray* indicates sites for which we have the greatest number of years. **b** Relationship between temperature synchrony and the Euclidean distance between the 609 sampling sites ($n = 148{,}368$). The *intersection* between the two *dashed lines* represents a measure of the spatial scale of temperature synchrony, whereas the *intersection* between the two *dotted lines* represents the synchrony at close distance; 95 % confidence intervals are also shown

than 3 consecutive years missing were discarded to minimize the influence of missing information on our results. The number of zero counts ranged from zero to 13, depending on the time series (mean 0.89; SD 2.16).

Daily air temperature data from 1982 to 2010 were provided by Météo France. This database (SAFRAN; Le Moigne 2002), is a regular 8-km grid, in which the daily air temperature was calculated for each cell by optimal interpolation of climatically homogeneous zones (for further details see Le Moigne 2002). Studies have shown that air temperature provides a reliable proxy for water temperature (e.g., Caissie 2006). Since warm temperatures during the summer have been shown to affect fish population synchrony (Grenouillet et al. 2001; Cattanéo et al. 2003), we calculated the mean air temperature during the warmest month of each year for each site. We then used this measure to estimate the degree of temperature synchrony (i.e., a proxy of the Moran effect) between the different sampling sites to determine whether it influenced fish population synchrony.

Definition of TSTs and estimation of time series features

Population time series were considered in four different ways: as raw data, as residuals obtained from a linear model with the year as a covariate to eliminate the long-term trend (detrended data), as residuals obtained from a stock-recruitment Ricker model (Ricker 1958) to eliminate temporal autocorrelation due to intrinsic population dynamic (prewhitened data), and as residuals obtained from a stock-recruitment Ricker model that included the year as a covariate to eliminate both the long-term trend and the temporal autocorrelation due to intrinsic population dynamic (prewhitened and detrended data). The precise specifications for the four types of time series are presented in the electronic supplemental material (ESM; Appendix S1). The models used for TSTs were fitted to the raw data using the iteratively reweighted least square method (McCullagh and Nelder 1989). The coefficients of these models (i.e., trend and density dependence) were then extracted, and used to characterize the raw time series. All calculations were performed in R (R Core Team 2013).

Synchrony analyses

Measuring synchrony: populations, species and scales of synchrony

For each species and the four types of time series, we measured population synchrony by computing Spearman cross-correlation coefficients (CCCs) between all pairs of time series with at least 8 years in common (Buonaccorsi et al. 2001). From these CCCs, we calculated species synchrony as the average of the CCCs weighted by the number of overlapping years of data between pairs of time series. To determine whether species synchrony was significantly different from zero, we used a bootstrap procedure with resampling of time points within each time series, and then recalculated the mean between all the CCCs computed

from the resampled time series (Lillegård et al. 2005). To rule out the effect of dispersion, the same analysis was conducted considering only the populations situated in different catchments (i.e., between which dispersion is theoretically impossible).

As the variable distances over which the different populations were sampled could influence species synchrony levels [species with aggregated populations generally displaying higher synchrony levels (Sutcliffe et al. 1996)], and thus the subsequent analysis (see below), we tested whether the species geographic range size (GRS) had an influence on our measure of species synchrony using Spearman's cross-correlation coefficients. For each species, GRS was measured as the area (km^2) of the smallest convex set of the subset of sites occupied by the species [i.e., the convex hull (Barber et al. 1996)].

The scale (i.e., the spatial extent) of synchrony is the distance beyond which population synchrony is overall no longer significantly different from zero (Bjørnstad and Falck 2001). To estimate the spatial extent of population synchrony for each species, we first calculated the Euclidean distance between each population. We chose the Euclidean distance because we considered this metric to be more representative of the similarity of the environmental conditions experienced by the different populations than a metric based on the distance along the river segments. Then, for each species and all four types of time series, we used generalized additive models to study the relationship between CCCs and distance, weighted for the length of the time series. We used the *x*-intercept (i.e., the intersection with the line $y = 0$) of this relationship as a measure of the spatial scale of species synchrony (Bjørnstad and Falck 2001), whereas the *y*-intercept was used as a measure of species synchrony at small distances (i.e., for sites that were located close to each other; see Fig. 1b for an example).

Determinants of population synchrony: distance between sites and temperature synchrony

For each species and all four types of time series, we used Mantel tests (Mantel 1967) to determine whether population synchrony (i.e., CCC) was significantly influenced by the Euclidean distance between sites as well as by temperature synchrony. The scale of temperature synchrony was measured over all the study sites (Fig. 1b) using the same procedure as the one used to estimate the spatial extent of population synchrony for the different species.

Influences of TSTs

As we performed multiple tests to compare the results obtained from each TST relative to raw data, the reported *P*-values were adjusted according to the sequential Bonferroni procedure to conserve an initial error rate of 5 %.

