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Time series analysis of interrupted long-term data set (1961-1991) of zooplankton abundance in Gulf of Maine (northern Atlantic, USA)

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Abstract − The main interannual and seasonal signals have been extracted from a multi-decadal data set of zooplankton collected with the Continuous Plankton Recorder in the Gulf of Maine, from January 1961 to December 1991. The monthly abundances of seven species or genera of copepods representing the dominant biomass in the area were considered. The presence of a large consecutive gap (35 months) prevented the use of statistical methods for the prediction of missing data. The eigen-vector filtering (EVF) method was then used on the original time series, while retaining the missing values. For each zooplankton taxon, two principal modes of variability (F_1 and F_2) were extracted, representing the interannual and seasonal variations, respectively. Results of EVF allowed the classification of the different genera or species, according to their main type of variability, into taxa 'interannually dominated' (*C. finmarchicus*, *Metridia lucens*, *Oithona* spp.), 'seasonally dominated' (*Centropages typicus*), and taxa characterized by both 'interannual and seasonal variation' (*Pseudocalanus* spp., *Temora longicornis*, *Acartia* spp.). A comparison between the interannual trends of 'interannually dominated species' and sea surface temperature (SST) indicated that all the species were more or less correlated with this important environmental factor. In particular, a strong negative correlation was found between *C. finmarchicus* and SST at a lag of about 0 months, showing that lower values of SST correspond to higher abundances of *Calanus finmarchicus* at this latitude. © 2001 Ifremer/CNRS/IRD/Éditions scientifiques et médicales Elsevier SAS

Résumé − Analyse de séries temporelles à long terme (1961–1991) interrompues sur le zooplancton du golfe du Maine (Atlantique Nord). La variabilité temporelle d'une série zooplanctonique a été estimée dans le golfe du Maine (de janvier 1961 à décembre 1991). Les prélèvements ont été réalisés par l'échantillonneur de type CPR (*Continuous Plankton Recorder*). Les données représentent l'abondance mensuelle moyenne de sept espèces de copépodes, ou catégories, lesquelles correspondent à la plus forte biomasse planctonique du golfe. Une importante lacune dans les enregistrements (35 mois consécutifs sans observations) dénie la possibilité de prédire statistiquement ces données manquantes. C'est pourquoi la méthode de décomposition des séries correspondant au filtrage par les vecteurs propres a été utilisée en conservant les données manquantes. Par la méthode de filtration des vecteurs propres, pour chaque taxon, deux séries F_1 et F_2 ont été décelées qui correspondent respectivement à deux échelles de variations, interannuelle et saisonnière. À partir de ces évolutions, une classification des taxons a été obtenue : *Calanus finmarchicus*, *Metridia lucens*, *Oithona* spp. sont principalement marqués par des phénomènes interannuels ; *Centropages typicus* au contraire ne répond qu'à l'échelle saisonnière. Enfin *Pseudocalanus* spp., *Temora longicornis*,

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Acartia spp. réagissent aux deux échelles de variation F_1 et F_2. Une corrélation a été trouvée entre la tendance générale F_1 des espèces à dominance interannuelle et la température de surface de la mer. En particulier une corrélation négative très forte apparaît entre *C. finmarchicus* et la température de surface de la mer, sans prendre en compte un décalage temporel ce qui signifie qu'à cette latitude, ce copépode est d'autant plus abondant que les eaux sont froides.

***Calanus finmarchicus* / Gulf of Maine / missing data / time series analysis / zooplankton**

***Calanus finmarchicus* / golfe du Maine / données manquantes / séries temporelles / zooplancton**

1. INTRODUCTION

The Gulf of Maine is an area of intense productivity (Sherman et al., 1988). Near the coast, hydrography is mainly influenced by tidal currents, while in the central part of this region circulation is due to a large cyclonic gyre that tends to be stronger in the spring (Bigelow, 1927; Bumpus and Lauzier, 1965). Tidal mixing and upwelling from the Jordan basin has implications for primary and secondary production in the western part of the Gulf of Maine (Townsend et al., 1987).

Bigelow (1926) first described the zooplankton community of the Gulf of Maine. However, systematic monitoring programs started quite later in the 1960s with the Continuous Plankton Recorder (CPR) (Hardy, 1939) survey, and in the 1970s with the Marine Resources Monitoring, Assessment and Prediction (MARMAP) program (Sherman, 1980). These two programs contributed to identifying about 390 zooplanktonic taxa over the continental shelf. Among these, twelve copepods account for 85 % of the total biomass. Seventy-five percent of the twelve taxa is due to *Calanus finmarchicus*, *Pseudocalanus* spp. and *Centropages typicus* (Sherman et al., 1988).

Within the US GLOBEC program, Georges bank, a region with hydrographic properties related to those of the Gulf of Maine was chosen as a target study area, as one of the most productive in the USA, and both *Calanus finmarchicus* and *Pseudocalanus* spp. were selected as target species. The median annual cycles of *Calanus finmarchicus*, *Pseudocalanus* spp., *Centropages typicus* and *Metridia lucens* on Georges bank over the period 1977–1981 are shown by Sherman et al. (1987). Meise and O'Reilly (1996) described the large-scale spatial and seasonal patterns of *Calanus finmarchicus* in the Gulf of Maine and Georges bank over the period 1977 and 1987. The variation in the seasonal cycle of the same species over a 30-year period, and its relationship with the North Atlantic oscillation (NAO) was described by Conversi et al. (2001).

The precious information contained in the Gulf of Maine time series is however difficult to analyze because of several large gaps in data coverage in the first half of the series. Indeed, the analyses so far published on this series (Jossi and Goulet, 1993; Sherman et al., 1998) utilize yearly averaged data. The aim of the present study is to characterize, for seven of the most abundant species/genera of copepods in the Gulf of Maine, the interannual trends, by extracting without simulating missing data or resorting to annual averages. For this reason we have applied the eigen-vector filtering (EVF) method (Ibanez and Etienne, 1992) on monthly abundances of *Calanus finmarchicus*, *Pseudocalanus* spp., *Centropages typicus*, *Temora longicornis*, *Acartia* spp., *Metridia lucens* and *Oithona* spp. This is the first usage of this method on real data with missing values. The comparisons of the principal trends of each taxonomic category permitted us to distinguish species mostly characterized by a seasonal cycle and species with a strong interannual component. The latter were compared with long-term fluctuations of surface water temperature (SST).

