A new application of principal response curves for summarizing abrupt and cyclic shifts of communities over space

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Abstract. There is a growing need to easily describe and synthesize the dynamics of ecosystems' components in space and time. Most multivariate analyses provide ordination diagrams or biplots that are too cluttered to allow simple reading and are unfamiliar to most users. To overcome such difficulties, a novel application of principal response curves (PRCs) is proposed. Principal response curves are traditionally used to assess treatment effects on community structure measured repeatedly over time. In this new application, the tested factor and the repeated-observation axis are replaced by time and space, respectively. The georeferencing of sampling sites permits to produce an easy-to-read map that summarizes both the temporal dynamics of the community and the contribution of each species to these dynamics at each sampling site. A 24-yr-long time series of scientific surveys monitoring 77 fish and cephalopod species in the Eastern English Channel is used to illustrate the novel application of the PRC method. This new application could prove a relevant tool for the ecosystem approach to human activities management by providing spatialized indicators of community changes, as spatial monitoring tools are increasingly recommended for measuring the effectiveness of management actions.

Key words: fish communities; multivariate analyses; partial redundancy analysis; spatial management tools; spatio-temporal dynamics.

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INTRODUCTION

Many ecosystems need to be monitored, notably those that provide services to human communities. Consequently, there is a growing need for integrated assessment and ecosystem-based management (Pikitch et al. 2004, Link and Browman 2014). This objective requires methods to easily describe and summarize the complexity of ecosystems' ecological components, and notably how communities change over time and space. Classical ecological surveys provide species datasets in three dimensions (a measure of presence or abundance per species × sampling date × sampling site) that are statistically analyzed and summarized into straightforward representations.

Because of the multidimensional nature of survey-based ecological datasets (the dimensionality could be enlarged beyond the three above-mentioned basic dimensions by further considering individual traits such as size, sex, maturity), several difficulties for interpretation are encountered when summarizing community structural patterns and their spatio-temporal dynamics.

Many multivariate analyses are actually available to achieve such objective of describing and summarizing community dynamics (Clarke 1993) and have been popularly used for several decades. These statistical methods are useful for reducing the number of dimensions of community data and characterize both their structural patterns and their spatio-temporal dynamics.

Multivariate analyses are also commonly used to identify factors that best explain species composition variation between samples. Among purely descriptive methods, principal component analysis is the most commonly used one (Jolliffe 1986, Ter Braak 1995). Nevertheless, the majority of these analyses provide ordination diagrams that impede simple reading for most non-specialists (Van den Brink and Ter Braak 1999). The problem is also that craggy trajectories do not allow appreciating differences between factor modalities' effects (e.g., Figure 1 in Van den Brink and Ter Braak 1999). A considerable number of studies present temporal dynamics of communities/environmental parameters on several sampling sites by producing a list of numerous bidimensional graphs/tables that prevents a global overview of data. To overcome such difficulties and provide a simple representation of complex datasets, we propose a novel application of the principal response curve (PRC) method initially developed by Van den Brink and Ter Braak (1999).

The PRC analysis is a multivariate method initially developed in the field of ecotoxicology for assessing the effect of toxicants on freshwater communities, especially macroinvertebrates (Van den Brink and Ter Braak 1999, Van Wijngaarden et al. 2006, Brock et al. 2009). In this context, the tested factor was the toxicant, while time was the dimension along which repeated measures were performed and patterns of change were identified. From both a methodological and a conceptual point of view, this method is not limited to testing factors such as toxic chemicals or related anthropogenic disturbances. In addition to providing community-level insights into the toxicant effects, the original application of the PRC method also enables a quantitative assessment of its effects at the species level. In contrast with classical multivariate methods, this analysis facilitates our understanding of communities' temporal dynamics in response to the factor of interest (typically a toxicant treatment) through an easy-to-read graphical representation (Van den Brink and Ter Braak 1999).

In this paper, we propose to apply the PRC analysis in a new configuration where the tested factor and the repeated-observation axes are replaced by time and space, respectively. Here, we aim to assess the temporal changes in communities and species across space. In addition to

this statistical variable shift, we also propose to map geographically the results of the PRC analysis in order to produce an easy-to-read representation that summarizes both the temporal dynamics of communities and the contribution of each species to their global response at each sampling site across the studied area.

This paper is organized as follows. We first describe the principle of PRC analysis and its original application. The new application of the PRC to describe spatio-temporal community dynamics is then introduced. As an illustration, the new PRC application is used to analyze a 24-yr-long time series of scientific surveys monitoring 77 fish and cephalopod species in the Eastern English Channel (EEC). The final section summarizes advantages and limits of this new application of the PRC.