To find out whether the influence of TSTs on the time series and the level of population synchrony depended on the features of the time series, we used linear mixed-effect models. As the results did not changed depending on whether the coefficients of trend and density dependence were estimated separately (using TST I and TST II) or simultaneously (using TST III), only the results obtained from the latter are presented. The same analysis was repeated on simulated time series with known properties to confirm the results obtained empirically (the detailed description of the procedure used to simulate the time series is presented in the ESM; Appendix 3). To check for violations of model assumptions, we performed a visual inspection of the residuals for all reported models.

The ability to remove trend and temporal autocorrelation

For the four types of time series, we assessed the number of time series that showed a significant trend or temporal autocorrelation using a non-parametric Mann–Kendall trend test (Kendall 1955) and the autocorrelation function implemented in R (Venables and Ripley 2002), respectively. For the latter, we only considered the autocorrelation with a 1-year lag. We then compared the number of time series that displayed significant trend or temporal autocorrelation for the four types of time series, to assess whether the component of interest (e.g., trend) had in fact been eliminated by the corresponding TST (e.g., detrending), and whether the other (e.g., temporal autocorrelation) had not been affected.

Effects of TSTs on the time series

To determine the extent to which TSTs modified the raw time series, we computed Spearman cross-correlation coefficients between the raw time series and the time series obtained with each TST. This led to the creation of three variables representing the degree of similarity between the raw time series and the time series altered by each TST. A high correlation would indicate a high similarity (i.e., a low influence of TST) whereas a low correlation would indicate a low similarity (i.e., a strong influence of TST). We then used Wilcoxon-paired tests to find out whether the average correlation calculated between the raw time series and the modified ones depended on the TSTs. The same procedure was performed on the simulated time series (Appendix S3).

To determine whether the similarity between the raw time series and the time series altered by each TST depended on the features of the raw time series, we computed three linear mixed-effect models with the length of the time series and the estimated coefficients of trend and

density dependence as independent variables. The last two variables were entered into the model as absolute values so as to focus on the effect of their strength. To account for species variability, we added random effects on the intercepts and slope coefficients of each independent variable. The three dependent variables (i.e., similarities between the raw time series and the modified ones) were normalized using a Box-Cox power transformation (Box and Cox 1964). Model equation and parameter descriptions are presented in the ESM (Appendix S2). The same procedure was performed on simulated time series (Appendix S3).

Effects of TSTs on population synchrony

To quantify the degree to which population synchrony was influenced by TSTs, we calculated the differences between the CCCs estimated using each of the TSTs and those estimated using the raw data. We thus obtained three variables representing the degree of dissimilarity between the CCCs obtained with each TST relative to those obtained with the raw data. To focus on the magnitude of these differences, we took the absolute values of these three variables. A high value would indicate a strong influence of TSTs whereas a low value would indicate a low influence. We then used Wilcoxon-paired tests to find out whether the average differences in the CCCs varied depending on the TST used. The same procedure was performed on the simulated time series (Appendix S3).

To determine whether the features of the raw time series influenced the differences between the CCCs calculated using the raw time series and those calculated using each TST, we computed three linear, mixed-effect models. For the length of the time series, we considered the common length used in calculating the CCCs. For density dependence and trend we focused on whether these processes were significantly detected in the time series using the autocorrelation function and the Mann–Kendall trend test, respectively. Thus, density dependence and trend were represented by ordinal variables coded from zero (neither of the two time series under consideration displayed significant values) to two (significant values in both time series). The models were constructed separately for each species to reduce their complexity and improve model convergence. To account for the variability associated with the sites involved in the calculation of the CCCs, we added random effects on the slopes and intercepts of the trend and density-dependent variables. The three dependent variables (i.e., differences calculated between CCCs estimated with raw data and those estimated with each TST) were Box-Cox transformed. Model equation and parameter descriptions are presented in the ESM (Appendix S2). The same procedure was performed on the simulated time series (Appendix S3).

Effects of TSTs on synchrony measurements and the determinants of population synchrony

We used Wilcoxon-paired tests: (1) to find out whether TSTs had a significant influence on the different statistics calculated for the 34 fish species using the raw data (i.e., overall synchrony, inter-catchment synchrony, scale of synchrony, and synchrony at small distances); and (2) to determine whether TSTs modified our ability to identify the determinants of population synchrony for the 34 fish species (i.e., how TSTs modified the relationship between population synchrony and the Euclidean distance between populations as well as that between population synchrony and temperature synchrony).

Results

For the four types of time series, we failed to find any significant ($P > 0.05$) influence of GRS on our measure of species synchrony. Our results are therefore expected to be weakly influenced by the variable distances over which the species were sampled.