2. MATERIALS AND METHODS

2.1. Data

Zooplankton data were obtained with the Continuous Plankton Recorder sampler (270-µm mesh), in the framework of US CPR program (Jossi and Goulet, 1993), by horizontal tows at 10 m depth, on transect across the Gulf of Maine (*figure 1*). Sampling was made with monthly frequency from 1961, but during the first part of

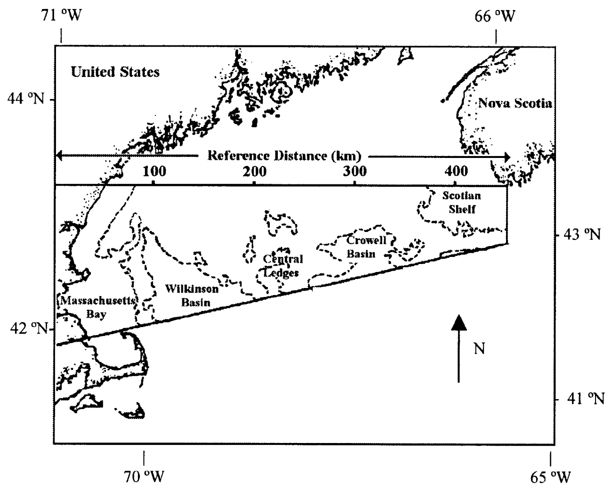

Figure 1. Gulf of Maine. Continuous Plankton Recorder (CPR) sampling from 1961 to 1991.

the series there were many missing months, and no sampling at all between 1974 and 1977. The sampling protocol, identical for the UK and US collections, is described by Colebrook (1975) and Warner and Hays (1994).

For this work, the most abundant species or genera of copepods in the area were studied: *Calanus finmarchicus* (Copepodites V and VI), *Pseudocalanus* spp. (CVI), *Centropages typicus* (unstaged), *Temora longicornis* (unstaged), *Acartia* spp. (unstaged), *Metridia lucens* (CV-CVI) and *Oithona* spp. (CIV-CVI). 'Total copepod' abundance, which is the sum of all 'small' copepods, below 2 mm, was also used. This category includes all the groups mentioned above except for *Calanus finmarchicus* and *Metrida lucens*, which are larger (Warner and Hays, 1994). The central part of the Gulf of Maine transect (291 km, between 69°50' W and 66°29' W) was chosen because it provided higher temporal coverage than the other parts of the transect, and because it was less influenced by the shelf and estuarine environments. Previous cluster analyses by Jossi and Goulet (unpublished) have shown that the above zooplankton species are homogenous within this spatial section. Zooplankton abundances included day and night samples combined, except for *Metridia lucens* for which just night records were retained. Log-transformed zooplankton abundances ($\log_{10}$ ind·100 m^{-3}) for each month were averaged along this subset of the transect so as to give a unique, pooled spatial value (henceforth called 'Gulf of Maine').

Sea surface temperature (SST) for the Gulf of Maine region was derived from the Comprehensive Ocean-Atmosphere Data Set (COADS).

2.2. Numerical Analyses

2.2.1. Biological variables

2.2.1.1. Step 1. Zooplankton data set: compression of the series to avoid missing values

The zooplankton data set was composed of monthly abundances during the period 1961–1991 (372 total observations) for the eight descriptors (seven taxonomic groups and total copepods), with 157 missing months, corresponding to 42 % of the total values for all the groups except for *Acartia* spp. and *Metridia lucens*, which had a greater number of missing values, respectively 43 and 50 %. The missing months were distributed mostly in the first part of the series, until the end of the 1970s. For each taxonomic group a new series, with n^* observations in it (where $n^* = n -$ missing values), was calculated by eliminating the gaps and compressing the series (*figure 2*).

2.2.1.2. Step 2. Extraction of the interannual trends by eigen-vector filtering (EVF)

In this work, 'trend' means the main tendencies of any shape over the decades of the series (e.g. interannual and annual trends).

The eigen-vector filtering (EVF) method (PASSTEC package, Ibanez and Etienne, 1998), proposed by Colebrook (1978) and used in benthic ecology by Ibanez and Dauvin (1988) and Ibanez (1991), was utilized in order to extract the main trends in each taxonomic group (*figure 2*).

EVF, using principal component analysis (PCA), acts as a weighted moving average. Its main property is the capacity of eliminating all the frequency bands equal or higher than the annual cycle. Compared to other well-known techniques, eigen-vector filtering has the following advantages: no observations are lost at the boundaries of the series, and no arbitrary choice is required regarding the shape of the trend.

With EVF the following steps are implemented on each variable or series (appendix 1):

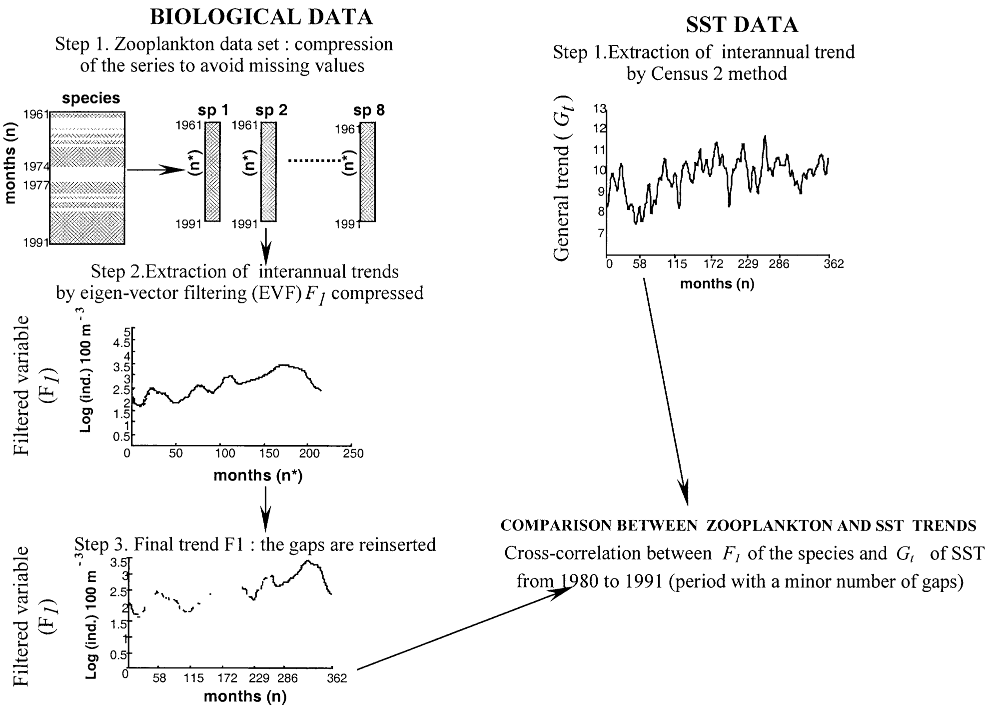

Figure 2. Different steps of the numerical procedure applied to the zooplankton and to the sea surface temperature (SST) data sets in the Gulf of Maine from 1961 to 1991.