THE PRC METHOD: PRINCIPLE, ORIGINAL, AND NEW APPLICATIONS

Principle and original application of PRCs

In its original application (Van den Brink and Ter Braak 1998), the PRC method is meant to assess the temporal response of community composition to toxicants relative to a control treatment. Statistically, it is a special case of partial redundancy analysis (RDA) where explanatory variables are the chemical treatment and the interaction between treatment and time (treatment × time) and where time, along which repeated measures of community composition are performed, is the covariable (or conditioning variable) whose effect is partialled out. As time effect represents a change in community composition in the control treatment, it results that the treatment effects are expressed as deviations from the control at each point in time. In practice, the PRC method also allows summarizing and plotting the partial RDA results in a way that improves the readability and the interpretation compared to traditional ordination biplots that are typically highly cluttered. In the latter, differences between treatment effects might indeed be difficult to assess because of strong irregularities in trajectories, and their temporal development might be masked because time is not one of the ordination biplot axes (Van den Brink and Ter Braak 1999). It results that, although ordination biplots illustrate the temporal changes in species composition in each treatment,

they are difficult to interpret in terms of how the difference between actual treatments and control evolves through time. To overcome these illustration difficulties, the PRC extracts and illustrates directly the differences in species compositions between the treatments and the control at each date (see Figure 3 in Van den Brink and Ter Braak 1999). In practice, this is achieved by plotting the canonical coefficients of the treatment effects along the first canonical axis of the partial RDA against time. As a result, the vertical axis of a PRC diagram contrasts each treatment effect on community composition with the control. These visual advantages of the PRC can be appreciated by comparing the partial RDA ordination biplot and the corresponding PRC plot (e.g., Figures 1 and 3, respectively, in Van den Brink and Ter Braak 1999).

The corresponding model is defined by Eq. 1 (Van den Brink and Ter Braak 1999)

$$y_{d(j)tk} = \bar{y}_{0tk} + b_k c_{dt} + \varepsilon_{d(j)tk} \tag{1}$$

where $y_{d(j)tk}$ is the log-transformed abundance of species k in replicate j of treatment modality d at time t, $\bar{y}_{0tk}$ is the mean log-transformed abundance of species k at time t in the control ($d = 0$), c_{dt} is the canonical coefficient of treatment modality d at time t (i.e., the coefficient quantifying the community response pattern relative to the control) along the first canonical axis of the partial RDA, b_k is the multiple of the canonical coefficient for species k and thus $b_k c_{dt}$ gives the response pattern of species k expressed relative to the control, and $\varepsilon_{d(j)tk}$ is an error term with mean zero and variance σ_k^2. Only the first canonical axis is considered here, as it permits to produce an easy-to-read plot that contains the main trend in communities' response to treatments, but a PRC can be generated for each canonical axis of the partial RDA if needed. In terms of visual display, instead of usual multivariate ordination diagrams, the PRC analysis plots the canonical (regression) coefficients c_{dt} (y-axis) along a single axis corresponding to the dimension of repeated observations (i.e., time, x-axis) and species weights b_k on a separate vertical axis (Fig. 1A). The representation of c_{dt} values therefore permits a direct visual assessment of community response to treatments relative to control. Note that $c_{0t} = 0$ for every t because $b_k c_{dt}$ is defined as a deviation relative to the control

($d = 0$) abundance of species k thanks to the partialling out of the time covariable effect. In addition to the PRC diagram, a permutation test can be performed in order to assess the significance of the first canonical axis on the response matrix (Borcard et al. 2011).

In the original PRC application to experimental data based on repeated measures through time such as those gathered in BACI (before-after-control-impact) designs (Van den Brink and Ter Braak 1998, Maccherini et al. 2014), the initial data table has three dimensions, namely abundance per species, factor modality, and time (Fig. 1A). From this data table, the PRC provides a two-dimensional graph (canonical coefficients c_{dt} against time) that describes the community response to the factor of interest (typically a chemical treatment) over time. The absolute value of the canonical coefficient c_{dt} quantifies, at each sampling date, the amplitude of the factor effect on the global structure of the community compared to the control situation represented by the x-axis (Fig. 1). The corresponding curves (one curve per modality of the tested factor) can be therefore interpreted as the PRCs of the community.