Features of the time series

The percentage of time series showing a significant long-term trend ranged from 9 to 60 % (mean 34.2 %; SD 10.6 %) depending on species (Appendix S4, Table S1), between 0 and 48 % of time series showing a positive trend (mean 20.5 %; SD 11.5 %), and the percentage of time series with a negative trend ranged from 0 to 26 % (mean 13.6 %; SD 5.8 %). Time series showing a significant negative density-dependent coefficient ranged from 27 to 93 % depending on species (mean 73.9 %; SD 14.7 %). When both components were estimated simultaneously, the percentage of time series displaying significant trend and density dependence differed from when they were estimated individually (Appendix S4, Table S1), thus revealing an inter-dependency among coefficients.

Influence of TSTs

A visual example of the effect of each TST on two observed time series is presented in Fig. 2. For the four types of time series, this figure also provides estimates of the level of synchrony between the two time series as well as an estimation of their coefficients of trend and temporal autocorrelation (the R code used to transform the time series and to estimate these coefficients is provided in Appendix S5).

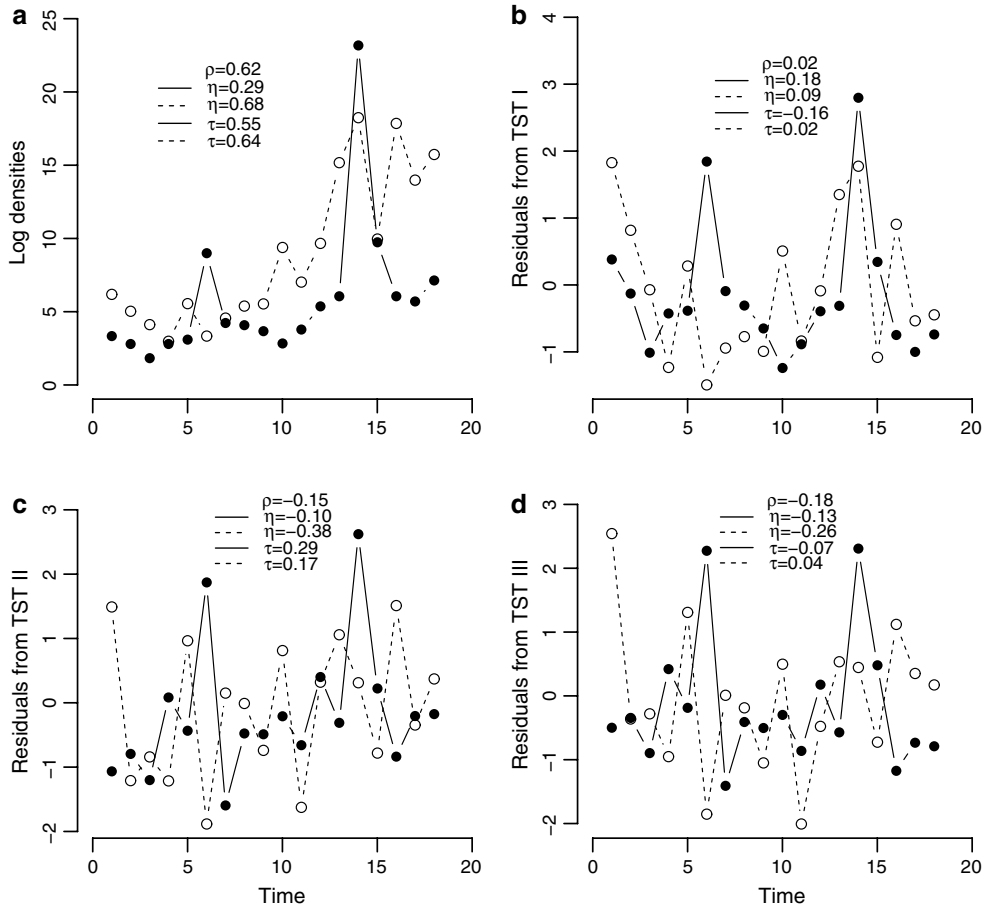

Fig. 2 Two observed time series with their estimated trend ($\tau 1$, $\tau 2$), their estimated lag-1 temporal autocorrelation ($\eta 1$, $\eta 2$), and the degree of synchrony between them (ρ). *Solid lines* correspond to the coefficients of trend associated with each time series, *dashed lines* correspond to the temporal autocorrelation associated with each time series. **a** Raw data (the densities were log transformed to reduce the variance in both time series to facilitate graphical representation; the coefficients associated with each time series were calculated on the raw densities), **b** residual from time series transformations (*TST*) I, **c** residual from TST II, **d** residual from TST III

The ability to remove trend and temporal autocorrelation

Among the 3131 time series considered, we found that 606 (19 %) showed a significant long-term trend, whereas 153 (5 %) displayed significant temporal autocorrelation. Once the long-term trend had been eliminated, seven (0.2 %) time series still displayed a significant long-term trend, while 105 (3 %) showed significant temporal autocorrelation. When accounting for intrinsic population dynamic, 18 (0.6 %) out of the 153 time series still showed significant temporal autocorrelation, whereas 153 (5 %) displayed a significant long-term trend. When both components were removed simultaneously, 30 (1 %) time series presented significant temporal autocorrelation, whereas one time series (<0.1 %) still displayed a significant long-term trend.