– Taking a series x_t, t varying between 1 and N, shifting in time x_t, a matrix X composed of r shifted series is constructed. Each r column of X has N–r+1 values, i.e. the first column has t = 1,...,N–r+1 values, the second one t = 2,...,N-r+2 values, ..., the last column (the rth) has t = r,...,N terms. The judicious choice of the number of shifted series, r, may be estimated as the lag at which the autocorrelation function of x_t goes to zero (Takens, 1981; Ibanez and Etienne, 1992).

– The r eigenvalues and eigenvectors of the $r \times r$ covariance matrix (thus the autocovariance matrix) are extracted and the principal components are computed. The first principal component (C_1) from the autocovariance matrix is associated with the highest variance of the series x_t. The second principal component, C_2, corresponds to the main signal after removing C_1, and so on, with the successive components reflecting less and less variability, indicating by their corresponding row eigenvalues. In most cases (see later), C_1 will represent the interannual trend of the series and C_2 the seasonal cycle.

In order to extract the major trends or filtered variables F_i, the matrix $\hat{X}$ is predicted using the corresponding row eigenvector U_i from the autocovariance matrix, and principal component column vector C_i:

$$\hat{X}_i = C_i\, U_i' \text{ where } i = 1,2,...,r.$$

– To build a unique series, F_i requires averaging the values of $\hat{X}$. Like in table X, in table $\hat{X}$ there are (n–2r) observations which are repeated r times and then the others that are repeated (r–1),(r–2),…,1 time, according to the shift in time done between the columns.

However, Ibanez and Etienne (1992) showed that F_i could be directly estimated as soon as U_i is obtained. F_i may be calculated by a weighted moving average (WMA) on the original series, x_t of order r–1, containing 2(r–1)+1 terms. For each principal axis F_i the ith weight is a linear combination of the elements of corresponding eigenvectors U_i (see appendix 2 for details).

Although the principal components are independent, the Fs may present significant correlations because of the embedded moving averages. This property is however more ecologically meaningful than complete independence, since for marine species very often the amplitude of the seasonal variation is positively linked to the amplitude of the interannual variation (Ibanez et al., 1993).

The EVF method was applied to each zooplanktonic series of monthly observations in the Gulf of Maine, after compressing the original data to eliminate missing values. The autocorrelation function for each species went to 0 (with 95 % confidence) at around 7 months. Thus *r* was chosen for all species as equal to 7, considering that it gives a weighted moving average of thirteen successive observations, which is most appropriate when dealing with planktonic species since they all have some degree of autocorrelation at the annual scale. Then the major trends of the seven taxonomic groups and of the total copepods were extracted.

Harmonic analysis (Kendall, 1976; Legendre and Legendre, 1998) was performed on the filtered variables F_1 and F_2 of each taxa calculated during the period May 1982–April 1991 (until December 1990 for *Acartia* spp.), to verify their periodicities. This part of the time series was chosen because it contained just a few (< 4 %) non-consecutive missing values allowing their estimation by interpolation. The significance of each harmonic was tested according to the associated percentage of variance (Anderson, 1971). Since an accurate test of significance would require the stationary distribution of F_1 and F_2, this procedure was carried out only to have an indication of the periodicity of filtered variables.

2.2.1.3. Step 3. Reconstruction of the actual F_1 and F_2 and classification of the trends

After the extraction of F_1 and F_2, the gaps are inserted again in the filtered variables, so that they are restored to original length. Taking into account the order of the weighted moving average, the *r*–1 values before and after each gap are biased, thus for $r = 7$, six values are more or less biased at each side of gap. At a point P_1 just at the boundary of a gap, the smoothed estimate of P takes into account seven of its adjacent values and six values on the other side of the gap. These points at the boundaries are the most biased. Then, the first adjacent point of P_1, P_2, is estimated from eight adjacent values and five values from the other side of the gap. The next point P_3 with nine correct values and four incorrect, etc. Finally, when calculating P_7 the estimation is unbiased.

F_1 and F_2 can outline three different characteristic situations, considering the difference (Δ) between the corresponding eigenvalues λ_1 and λ_2 (Ibanez, 1991; Souprayen et al., 1991; Ibanez et al., 1993):

– when Δ is very high (λ_1 is almost twice λ_2) and the correlation between F_1 and F_2 is low, only the year to year variation is important.

– when Δ is very low (less than 1/10) and the correlation between F_1 and F_2 is significant, the seasonal variation is dominant in the series.

– when Δ corresponds to an intermediate value, an interannual trend is certainly present but the seasonal variation is not negligible.

The difference (Δ) between the eigenvalues λ_1 and λ_2 was calculated for all seven taxonomic groups and it corresponds to the difference between the percentages of variance associated with the filtered variables F_1 and F_2. The seven genera or species (total copepods were omitted from this calculation as it was targeted toward genera or species) were classified, following the criteria explained above, into ‘interannual’, ‘seasonal’ and ‘interannual seasonal’ taxa (see *table I*). As the Δ average of the seven taxa is 8, this value was arbitrarily chosen as the threshold separating species with a dominant seasonal variation or an intermediate situation, from species with a dominant interannual trend. The latter were then chosen for comparison with environmental data.

Table I. Classification of the principal copepods of the Gulf of Maine, on the basis of the results of eigen-vector filtering (EVF). The columns F_1 and F_2 indicate the % of variance (also shown for total copepods) associated to the first two principal components extracted from the autocovariance matrix. The column code indicates three categories of species, having different type of variation: + + 0: species with a strong interannual cycle; + +: species with dominant seasonal cycle; + + +: species with interannual cycle and not negligible seasonal cycle. $R_{F1 \cdot F2}$ indicate the correlation between F_1 and F_2.