The sign of the canonical coefficient c_{dt} indicates the type of community response and must be interpreted by comparison with the signs of species weights b_k. Indeed, in addition to the community level (c_{dt} canonical coefficients), the PRC analysis allows an interpretation at the species level. The absolute value of the species weight b_k quantifies the contribution of each species to the global change in community structure. Species weights can then be plotted on a separate vertical axis (Fig. 1A). Taxa with near-zero weight correspond to those showing no response to the tested factor and/or to those for which abundance was anecdotic in the time series whatever the factor modality. The signs of b_k and c_{dt} coefficients are identical (or opposite) for species that are more (or less) abundant in treated samples than in control ones. For example, in Fig. 1A, species 1, 3, and 4 were less abundant in treated samples than in controls on dates 3, 4, 5, and 6. Conversely, species 2, 6, 5, and 7 were more abundant on these dates (Fig. 1A). Concerning the amplitude of abundance changes, the proportional change in species k in the tested factor modality d at time t relative to its geometric mean abundance in the control is given by exp
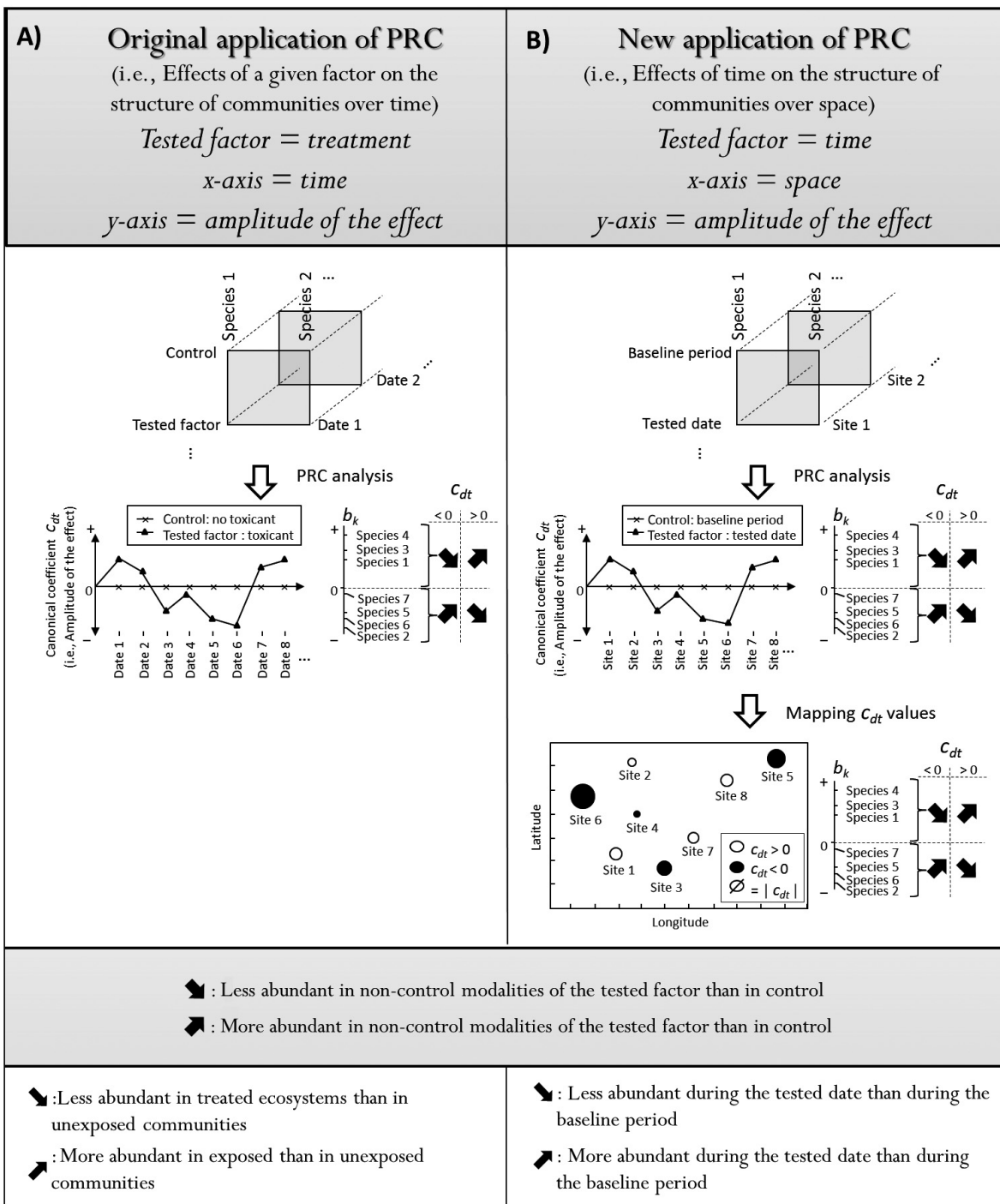
Fig. 1. Schematic description of the principal response curve (PRC) method and differences between its original (A) and new (B) application. In the original application of the PRC, canonical coefficients c_{dt} represent the amplitude of treatment effect on communities over time, while in the new version, canonical coefficients c_{dt} represent the effect of time on communities over space. Considering space as the repeated-measures axis allows mapping the analysis' results.

($b_k c_{dt}$). Most of the time, the high number of species considered prevents a clear overall representation and, thus, requires the selection of a species subset to solve this problem. For a complete description and discussion of the PRC method, the reader can refer to Van den Brink and Ter Braak (1998, 1999).