Effects of TSTs on the time series

The correlations calculated between the raw time series and the modified ones were on average greater when considering the time series obtained from TST I (median 0.89; SD 0.17), and smaller when using the time series obtained from TST III (median 0.75; SD 0.18) (Fig. 3a). We found intermediate levels of similarity between raw data and time series obtained with TST II that were nonetheless quite similar to those found with time series obtained from TST I (median 0.85; SD 0.19). Wilcoxon-paired tests revealed significant ($P < 0.001$) differences between these correlations. Thus, TST I and II had less influence on the time series than TST III. These results were confirmed by analyses conducted on the simulated time series (Appendix 6, Fig. S1a). However, the influence of TST II (median 0.56;

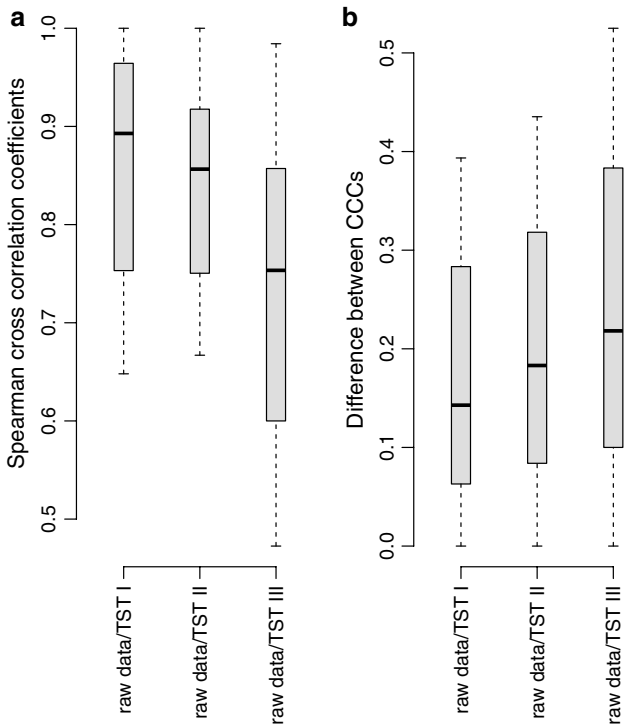

Fig. 3 **a** Correlations between the raw time series and the time series obtained with each of the TSTs ($n = 3131$). **b** Differences between the cross-correlation coefficients (*CCCs*; i.e., population synchrony) calculated using the raw data and those calculated using the TSTs ($n = 180{,}864$)

SD 0.27) on the time series was closer to the one of TST III (median 0.52; SD 0.26) which was far greater than the influence of TST I (median 0.91; SD 0.18).

With regard to the correlations calculated between the raw time series and the ones obtained with TST I, the mixed-effects model revealed a negative influence of the strength of the long-term trend ($P < 0.001$) and a positive influence of the strength of density dependence ($P < 0.001$; Appendix S6, Table S2). Thus, time series that presented a low density dependence, but a high long-term trend were modified by TST I to a greater extent than those with the opposite features. The same general pattern was found when considering correlations calculated between raw data and time series obtained from TST II and III (Table S2). These results were further confirmed by analyses conducted on simulated time series, which besides revealed a negative influence of the length of the time series (Table S2). Thus, long time series were modified to a greater extent by TSTs than short time series.

Effects of TSTs on population synchrony

Differences between the CCCs calculated using the raw time series and those calculated using the modified ones were on average higher for TST III (median 0.21; SD 0.21), and lower for TST I (median 0.14; SD 0.18; Fig. 3b). We found intermediate differences between the CCCs calculated with the raw time series and those calculated with TST II (median 0.18; SD 0.18). Wilcoxon-paired tests revealed that these differences were significantly influenced by TSTs ($P < 0.001$). Thus, relative to the raw data, TST I had less influence on the CCCs than TSTs II or III. The same general pattern was found on the simulated time series (Appendix 6, Fig. S1b).

Mixed-effect models relating the differences in CCCs to the features of the time series converged for 17 out of the 34 species when the difference in CCCs obtained using raw data and those obtained using TST I were considered (Appendix 6, Table S3). Among these, 14 (82 %) displayed differences in CCCs that were significantly ($P < 0.05$) positively related to the long-term trend, whereas four (23 %) and 11 (64 %) species displayed differences in CCCs that were significantly ($P < 0.05$) negatively related to the temporal autocorrelation and the length of the time series, respectively. Thus, the difference between the CCCs calculated using the raw data and those calculated using TST I was greater when no time series displayed significant temporal autocorrelation, both time series displayed a significant long-term trend, and the length shared by both time series was short. Even though the number of species presenting significant associations with time series features was lower, the same general pattern was found for the differences calculated between the CCCs estimated from raw data and those estimated from TSTs II and III (Table S3). These results were supported by linear models performed on the simulated time series (Table S3). However, contrary to empirical time series, we found that the differences between the CCCs calculated using the raw data and those calculated using either TST II or III were greater when both time series displayed significant temporal autocorrelation.