Type of variation	Species	F_1 (%)	F_2 (%)	Code	$R_{F1 \cdot F2}$
a) Interannually dominated					
	Calanus finmarchicus	34	21	+ + 0	0.30
	Metridia lucens	44	18	+ + 0	0.30
	Oithona spp.	44	18	+ + 0	0.28
b) Seasonally dominated					
	Centropages typicus	32	31	+ +	0.71
c) Interannual/seasonal species					
	Pseudocalanus spp.	34	26	+ + +	0.49
	Temora longicornis	30	19	+ + +	0.45
	Acartia spp.	27	20	+ + +	0.39
	Total copepods	34	26	+ + +	

2.2.2. Environmental variables

The Census 2 method (Shiskin and Eisenpress, 1957) was used on SST monthly data in order to remove the seasonality and to extract the interannual trend (Institut national de statistique, 1965; Béthoux et al., 1980; Fromentin and Ibanez, 1994). By means of successive moving averages, it displays a series of three components: the interannual trend, called 'general trend' G_t, the 'annual cycle' A_t, and the 'random component' I_t, which represents unusual events (*figure 2*). An important property of this method is that, by construction, the interannual and seasonal components present null values for the coherence function at the seasonal frequency. Census 2, more powerful for the decomposition of time series than the EVF, was chosen because of the regularity (no missing data) of the SST series, a necessary condition which prevented its use on our biological series.

Harmonic analysis was performed on the general trend, G_t, to compute its periodicity.

2.2.3. Comparison between biological and environmental variables

The classification method outlined above permitted distinguishing 'seasonally' and 'interannually' dominated taxa. One can reason that the latter are likely to be more easily influenced by large scale environmental changes. Hence the major trends (F_1) of *Calanus finmarchicus*, *Metridia lucens* and *Oithona* spp. (i.e. the three zooplanktonic group which were classified as 'interannually-dominated') were compared with the interannual trend of SST (G_t) in order to investigate the relationship between temperature, a proxy for large-scale environmental variations, and zooplankton variations. Taking into consideration the large number of missing values until the end of the 1970s, a cross-correlation was performed on a sub-series of 132 F_1 and C_t values, corresponding to the period January 1980–December 1991. The maximum lag chosen for the cross correlation was 30 months, in order to maintain a satisfactory number of degrees of freedom and a good estimation of the correlations coefficients.

3. RESULTS

The filtered variables F_1 and F_2 for the eight zooplanktonic categories are presented in *figure 3*, where the different species are ranked, according to the results of the classification of the trends shown in *table I*. The taxa *Calanus finmarchicus*, *Metridia lucens* and *Oithona* spp. (*figure 3a–c*) showed the highest interannual variability, taking into account the high difference between the eigenvalues λ_1 and λ_2 ($\Delta > 8$ %) and the low correlations between their filtered variables (*table I*). Harmonic analysis on the filtered variables of these taxa for the period 1982–1991 (*table II*) confirmed that F_1 represents the interannual component (from 36 to 54 % of variance associated to the $\propto$ period), showing a cycle of 54 months for *Metridia* and *Oithona*, while F_2 always represents the annual trend.

In the Gulf of Maine, *C. finmarchicus* is present year round with peaks between May and July (*figure 4a*). Considering F_1, which represented its interannual variability, this species showed from 1961 to 1991 an increasing trend, with about 3.5 log ind·100 m^{-3} more in 1987 (the year of maximum abundance) compared to 1963 (the lowest year). Because of the great number of missing data in the first part of the series, the interannual cycle of *M. lucens* has been studied over a shorter period, from 1979 to 1991. *Metridia*, which is mostly present in autumn (*figure 4b*), showed a decrease of around 2 log ind·100 m^{-3} from 1979/80 to 1984, maintained constant abundance until 1989 and thereafter increased again. The annual cycle of *Oithona* spp. from monthly averages of 1961–1991 (*figure 4c*) indicates that this copepod is generally less abundant from November to March, starts to increase in April and peaks in August and September. Considering the interannual trend (*figure 3c*), after 1963 *Oithona*'s abundances seemed to diminish, and a cycle of 11 years can be detected from 1979 to 1990.

Of all taxa, *Centropages typicus* is the only one that presents a dominant seasonal variability. F_1 and F_2 for this species, which has maximum abundance from August to November (*figure 4e*), are practically identical (*figure 3e*) and strongly correlated (*table I*), while harmonic analysis indicates that both F_1 and F_2 of *Centropages* represent a strong seasonal cycle (*table II*). On the other hand, *Pseudocalanus*, *Temora* and *Acartia* show both a strong annual variability and a non-negligible interannual cycle (intermediate Δ, $R_{F1 \cdot F2} > 0.35$ in *table I*). This pattern is also confirmed by the lower variance of $\propto$ period of F_1 for these taxa (between 16 and 25 %) with respect to 'interannually dominated species'. *Pseudocalanus* had two major peaks in 1979 and 1982 (*figure 3f*), while from 1982 onwards