New application of the PRC method

The new application of the PRC method aims at describing a community's temporal dynamics across space. To do so, we shift the tested factor to time and the repeated-measures axis to sampling site or more broadly speaking space (Fig. 1B). The tested factor time is at least composed of two modalities: One modality called baseline dates, which corresponds to a set of dates characterized by a community structure that is considered as a reference state, and one or several modalities called tested dates that correspond to dates at which the community structure will be compared to the reference state (Fig. 1B). Each modality of the factor time can correspond to one or several dates characterized by a similar community structure. The dates of each modality can be either consecutive, when community structure quickly switches from one stable state to another or when community structure gradually changes, or non-consecutive, when the community structure alternates between stable states several times during the studied period, typically following a cyclic pattern. In the case of regime shift or alternative community structure/ecosystem states, the baseline date is relatively simple to define/identify from responses following abrupt changes. In contrast, the identification of a baseline date in gradual changing states is less straightforward since the PRCs impose separation of entities in the continuum.

Regarding the spatial component, each sampling site is associated with a c_{dt} value that characterizes community change between baseline and tested dates at this site and that can be interpreted in terms of species composition by comparison with the species weights b_k as in the original application (Fig. 1B). In addition, each sampling site is characterized by its longitude and latitude, which allows mapping the results. Such easy-to-read maps summarize both the evolution of community structure compared to the baseline dates and the contribution of each species to the community's response at each sampling site of the studied area (Fig. 1B). More generally, sampling sites can be characterized by any geographical or environmental parameter considered relevant for studying the potential implication of spatial structure, emerging from processes such as spatial auto-correlation, or environmental gradients on community structure change between baseline and tested dates. Plotting canonical coefficients c_{dt} against the values of the geographical or environmental parameter of interest instead of the sampling site then allows identifying easily potential spatial structure or environmental gradients in community temporal change.

The new PRC application allows assessing community composition changes between tested and baseline dates at several sites, but it does not provide a way to test the statistical significance of change at each site (although a permutation test on the first canonical axis of the corresponding partial RDA provides a global test of community change significance across sites; see subsection *Principle and original application of PRCs*). Significance of community structure change between the tested and baseline dates can be evaluated at each sampling site using Monte Carlo permutation tests designed to correct for the increase in the family-wise type I error rate due to multiple comparisons (i.e., one per sampling site). Community composition data are correlated across sites because of a spatial correlation structure emerging from two processes. First, the abundance of two species (or more) can co-vary through space and thus be spatially correlated. Second, the abundance of a given species can be correlated with itself across space, that is, spatially auto-correlated. The resulting spatial correlation structure in community composition data implies that data used for tests of community structure change between the tested and baseline dates at different sites are correlated. The more correlated the data are between tests, the weaker the correction for multiple comparisons needs to be (Bretz et al. 2011, Groppe et al. 2011). This is better understood when considering the extreme situation in which data are perfectly correlated between tests: Then, all tests are strictly identical and are effectively equivalent to a single test, so that the test-wise type I error rate, that is, the nominal type I error rate for each single test, is equal to the

family-wise type I error rate. Multiple comparison methods that are based on the assumption that tests are independent, such as the widely used Bonferroni procedure, are too conservative, that is, prone to declare an effect non-significant when it is actually significant, when the data are correlated between tests.

In order to integrate information about the spatial correlation in the community composition data, we corrected for multiple testing using the maximum statistic/minimal P-value method that accounts for the degree of correlation between the multiple comparisons (Nichols and Hayasaka 2003, Bretz et al. 2011, Groppe et al. 2011). In practice, we approximated the distribution of the minimal P-value across sampling sites by repeating 1000 times (or more) the following two-step procedure (see Data S1 for R script):

1. Outer permutation: Permute randomly factor time modalities (baseline and tested dates, z-axis, Fig. 1B) while leaving matrices of abundance by species (x-axis, Fig. 1B) and sites (y-axis, Fig. 1B) unchanged; this allows randomizing any potential association between time and the abundance of each species at each site while preserving the spatial correlation structure of community composition.
2. Inner permutations: Perform a RDA on community composition at each sampling site using the permuted data with factor time as an explanatory variable and test for its significance using a Monte Carlo permutation test; record of the resulting minimum P-value across sampling sites.

The resulting distribution of minimal P-values (the number of minimum P-values being equal to the number of outer permutations, typically 1000) can then be used as the empirical null distribution against which the observed P-values at each sampling site are tested. The latter are computed for each sampling site through a RDA of the non-permuted abundance data with factor time as an explanatory variable followed by a Monte Carlo permutation test (equivalent to the inner permutation test above). A change in community structure at a given site is then considered significant when <5% of the minimum P-values in the empirical null distribution are lower than the observed P-values. Notice that

outer permutations are the critical step for the maximum statistic/minimal P-value method, while the inner permutation is only the base single-comparison test that can be replaced by any other type of tests (even parametric) depending on the nature of the data.