Effects of TSTs on species synchrony, spatial variation of synchrony and the determinants of population synchrony

Detailed results describing how: (1) synchrony measurements (overall and inter-catchment species synchrony, scale of synchrony and synchrony at short distance); and (2) the relationship between population synchrony and its determinants (temperature synchrony and the Euclidean distance between populations) changed depending on TSTs are presented in Appendix S6 (Table S4–S6). For the raw data, we found that more than half (64 %) of the species displayed significant levels of population synchrony even though these were weak (Table S4). When considering only the populations that were located in different catchments, we found that 67 % of the species displayed significant synchrony levels. Several species (30 %) were

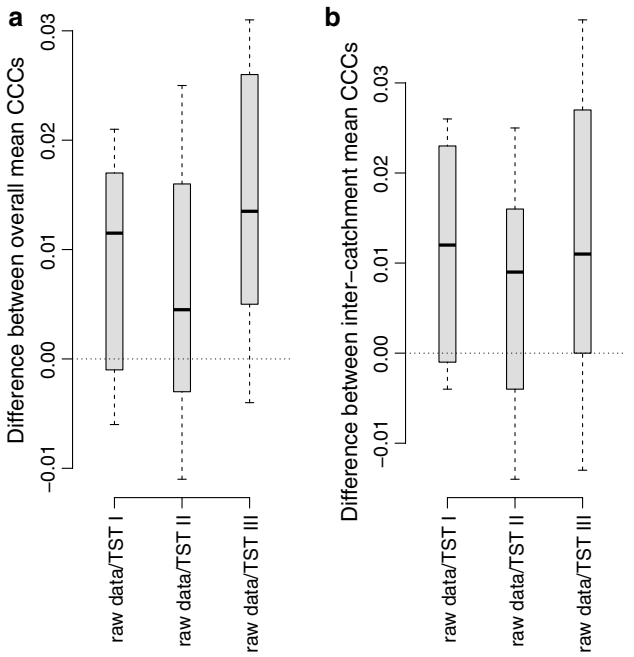

Fig. 4 Difference between **a** overall synchrony (i.e., mean of all CCCs) and **b** overall inter-catchments synchrony (mean of CCCs involving only population situated in different catchments) calculated for each species using the raw data and those calculated with TSTs ($n = 34$). The *horizontal dotted line* indicates the absence of difference between the results obtained using the raw data and those obtained with the TSTs. For abbreviations, see Figs. 1 and 2

synchronous over large distances (>200 km, Table S5), that significantly differed from zero (according to 95 % confidence intervals), which coincided with the scale of synchrony measured for temperature (i.e., >400 km; Fig. 1b). Less than half (41 %) of the species displayed significant levels of synchrony at close distances (Table S5). For 17 % of the species, the level of population synchrony was significantly related to the level of temperature synchrony (Table S6). Finally, for 30 % of the species, we found a significant ($P < 0.05$) negative relationship between the level of population synchrony and the Euclidean distance separating them (Table S6).

Whatever the measures considered, the results were globally biased downward by TSTs (Figs. 4, 5) but the influence of TSTs was highly variable depending on the metric and the species considered (see Tables S4–S6). Overall, we found no statistical differences ($P > 0.05$) between the results obtained with raw data and those obtained with TSTs either for species synchrony (both overall and inter-catchments species synchrony; Fig. 4a, b), the scale of synchrony (Fig. 5a), the synchrony at short distances (Fig. 5b), the relationship between population synchrony and Euclidean distance between populations (Fig. 5c) or the relationship between population synchrony and temperature synchrony (Fig. 5d).

Discussion

Our goals in this study were: (1) to determine whether a Moran effect had any influence on fish population dynamics at the regional scale, and (2) to quantify the influence of three commonly used TSTs on synchrony measurements as well as on our ability to identify the determinants of population synchrony. To do this, we used empirical time series of abundance data for 34 fish species, and computed several statistics commonly used in synchrony studies. We then compared the results obtained using the raw data to those obtained using the TSTs. Using both empirical and simulated time series, we also quantified the influence of TSTs on time series and population synchrony levels and tested whether this influence depended on the features of the raw time series.