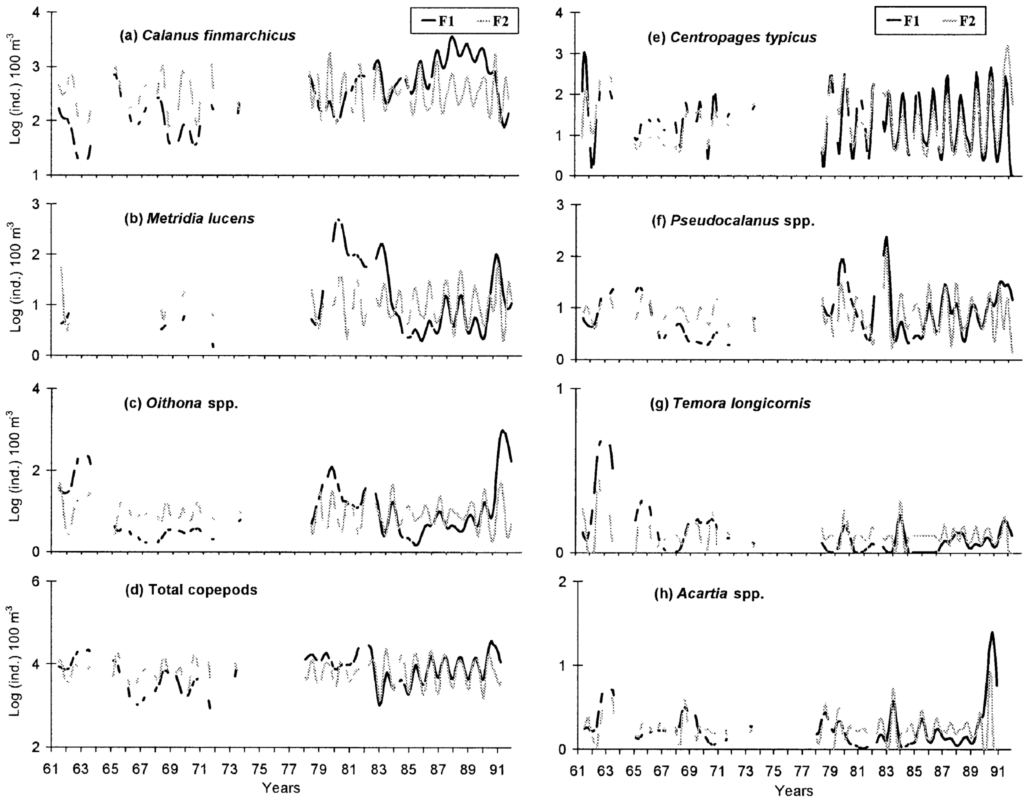

Figure 3. Gulf of Maine, 1961–1991. Filtered variables F_1 and F_2 obtained by eigen-vector filtering (EVF) for principal zooplanktonic species/genera and for total copepods. The species or genera are arranged according to the results of the classification of the trends, showed in *table I*. Note that scales are different.

showed an interannual cycle of 54 months (40 % of variance associated to this harmonic, *table II*). *Temora* and *Acartia* species had exceptional densities at the beginning and at the end of the time series (*figure 3g–h*), respectively. The annual periods of maximum abundance of these three taxa are indicated by the multi-year averages showed in *figure 4g–h*. The category 'total copepods', which does not include the species *C. finmarchicus* and *M. lucens*, show quite identical F_1 and F_2 (*figure 3d*).

Table II. Results of harmonic analysis on F_1 and F_2 of the principal copepods of the Gulf of Maine from May 1982 to April 1991 (* until December 1990 for *Acartia*). Significant harmonics and % of variance associated within each F_1 and F_2 are indicated. ∝ indicates the ∝ period representing variability associated to the general trend of the series. Periodicities having maximum variance are in bold.

	F_1		F_2	
	Significant harmonics (months)	% of associated variance	Significant harmonics (months)	% of associated variance
Calanus finmarchicus	∝	**54**	**12**	**52**
Metridia lucens	∝, 54	**36**, 29	13.5, **12**, 9.8	16, **34**, 13
Oithona spp.	∝, 54, 27	**40**, 26, 14	**12**	**60**
Temora longicornis	∝, 54, **21.6**, 18	16, 15, **23**, 18	**12**, 10.8, 8.9	**25**, 17, 18
Acartia spp.*	∝, 54, 20.8	**25**, 24, 18	**11.6**, 10.4, 9.5	**29**, 16, 18
Pseudocalanus spp.	∝, **54**, 12	20, **40**, 16	**12**, 7.2	**49**, 14
Centropages typicus	**12**	**84**	∝, 54, **12**	21, 14, **43**

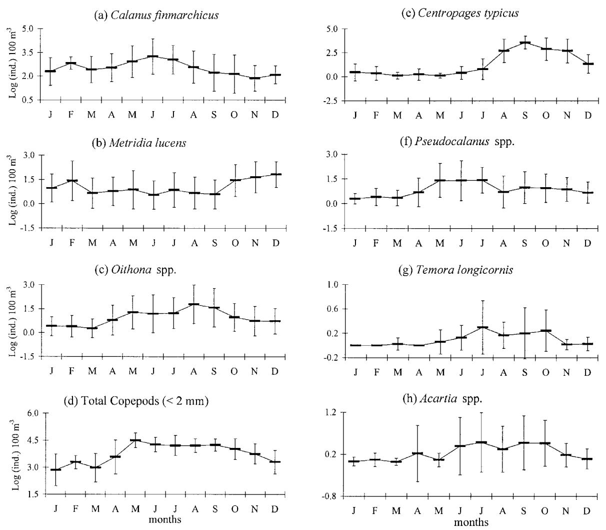

Figure 4. Gulf of Maine, 1961–1991. Thirty-year averages of each month ($\log_{10}$ ind·100 m^{-3}) and standard deviations of principal zooplanktonic species/genera and of total copepods. Note that scales are different.

The results of the classification of the principal trends are consistent with what is visible in the monthly abundance raw data ($\log_{10}$ ind·100 m^{-3}) per year (*figure 5*). For example, *C. typicus* (*figure 5e*) repeats the same pattern of high abundance over the period August–November and low abundance over the period March–May over time, without major changes from year to year. *C. finmarchicus* (*figure 5a*), on the other hand, shows an interannual variation, in addition to the seasonal variability, with lower densities in the first half of the series than in the second half (a linear, increasing trend already identified by Jossi and Goulet, 1993, and further discussed by Conversi et al., 2001). Analogously, the increasing of F_1 of *M. lucens* corresponds to the increasing abundance of this species between 1980 and 1990 (*figure 5b*). Within the interannual/seasonal taxa, *Acartia* spp. had two exceptional maxima of monthly abundance, at the end of the time series (*figure 5h*).

Sea surface temperature (SST) in the Gulf of Maine followed a seasonal cycle with minimum of around 4 °C in February-March and maximum of 16–17 °C in August-September. Harmonic analysis was performed on the interannual trend, G_t, extracted with the Census 2 method (*figure 6*), indicating a minor cycle of around 3–3.5 years and two major cycles of 15.5 and 30 years. G_t showed a decreasing trend from 1961 to 1965, an increasing trend from the mid-1960s to 1980, and a minor oscillation during the last 10 years of the series.

The interannual trend of SST, G_t was compared to F_1 of the zooplanktonic species with a strong interannual variability (*figure 7*). A cross-correlation was performed between these filtered variables during the period January 1980–December 1991 (*figure 8*). To distinguish the most important correlations between zooplankton and SST, only values with $P \leq 1\,\%$ level were retained, although the variables represented filtered series. The results of this analysis (*figure 8*) showed that a strong negative correlation exists between long-term variations of *Calanus finmarchicus* and sea surface temperature at a lag of about 0 months, meaning that low values of SST correspond to high abundances of the *Calanus* species. However, a positive correlation seems to be at a lag of 2.5 years, with temperature preceding *C. finmarchicus*, suggesting that the sign of correlation may change depending on the temporal scale investigated. At the same lag, *Oithona* spp. seems to show instead a significant negative correlation with SST, meaning that higher temperature proceeds 2.5 years lower densities of this copepod. High abundances of both *Oithona* spp. and *Metridia lucens* seem to precede by 2.5 years high values of SST (see positive correlation at lag of 30 months). Such correlations are meaningless.