The PRC analysis generates a loss of information as any other ordination method. Beyond quantitative approximation, this may generate misleading qualitative conclusions such as erroneous estimates of direction in species abundance variation. We propose to assess the global qualitative accuracy of the new application of the PRC analysis by comparing the matrix of predicted directions of species abundance changes between the tested and the baseline dates and that of directions of change observed in the data. More precisely, the first one or predicted direction matrix contains the sign of abundance change for each species k (columns) at each site t (rows) as predicted by the PRC, that is, obtained by comparing the sign of c_{dt} and b_k. The second one, or observed direction matrix, contains the sign of abundance change as observed in the original dataset by comparing average abundance between the tested and the control dates. The two matrices are then compared by computing their percentage of similarity, that is, the percentage of cells of the two matrices that have the same sign. The similarity or qualitative accuracy is expected to vary from 50% if the predicted direction matrix is completely random compared to the observed direction matrix to 100% if directions of changes are predicted perfectly.

ECOLOGICAL ILLUSTRATION: SPATIO-TEMPORAL DYNAMICS OF THE ENGLISH CHANNEL FISH COMMUNITY

Study area and data

The English Channel is one of the busiest maritime areas in the world enduring intense and diversified anthropogenic pressures: international mixed fisheries (Jennings and Kaiser 1998, Batsleer et al. 2013), intense commercial traffic, wind farm settlements, and aggregate extractions. Since 1988, a bottom trawl survey (Coppin and Travers-Trolet 1989) is conducted annually in October in the EEC and the southern North Sea (areas VIId and south of IVc defined by the International Council for the Exploration of the Sea) in order to

monitor the bentho-demersal fish community. While this survey primarily aims at producing abundance indices to be used in commercial fish stock assessments, data are collected on all species caught and thus allow following the spatio-temporal dynamics of the local bentho-demersal fish community (Appendix S1: Fig. S1). Based on these data, Auber et al. (2015) documented a regime shift in the fish community structure of the EEC during the mid-1990. This regime shift seemed likely triggered by a large-scale and multidecadal hydro-meteorological process in the Atlantic Ocean, detected from the Atlantic Multidecadal Oscillation signal during the mid-1990s. However, the regime shift was characterized at the entire EEC basin scale without considering potential spatial heterogeneity in community change at smaller scale. The new application of the PRC proposed here would provide better understanding of the spatial distribution of temporal changes, using the pre-regime shift period as a reference state for community structure and thus baseline dates.

Because weather conditions sometimes prevented sampling, we chose to delete all sampling sites that had not been visited for at least three consecutive years. As a result, 79 sampling sites were kept. Overall, 77 taxonomic groups of fish and cephalopod were recorded since 1988. In this paper, we loosely define fish communities as encompassing fishes and cephalopods. The abundance indices at each sampling site were standardized to density (number of individuals/ km^2), which we will refer to as abundance hereafter. Therefore, data consisted of a three-dimensional table of abundance according to fish species, sampling year, and sampling site (Fig. 1B). Before applying the PRC analysis, abundance data (x) were $\ln(Ax + 1)$-transformed (Van den Brink et al. 2000), where Ax must be equal to 2 for the lower x value in the dataset. In this case study, the coefficient A was equal to 0.1.

Results

Since the regime shift in the fish community was detected between years 1997 and 1998 (see Auber et al. 2015 for details), the period (1988–1997) was selected as the "baseline dates" and the period (1998–2011) as the tested dates. The PRC method was applied on the table of log-transformed fish abundance data according to the new

scheme, that is, with time as the tested factor characterized by two modalities (baseline dates and tested dates) and sampling sites as the repeated-measures axis (package vegan in R version 2.15.1; Oksanen et al. 2015, R Core Team 2015).

Sampling sites explained 40.1% of spatio-temporal variance in species abundance data (implicitly displayed on the horizontal axis, Fig. 2A), whereas time was responsible for 6.2%, 36.5% of which is represented by the first canonical axis of the PRC analysis (vertical axis, Fig. 2A), 10.9% by the second one, and 7.1% by the third one (not displayed). The variance explained by the factor time corresponded to a significant difference in terms of community structure between the two periods corresponding to baseline and tested dates (permutation test: $P < 0.001$). These first results illustrate two points. First, one interest of the new application of the PRC method is to allow detecting temporal changes while accounting at the same time for strong spatial variability (by defining sampling sites as conditioning variable) that in other analyses would either mask the temporal effects or be neglected (analyses on spatially averaged data). Second, they show that, in this case study, the first PRC can be used alone to assess the temporal changes in community composition as it represents more than one-third of the temporal effect, while the second and third PRCs represent one-tenth or less.