Evidence for a Moran effect

Using the raw data, we found that population synchrony, though generally significant, was weak for all 34 fish species found in French rivers. Such weak patterns of population synchrony have already been shown in birds (Paradis et al. 2000), fish (Grenouillet et al. 2001) and amphibians (Trenham et al. 2003), and can be explained by several factors. For instance, most populations of the same species did not have the same density-dependent structure, (which violate Moran's assumption of identical density-dependent dynamics) and can explain the low levels of synchrony observed between populations (Hugueny 2006). Chaotic (Kendall et al. 2000) or non-linear (Benton et al. 2001) population dynamics can also reduce population synchrony, and we cannot exclude the possibility that some of the populations studied here may have had such dynamics. Moreover, Grenouillet et al. (2001) have shown that for age-structured species the different age classes can be governed by different processes (density dependent vs. density independent), which reduces synchrony at the population level. Finally, the presence of measurement errors in population time series has been shown to biase downward synchrony levels (Santin-Janin et al. 2014).

For most of the species we found a negative relationship between population synchrony and the Euclidean distance between sites, which is consistent with previous studies. Such a relationship can be explained by dispersal (Ranta et al. 1995), as well as by the Moran effect (Koenig 2002). However, given that dispersal between catchments is unlikely for fish, and that some species were synchronous across catchments, fish population synchrony could partly be attributed to the Moran effect. Moreover, temperatures were synchronous over scales comparable to the scale of synchrony found for some species, thus reinforcing the

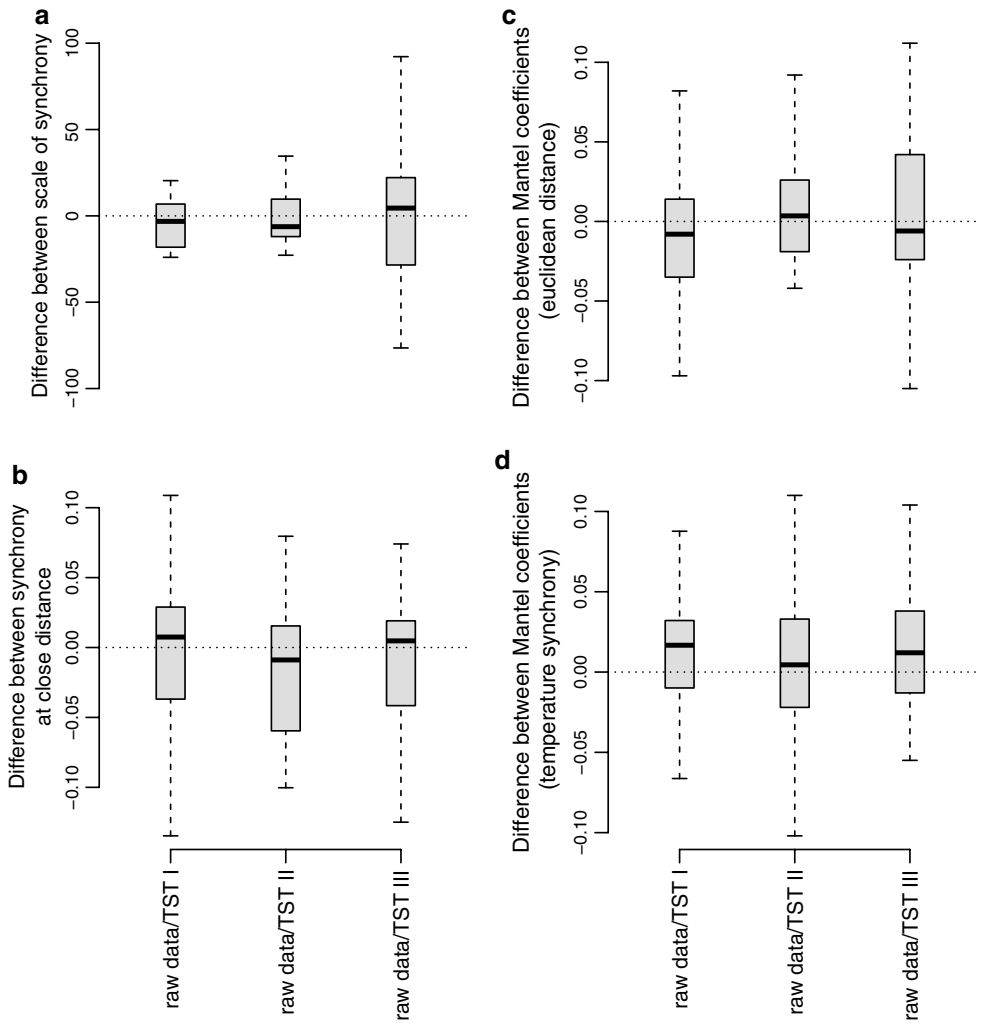

Fig. 5 Difference between **a** the scale of synchrony estimated using the raw data and the scales estimated using TSTs, **b** the synchrony at short distances estimated using raw data and the synchrony estimated using the TSTs, **c** the relationships between population synchrony and the Euclidean distance estimated using raw data and the relationships estimated using TSTs and **d** the relationships between population synchrony and temperature synchrony estimated using raw data and the relationships estimated using TSTs ($n = 34$). The *horizontal dotted line* indicates the absence of difference between the results obtained using the raw data and those obtained with the TSTs

Moran effect hypothesis. Further support for climate-driven population synchrony was provided by the significant relationship between population synchrony and temperature synchrony. Nevertheless, as this relationship did not hold for all the species displaying significant synchrony, other climatic factors (e.g., rainfall) may be involved in both fish population dynamics (Lobon-Cervia 2008) and synchrony (Cattanéo et al. 2003).