4. DISCUSSION

A major problem with biological decadal time series is that often, for economical or logistic constraints, there are suspensions in the program, which result in gaps in the time series. Several statistical analyses require series without gaps, and therefore several methods have been devised (e.g. splines functions: Lancaster and Salkauskas, 1986; area interpolation: Fox and Brown, 1965; principal component analysis: Jolliffe, 1986) to predict the missing data. However, the original information is modified by the insertion of simulated data. The CPR time series in the Gulf of Maine is a particularly difficult case because it contains a large gap (35 consecutive months) that prevents the simulation of missing data. Because of this, all previous studies have used annually averaged data (Jossi and Goulet, 1993; Conversi et al., 2001) thus loosing the monthly information. With this work, we have used a different approach, that of extracting statistically reproducible trends while retaining the missing data, utilizing the EVF method. This way we

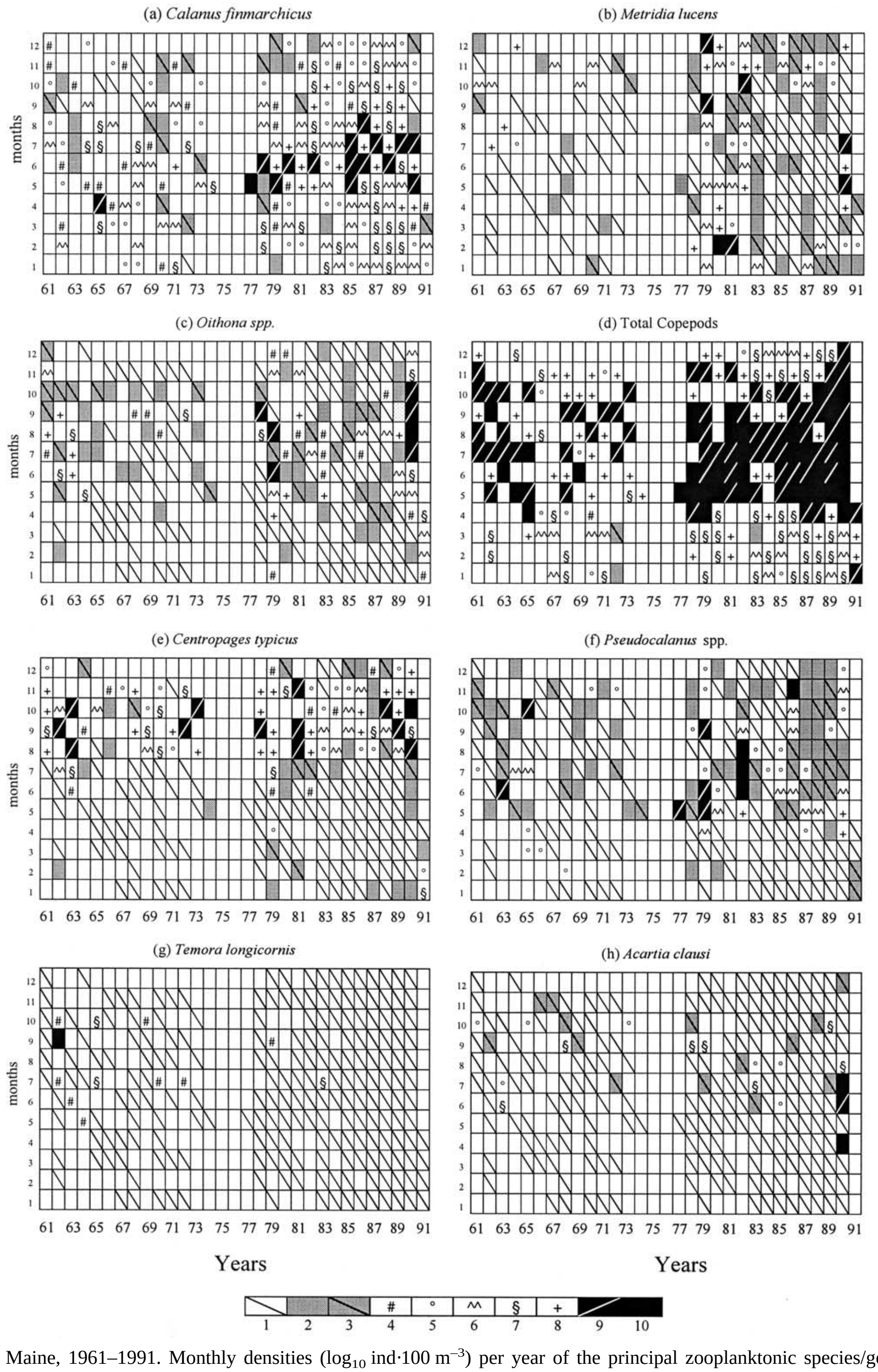

Figure 5. Gulf of Maine, 1961–1991. Monthly densities ($\log_{10}$ ind·100 m^{-3}) per year of the principal zooplanktonic species/genera and of total copepods. The values are expressed as classes of abundance, which are detailed as follows : 1: 0–0.5; 2: 0.5–1; 3: 1–1.5; 4: 1.5–2; 5: 2–2.5; 6: 2.5–3; 7: 3–3.5; 8: 3.5–4; 9: 4–4.5; 10: 4.5–5.5.

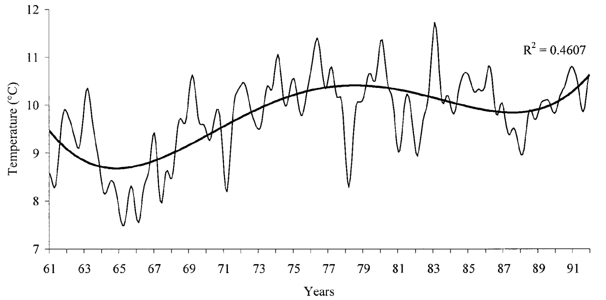

Figure 6. Gulf of Maine, 1961–1991. Interannual trend G_t for the SST obtained by Census 2 method. Fourth-order polynomial fit is superimposed and the correlation coefficient R^2 indicated.