All sampling sites were characterized by negative c_{dt} values (Fig. 2A), which indicates a qualitatively identical type of fish community change between time periods at all sites in the sense that the direction of species abundance variation between the two periods was the same whatever the considered site. However, because c_{dt} values were different from one site to another, the amplitude of the community's structure variation was relatively heterogeneous in space. Species weights b_k indicated that the common response pattern across sites was mainly characterized by a diminution in the density of horse mackerel (*Trachurus trachurus*) and poor cod (*Trisopterus minutus*; strongly positive b_k values for negative c_{dt} values, which corresponds to a diminution of about 20,000 individuals/km^2 between the periods [1988–1997] and [1998–2011]; Fig. 2A). These two dominant species were the main ones involved in the mid-1990 regime shift as documented in Auber et al. (2015). The PRC also
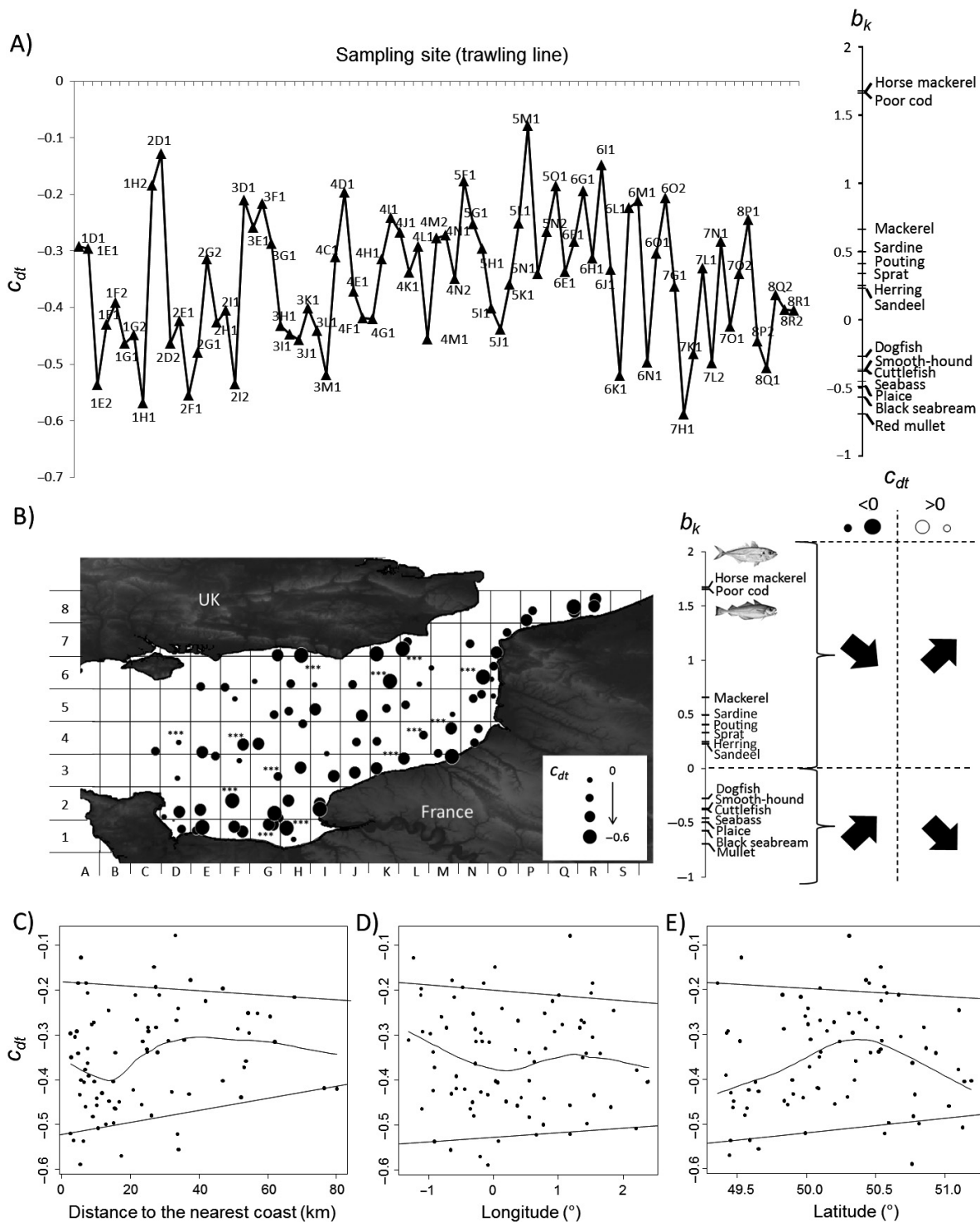
Fig. 2. Distribution of c_{dt} values across sampling sites. (A) Principal response curve, only species for which the b_k coefficient was in the first or the last decile were included in the graph (36.5% of the inertia is explained by the first canonical axis). Sampling sites are ordered from south to north, and labeled by three characters as follows:

(Fig. 2. *Continued*)
The first character corresponds to the latitudinal row of the sampling grid from south to north (see B), the second character corresponds to the longitudinal column of the sampling grid from east to west, and the third character corresponds to the number of the sampling site within a given cell defined by a row and a column (each cell of the sampling grid contains a maximum of two sampling sites). (B) Map showing the amplitude of the fish community change between the baseline [1988–1997] and the tested period [1998–2011] at each sampling site and trend (positive or negative) in abundance for each species. Sampling sites for which a significant change in the community structure occurred are shown by asterisks (***P < 0.001; **0.001 < P < 0.01; *0.01 < P < 0.05). This map was produced using ArcGIS version 9.3.1 (ESRI, 2009). (C) Relationship between c_{dt} values and distance to the nearest coast (in km) with the first/last decile lines and smooth curve. (D) Relationship between c_{dt} values and longitude with the first/last decile lines and smooth curve. (E) Relationship between c_{dt} values and latitude with the first/last decile lines and smooth curve.