Nonetheless, we found that removing temporal autocorrelation due to intrinsic population dynamics (prewhitening procedure) reduced population synchrony levels to a greater extent than removing the long-term trend (detrending procedure), suggesting a higher contribution of local processes to population synchrony than regional ones (Bjørnstad et al. 1999). This contrasts with the fact that the number of time series presenting significant long-term trends was more than two times higher compared to those presenting significant temporal autocorrelation. Such difference between the detrending and the prewhitening procedure can be explained by a high uncertainty in the estimation of the long-term trend coefficient relative to the density-dependent coefficient. Indeed, simulated time series revealed that the efficiency of the stock-recruitment Ricker model to estimate long-term trend was low (Fig. S2a) which contrasted with its ability to estimate density dependence (Fig. S2b). This model has been widely used in synchrony studies (e.g., Myers et al. 1997; Cattadori et al. 2000) and its choice here was motivated by the high proportion of time series (>80 %) presenting a significant negative relationship between $\log(N_{t+1}/N_t)$ and N_t. Such a

low propensity of this model to estimate long-term trends in abundance time series raises concerns about its ability to remove this component.

Influences of TSTs

Removing trend and/or temporal autocorrelation was not always efficient as some time series still presented significant signals once TSTs had been applied. This could be explained by the method used to remove the component of interest. For instance, several competing methods exist to remove the long-term trend (Buonaccorsi et al. 2001) and we cannot exclude the possibility that another method would have done a better job. However, considering the number of time series analyzed in this study (i.e., 3131), a unique method is not expected to be efficient in all cases. We also found that removing one component in the time series without affecting the other is not straightforward. For instance, if removing temporal autocorrelation also removes some part of the long-term trend then, one could wrongly conclude that populations are not influenced by a large-scale climatic factor, which could have dramatic consequences in a conservation perspective as population synchrony is, to some extent, related to species extinction risk (Hanski and Woiwod 1993).

We expected that time series with a low long-term trend would be weakly affected by TST I, as would time series that displayed low density dependence and TST II. However, although we found the expected pattern for the long-term trend and TST I in both empirical and simulated time series, we found that time series that displayed low density dependence were affected by TSTs to a greater extent than time series displaying high density dependence, which contradicts the result obtained from simulated time series (i.e., for which we found the expected pattern). Estimating density dependence in population time series has always proved to be challenging (Dennis et al. 2006), notably because it depends on several time series features (Clark and Bjørnstad 2004). For instance, even though the sampling procedure is considered efficient (as is the case in this study), population time series usually present census errors (Freckleton et al. 2006), which strongly influence the strength and evidence for density dependence (Knape and De Valpine 2012). To take these errors into account, state-space models have been used, and studies have shown that they usually provide less biased estimates of density dependence (e.g., Freckleton et al. 2006). However, state-space models could present identifiability issues when process and error variance are both unknown, which could lead to large variances in parameter estimates (Knape 2008). This is particularly true when the time series are short. Other features, such as the number of missing values in the time series or the variance around the mean of population censuses, could bias the estimation of density dependence (Brook and Bradshaw 2006), and could explain why time series with low density dependence were modified to a greater extent than others. Overall, this complexity might explain why population synchrony levels measured on the empirical data set were modified to a greater extent when both time series did not present evidence of temporal autocorrelation.

On average, we found that detrending and/or prewhitening decreased the measures of synchrony, which was consistent with the findings of previous studies. For instance, it has been shown that overall synchrony tends to be higher when measured using raw data than when measured using detrended data (Batchelder et al. 2012). This decrease after detrending has classically been interpreted as evidence for a Moran effect, and it can be explained if a long-term trend is an important and shared source of variation in the data (Pyper et al. 1999). Similarly, temporal autocorrelation in a time series is known to inflate cross-correlation coefficients (Pyper and Peterman 1998; Pyper et al. 1999). Consequently, eliminating temporal autocorrelation can be expected to reduce the population synchrony and, therefore, the overall species synchrony. However, Cheal et al. (2007), using detrended time series of coral reef fish populations, found that eliminating temporal autocorrelation did not change their measures of synchrony. Likewise, even though we observed an overall decrease in fish population synchrony, no significant influence of prewhitening was observed. Nevertheless, we found that, depending on the species considered, TSTs can reverse conclusions on synchrony significance. For instance, once temporal autocorrelation had been eliminated, overall synchrony was no longer significant for *Alburnoides bipunctatus,* while it had become significant for *Alburnus alburnus* (Tables S4).