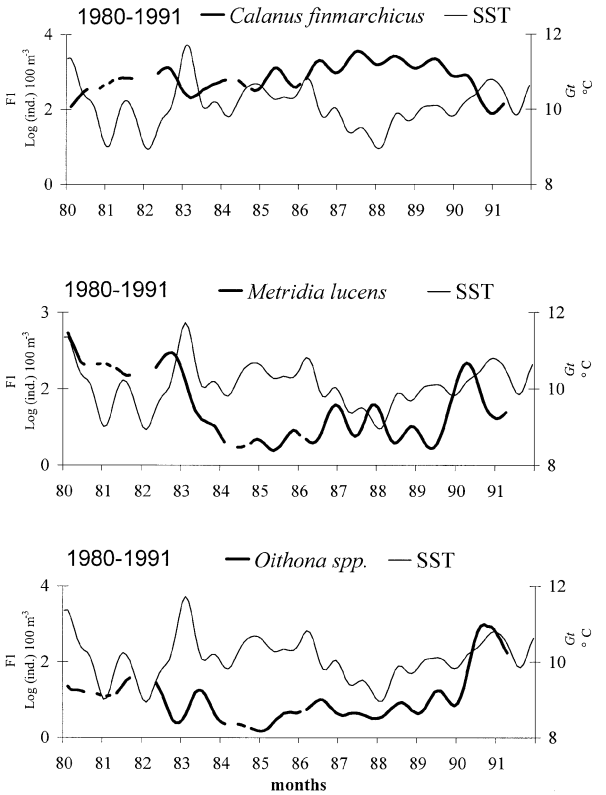

Figure 7. Gulf of Maine, 1980–1991. Interannual trend for the SST, G_t, compared with interannual trends F_1 of the principal zooplanktonic species or genera, which showed the greater variations at a long time scale. Note the scales are different.

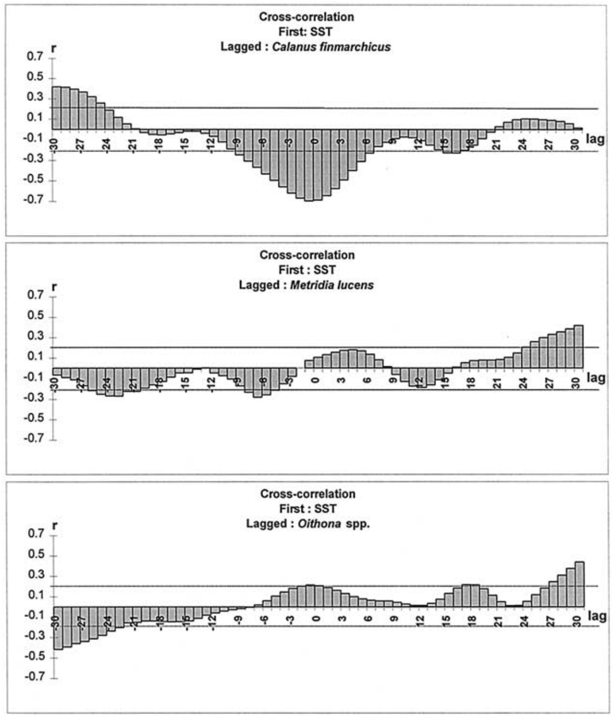

Figure 8. Gulf of Maine, 1980–1991. Cross-correlation function between the interannual trend of SST (G_t) and the interannual trend (F_1) of the most interannual zooplanktonic taxa. Straight lines indicate the 99 % confidence interval.

have been able to use the full information contained in the monthly sampling without resorting to annually averaged data.

The trends F_1 and F_2 extracted with the EVF represent the major modes of variability of the zooplanktonic species under study, which are the interannual and annual variability, as shown by harmonic analysis of the F_i (*table II*) and comparisons of such patterns between taxa and environmental variables can be made.

The taxa studied here are the numerically dominant zooplankton species in the Gulf of Maine. Thus, changes in their abundance can have far-ranging consequences in the trophic chain. The Gulf of Maine area, together with the Gulf of St. Lawrence, seems to be a source of *Calanus finmarchicus* (Meise and O'Reilly, 1996; Bucklin and Kocher, 1996) for the highly productive Georges bank area, an area which has been selected as a GLOBEC study area for its importance and strategic location (Wiebe et al., 2001).

EVF allows the classification of zooplanktonic species according to their main type of variability, indicating *Calanus finmarchicus*, *Metridia lucens* and *Oithona* spp. as 'interannually dominated' taxa, *Centropages typicus* as 'seasonally dominated' taxa and *Pseudocalanus* spp., *Temora longicornis*, *Acartia* spp. as intermediate between the two. This classification can be helpful to identify species whose major variance mode is interannual which are potential indicators of environmental and in particular climatic variations.

This classification is consistent with what is shown by the raw data (*figure 5*), and for some species such as *C. finmarchicus*, with the finding of other authors in the same area (Jossi and Goulet, 1993). On the other hand, the interannual variation of *Oithona* spp. and *Metridia lucens* shown by our analyses (*figure 3b, c*; *table I*) could not be detected by the linear method used by Jossi and Goulet (1993). Anyway, the decline in abundance of *M. lucens* after 1983, was indicated by Sherman et al. (1998) from MARMAP data series.

The species whose variance is mostly in the interannual range (*Calanus finmarchicus*, *Metridia lucens* and *Oithona* spp.) are of special interest because they may be particularly sensitive to environmental and climatic changes. One of these species, *C. finmarchicus*, is a major species in the whole northern Atlantic as well as a GLOBEC target species. The results (*figure 8*) of a preliminary comparison with an environmental variable, SST, indicate that for these three species, and in particular for *C. finmarchicus*, temperature can be an important factor, and can possibly be used for prediction. The high values at the edge of the cross-correlation chosen interval (*figure 8*) may indicate that the scale of the interannual relationship is longer than what we can detect with the given data. The relationship between species and temperature can be different at different temporal scales (as in the case of *C. finmarchicus*). *Calanus finmarchicus* shows a strong negative correlation with SST at about lag 0 month, which suggests that in this area, which is on the southern fringe of *C. finmarchicus*' distribution, a small change in the SST may have immediate effects (of opposite sign) on its abundance. Other authors already indicated *Calanus* as a cold water species, in this same area (Meise and O'Reilly, 1996) and in the North Sea (Fromentin and Planque, 1996; Reid et al., 1998), but they also pointed out that this correlation is more likely due to the area hydrography than to a direct temperature effect. On the other hand, on a longer temporal scale (30 months or 2.5 years), there seems to be a positive correlation, although it is difficult to define as we are at the limit of the series. This would be consistent with the findings by Conversi et al. (2001), who, using CPR data annually averaged, find a significant, positive relationship between *Calanus finmarchicus* and SST in the Gulf of Maine, with temperature preceding *C. finmarchicus* variations by about 2 years. It is likely that correlations at 0 lag indicate short-term links (direct or quasi-direct effects) with the temperature, while lagged correlations beyond the year may indicate (as Conversi et al., 2001, suggest) a change in the water column structure of advective type and possibly of climatic origin.