revealed a moderate decrease (i.e., a diminution ranging from 1000 to 6000 individuals/km^2 on average according to species) in mackerel (*Scomber scombrus*), sardine (*Sardina pilchardus*), pouting (*Trisopterus luscus*), sprat (*Sprattus sprattus*), herring (*Clupea harengus*), and sandeel (*Hyperoplus* genus) abundance (moderately positive b_k values for negative c_{dt} values; Fig. 2A), and a very low increase (i.e., rise of about 60 individuals/km^2 between the periods [1988–1997] and [1998–2011]) in the abundance of some species such as red mullet (*Mullus surmuletus*) and black seabream (*Spondyliosoma cantharus*; Fig. 2A). The b_k coefficients of the 32 other species were close to zero, indicating that these species' abundance was similar between the two periods and/or anecdotal throughout the time series.

Since all sampling sites were georeferenced, c_{dt} values could be mapped for easier inspection of the temporal variation in fish community over space (Fig. 2B). The resulting map clearly demonstrates the relative spatial heterogeneity in the amplitude of community change already suspected from the raw PRC itself (Fig. 2A). This representation suggests that sampling sites with the highest c_{dt} values are globally located close to the coast. However, no significant correlation between c_{dt} values and three different environmental parameters characterizing sampling sites, distance to the nearest coast, longitude, and latitude, was detected, suggesting the absence of environmental gradient in community change associated with these parameters (Table 1, Fig. 2C–E).

Monte Carlo permutation tests correcting for multiple comparisons showed that changes in community structure were significant at 13 out of the 79 sampling sites (Fig. 2B). In addition to

community-level patterns, the resulting map facilitates comparison of the amplitude of temporal variation in each species' abundance between sites (i.e., by looking simultaneously at the circles' size representing c_{dt} absolute value and the absolute value of b_k; Fig. 2B).

The PRC analysis estimated the correct direction of species abundance change for 4824 out of the 6083 (79 sampling sites × 77 species) cases observed, which corresponds to a qualitative accuracy of 79.3%. As explained before, the qualitative accuracy is expected to vary between 50% (random prediction) and 100% (perfect prediction). The observed accuracy therefore indicates that PRC predictions are much better than random but also not perfect. The good degree of qualitative accuracy is probably related to the amplitude of the regime shift observed in this ecosystem in the mid-1990s.

General Discussion

We proposed here a new application of the PRC analysis for studying community temporal

Table 1. Results from regressions and quantile regressions between c_{dt} values and the distance to the nearest coast, longitude, and latitude.

Variables	Regression (P)	Quantile regression (P)	
		First decile	Last decile
c_{dt} ~ distance to the nearest coast	0.06	0.06	0.64
c_{dt} ~ longitude	0.65	0.62	0.54
c_{dt} ~ latitude	0.37	0.32	0.71

dynamics across space. As shown here, applying the PRC on species abundance tables, with time as the tested factor and site as the repeated-measures axis, is well adapted for providing a simple and rapid overview of community structure changes and for simultaneously qualifying and quantifying site-specific community structure and species abundance temporal changes. This new application clearly provides a highly accurate synthesis of community-level dynamics at numerous sampling sites as illustrated for the EEC fish community. The geographical representation of canonical coefficients (c_{dt}) allows a rapid identification of sites where community changes occur, as well as of the type and the magnitude of community response at each site. Complementary to c_{dt} coefficients, b_k coefficients are very useful to assess the direction and amplitude of species abundance changes at each sampling site and thus to rapidly identify species that can be considered as indicator species. We must note that the new application of the PRC proposed here does not rely directly on the spatial location of data points as sampling sites are identified as factor modalities and not through their geographical coordinates. This means that the PRC must be completed by additional analyses to investigate potential spatial patterns in community temporal changes. Hence, the novel PRC application could be useful in revealing spatial structures or environmental gradients in temporal community changes by evaluating spatial autocorrelation in c_{dt} values or by relating them to environmental parameters. Although no environmental gradient has been evidenced for the EEC example, the canonical coefficient c_{dt} representing community changes could still be related to abiotic or biotic parameters that characterize sampling sites but that we did not consider (e.g., bathymetry, temperature, salinity, productivity). Beyond community data, the PRC analysis could be applied in its new configuration to environmental parameters data in order to easily characterize and quantify the spatio-temporal dynamics of ecosystems' abiotic conditions.