When considering the determinants of population synchrony (i.e., distance between populations and temperature synchrony), we also found that TSTs could lead to opposite conclusions depending on the species considered. For instance, once temporal autocorrelation has been removed, we found that the main driver of population synchrony for *Salmo trutta* was temperature synchrony, whereas the distance between populations was the main driver when the raw data were used. Likewise, on a study involving 60 bird species, Paradis et al. (2000) found that detrending did not influence the relationship between synchrony and distance for 34 of them, whereas the relationship was strengthened for 12, and weakened for 14. Thus, depending on the species considered and the TSTs applied to the time series, the conclusions could be very different, which could have major implications for defining specific management plans.

Prospects for the future and guidelines for further research

For several species, we found some evidence of an effect of correlated environmental noise (i.e., a Moran effect) on population dynamics as: (1) populations were synchronous on a large spatial scale and across catchments, (2) population synchrony was related to temperature synchrony, and (3) eliminating the long-term trend in time series reduced the overall synchrony of the species. However, although temperature appeared to be a plausible factor driving population synchrony for some species, other factors are also likely to be involved (e.g., the frequency and intensity of river discharges). Moreover, we only considered the influence of temperature during the warmest month of the year, which could have biased our conclusions. Indeed, other climatic descriptors (e.g., the temperatures during the coldest month) could have affected the observed relationship between population synchrony and temperature synchrony. Further studies are clearly needed to add to our knowledge about the factors that drive fish population synchrony in France.

In some cases, TSTs can be very helpful for quantifying the influence of various processes on population dynamics. For instance, eliminating a long-term trend that is due to common climatic influences makes sense if all the populations are either increasing or decreasing, because it makes it possible to focus on local rather than global processes (Buonaccorsi et al. 2001). However, removing long-term trends for other purposes is more questionable. For instance, a trend can be caused by local processes (e.g., local pollution) and its removal could make it more likely that we could detect an apparent correlation between two time series when in fact there was none. Likewise, it is common to remove long-term trends because their presence could give "spurious" correlations (inflation of CCCs) whereas their removal could eliminate important information that would reduce our ability to detect a real causal relationship (Brown et al. 2011). Another problem with TSTs is that the different components in the time series are not independent of each other. For example, removing the temporal autocorrelation in the time series could affect the detection (as shown in this study) and the estimation of the magnitude (Hamed and Rao 1998) of the long-term trend and vice versa. Therefore, if two series do have a causal relationship that manifests itself, for example, as a trend in each series, this could be masked by the prewhitening procedure. Thus, a serious problem with using TSTs is that it is difficult to know exactly what has been eliminated, and so what has been measured. This problem is further complicated by the fact that the influence of TSTs depends on the features of the time series. Thus, the use of TSTs should be subject to great care and should depend on the features of the time series. As a first step, we therefore recommend that the features of the time series should be estimated, and TSTs used in the light of these estimations. For this purpose, we suggest using population dynamic models (e.g., Ricker or Gompertz population models, depending on the data), as they make it possible to estimate both the density dependence and the long-term trend. Nonetheless, the efficiency of the stock recruitment Ricker model to estimate long-term trends has raised concerns and further studies are needed to determine whether it is also the case for other statistical models. If one wants to focus on local processes, we recommend removing the long-term trend only if all the time series are either increasing or decreasing (Buonaccorsi et al. 2001). When studying global processes, the data should not be detrended. If the time series do not provide any evidence of density dependence (i.e., of lag-one temporal autocorrelation), we recommend not removing temporal autocorrelation, as this transformation strongly modifies the time series and therefore any subsequent analyses (e.g., estimation of population synchrony). If the time series display density dependence, we propose using population dynamic models to remove temporal autocorrelation, because they can be used to account for more complex population dynamics than simple linear autoregressive models (e.g., by integrating non-linear density dependence). One interesting possibility for this purpose would be to use state-space models to account for observation errors in population censuses.

When using TSTs, we advocate always checking: (1) whether the component of interest has really been eliminated, and (2) whether the other component has not been affected. Finally, because TSTs can lead to differing (and sometimes even opposite) results depending on the species considered, we recommend using different TSTs, and interpreting the results in the light of the features of the time series, taking all the transformations into account.

We believe that analyzing time series in this way could improve our understanding of the processes that drive population synchrony by quantifying the relative importance of long-term trends and temporal autocorrelation.

Author contribution statement M. C. and G. G. formulated the idea; M. C., G. G. and J. B. F. developed the methodology; M. C. conducted the analyses and wrote the manuscript; G. G. and P. L. supervised the work.

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