Oithona spp. shows at the same time scale (2.5 years) a negative correlation with SST. This fact may suggest a switch from small to larger copepods over time, but such a hypothesis needs to be investigated with additional species composition data before it can be supported.

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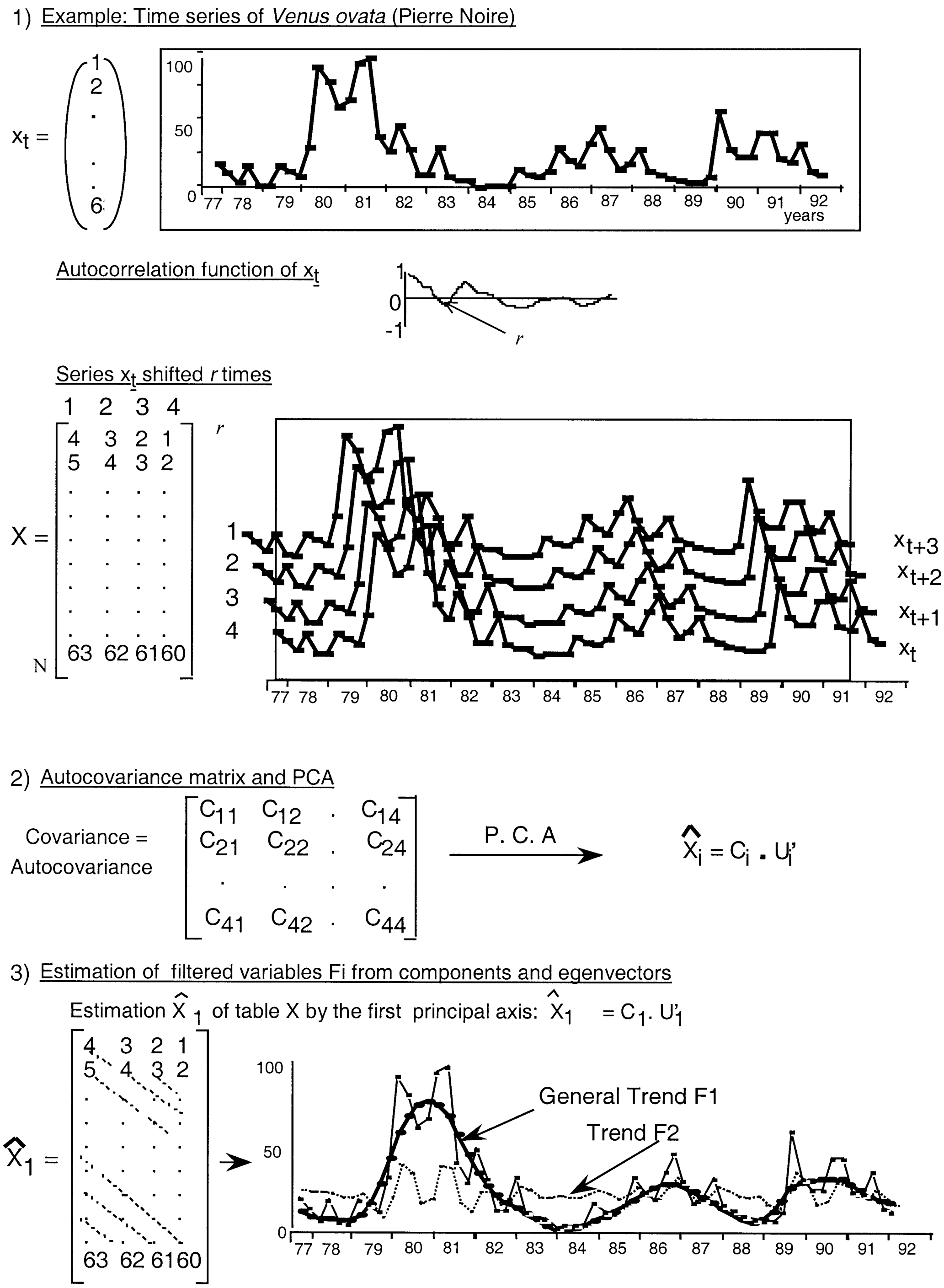
Appendix 1.

Simplified scheme of the different steps of the EVF method. X_t: initial series; X_i: *i*th predicted matrix; *Ci*: *i*th principal component; U_i: ith eigenvector.



Appendix 2.

Numerical procedure utilized for calculating filtered series F_i with EVF method.

Ibanez and Etienne (1992) showed that the filtered series F_i, corresponding to the principal axis f_i, may be calculated by a weighted moving average (WMA) on the original data set. With the r shifted series, WMA is of order r–1 and has 2(r–1)+1 terms. For the principal axis f_i, j being the term of the WMA, the jth weight P_{jf} is a linear combination of the elements of corresponding eigenvector, U_{ik}:

$$P_{j,f} = \sum_{k=1}^{m-|j|+1} U_{k,f} U_{k + |j|,f}$$

with $m = r–1$, $–m < j < +m$ and $U_{k,f}$ the kth element of eigenvector f.

x_t being the original series (with $t = 1,...,N$), the smoothed variable $F_{t,f}$, corresponding to the eigenvector f at point t is calculated as follows:

– When $m < t < (N – m + 1)$

$$F_{t,f} = \sum_{\substack{k=-m \\ 1>k+t<n}}^{m} P_{k,f} x_{t + k} / (m + 1)$$

– When $t < m + 1$

$$F_{t,f} = \sum_{k=-t+1}^{m-1} \left(P_{k,f} \sum_{l=1}^{m-t+1} U_{l,f} U_{l - k,f} \right) x_{t + k,f} +$$

$$\sum_{k=m-t+1}^{m} P_{k,f} x_{t + k}$$

– When $t > (N – m)$

$$F_{t,f} = \sum_{k=N-t-m+1}^{N-t} \left(P_{k,f} \sum_{l=N-t+2}^{m+1} U_{l,f} U_{l - k,f} \right) x_{t + k,f} +$$

$$\sum_{k=-m}^{N-t-m} P_{k,f} x_{t + k}$$

The weights of the MAW allow to compute the gain function associated to each filtering thus to know which frequency bands have been eliminated. The gain function may justify a posteriori the choice of r.

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