The newly proposed application of the PRC is particularly well adapted for describing regime shifts or cyclic successions of alternative stable states (Collie et al. 2004). Such cases are characterized by low variability between replicates within each modality of the tested factor (time period or set of dates) relative to that between

modalities and are thus well accommodated by a discretized representation of time as the tested factor. However, when community/ecosystem dynamics are characterized by a gradual change, the PRC is less adapted since the community reference state is composed of a series of different, although contiguous, community structures that will complicate the determination of baseline dates and more generally the discretization of time. In this case, the accuracy of the assessment of time effect is likely to be reduced since the level of variation within each modality of the tested factor (i.e., time) relative to that between modalities will be higher than in cases of regime shifts or alternative stable states. As a consequence, caution must be exercised when aiming to apply the novel PRC configuration on biotic/abiotic compartments that do not present abrupt shifts. A critical prerequisite of the proposed application of the PRC method is that the number of sets of tested dates and the specification of dates in each set must be determined before applying the PRC itself. Several statistical methods exist for defining dates where abrupt changes occur in time series such as constrained/unconstrained hierarchical/non-hierarchical clustering methods (e.g., k means, multiple regression trees), but also piecewise regressions. The identification of the baseline period and the tested period was straightforward in the EEC example, as a regime shift occurred in this ecosystem. For gradual changes in communities, care must be taken when identifying the different periods or set of dates to be used. Options include subdividing the time series into two or an arbitrary number of contiguous periods, each consisting of a fixed number of dates, or using only the first (few) date(s) as a baseline and the last (few) dates as tested dates. When doubt exists about the definition of the sets of dates, an analysis of sensitivity to the discretization of time should be performed in order to assess uncertainty in the results due to these choices. In any case, we discourage the use of the new PRC application in case of gradual shift of community structure. It is also worth noting that considering several periods or sets of dates results in the production of several maps (one for each tested period or set of dates showing changes from the reference state).

In this study, only the first PRC (corresponding to the first canonical axis of the partial RDA) was

presented in order to illustrate the use and utility of the new PRC application to describe communities' spatio-temporal dynamics. However, according to the level of information required by users, additional PRCs can be generated and plotted using additional canonical axes. The first PRC provides the leading-order term in the spatio-temporal dynamics of the considered data (communities, environmental parameters, etc.), but more detailed information can be accessed using additional PRCs and canonical axes. Whatever their number, PRCs are still useful compared to standard ordination biplots since PRCs are much more efficient to assess and interpret the effect of the tested factor relative to its reference level (treatment vs. control, tested vs. baseline dates, etc.).

The ecosystem approach incorporates a range of objectives geared to maintaining healthy or sustainable environments (Pikitch et al. 2004, Convention on Biological Diversity, 1992) and offers schemes for integrated management (Busch et al. 2003). In this context, the achievement of ecosystem-based management objectives requires the use of quantitative indicators. Some of these indicators are general measures of ecosystem health, while others have potential to underlie decision rules such that a particular indicator value may trigger specific management action (Gislason et al. 2000, Rombouts et al. 2013). In the case of the novel PRC application, c_{dt} and b_k coefficients correspond to measures of community and species changes, respectively. This makes the PRC an interesting tool for implementing the ecosystem approach, in both marine and terrestrial ecosystems management. For instance, the new application of the PRC analysis could be useful for providing a rapid assessment of potentially sensitive areas that may contribute to endangered species extinction or invasive species proliferation. Likewise, it could be useful to describe spatio-temporal dynamics of functional rather than taxonomical community structure. Functional approaches based on species traits or ecological roles could indeed be more effective than traditional methods that only consider taxonomic community structure, especially for understanding mechanisms behind community dynamics and biodiversity–ecosystem functioning relationships (Dumay et al. 2004, Culp et al. 2010).

Our study illustrates the flexibility and versatility of this novel PRC application for a more straightforward representation and interpretation of temporal variations in communities, or more generally in multiple ecosystem components, at different spatial scales. Despite some limitations, it has the benefit of being an efficient monitoring tool for describing sequential and/or alternative changes in community/ecosystem states (e.g., seasonal patterns of biotic and abiotic components). It is also a potentially useful tool for ecological studies in either controlled (Van den Brink and Ter Braak 1999) or wild environments and it can be used to assess diverse biological responses to climate change as well (Heegaard and Vandvik 2004). Moreover, the geographical projection of PRC results on maps offers ease in readability and interpretation of spatial patterns in temporal changes possibly useful to environmental managers and conservationists for spatial management decisions such as the definition of preferential protected areas (Fogarty and Murawski 1998). This last advantage reinforces the relevance of the new PRC application for the ecosystem approach since spatial management tools are increasingly recommended in this context (Sainsbury et al. 1997, Babcock et al. 2005) and because decision-support tools are needed for designing and measuring the effectiveness of management actions. To conclude, this new PRC application is an efficient method for providing an initial and simplified overview of the temporal dynamics of communities and populations at various sites and we strongly encourage its application for future synecology research where time and space matter.

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SUPPORTING INFORMATION

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