Assessing ecological responses to environmental change using statistical models

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Summary

1. There is a clear need to improve our ability to assess the ecological consequences of environmental change. Because of the complexity of ecosystems, predictions are often reliant on models and expert opinion. These require validation with observed data; in this respect, long-term datasets are particularly valuable.

2. Innovative statistical methods are presented for identifying ecological trends and changes in seasonality in response to environmental change. These are illustrated through the example of Loch Leven, a shallow freshwater lake. 35 years of monitoring data are examined spanning periods of enrichment, ecological recovery and changing climate.

3. The use of additive models are illustrated for assessing non-monotonic annual trends and seasonal variability of responses, often typical of noisy and complex ecological time-series. Nonparametric regression models are used to consider seasonal trends and to investigate if seasonal patterns change throughout time.

4. Models are developed for phosphorus and nitrogen; temperature and rainfall; *Daphnia* grazers; and chlorophyll$_a$.

5. The analysis highlights a generally decreasing availability of phosphorus over the study period and generally increasing nitrate concentrations and rainfall. Increasing spring temperatures are also evident.

6. There have been no significant trends in annual mean grazer densities for the period 1971 to 2002. Significant changes in summer grazer densities were highlighted, with a decreasing trend until the early 1990s, followed by an

increasing trend to 2002.

7. Chlorophyll$_a$ models indicated significant declining trends for the period 1968-2002, driven largely by significant reductions in spring and summer early on in the first three years. Seasonality also changed, with a reduced and earlier spring peak and a more prominent "clear-water" period in late spring / early summer. These changes may be driven by the observed increasing trend in spring temperatures and consequent increasing spring *Daphnia* densities.

8. ***Synthesis and applications***. The analysis highlights the value of statistical models for assessing complex ecological responses to environmental change. The models outlined can examine key ecological impacts of climate change, particularly effects on the timing of seasonal events and processes.

Key-words: climate change, freshwater, Loch Leven, seasonality, statistical model, trend.

Introduction

There is a clear need to improve our ability to assess the ecological consequences of environmental change. Because of the complexity of ecosystems, predictions are often reliant on models and expert opinion (Sutherland, 2006). These require validation with observed data; in this respect long-term datasets are particularly valuable.

Assessing environmental change at an ecosystem level often requires assessing whether annual trends are significant and whether seasonality is changing. Ecological time-series, however, are often very complex with non-linear and non-monotonic trends over time and strong seasonality. More novel approaches to statistical analysis of ecological time series are, therefore, needed to account for these issues. It is of particular interest to explore the average pattern over the years (annual trend), the average pattern over the years within each season (seasonal trend) and the average pattern within the year (seasonality) for responses.

This paper details innovative statistical methods for identifying trends and seasonality in ecological responses in complex, long-term ecological datasets. These are illustrated through the example of Loch Leven, a shallow freshwater lake in Central Scotland. Over 35 years of monitoring of water quality and plankton populations has been carried out spanning periods of toxic pollution, nutrient enrichment, ecological recovery and changing climate.

The development and application of additive and nonparametric regression models are illustrated. Models are developed for: 1) SRP and nitrate ($N0_3$-N), the main nutrients potentially limiting phytoplankton production in this system; 2) temperature and rainfall, important climatic variables, 3) *Daphnia*, the dominant phytoplankton grazer in the system and 4) chlorophyll$_a$, a measure of phytoplankton standing crop and a key measure in the European Union Water Framework Directive (WFD) of the ecological status of freshwaters (European Parliament, 2001).

Materials and Methods

Study Site

Loch Leven is situated in lowland Scotland in the Perth and Kinross area. It is the largest shallow, eutrophic lake in Great Britain with an area of 13.3km^2, mean depth 3.9m and a maximum depth 25.5m. The water draining into the loch comes from direct rainfall and run-off from the agricultural catchment and is used by various industries downstream. The loch is an important trout fishery and is also a Ramsar site and National Nature Reserve. An action programme to improve the ecology and water quality of the loch, focused on reducing phosphorus loadings, began in the 1980's (Bailey-Watts and Kirika, 1987, 1999). For further site information see, Carvalho and Kirika (2003), Bailey-Watts (1978) and Jupp and Spence (1977).

Data

The Centre for Ecology & Hydrology have monitored approximately 150 variables at the the loch since 1968. Samples are predominately taken from Reed Bower, an area near the centre of the loch, and the sampling dates are a mixture of weekly, biweekly and monthly with large periods of missing data, especially in the 1980's (Ferguson et al., 2007).

There are six key variables for this study. For SRP, nitrate (NO_3-N), *Daphnia* and chlorophyll$_a$ the raw sampling dates have been aggregated to monthly means and a natural log transform has been applied to each variable. The data have also been aggregated to seasonal means to explore trends over time within each season, where winter is (Dec, Jan, Feb), spring is (Mar, Apr, May), summer is (June, July, Aug) and autumn is (Sept, Oct, Nov). For air temperature, mean daily values have been calculated using (max+min)/2 and then data have been aggregated to monthly and seasonal means. However, for rainfall, monthly and seasonal cumulative rainfall values are used here.

Statistical Methods

Classical approaches to modelling trends and seasonality in water quality data include Mann Kendall and Seasonal Kendall tests (see, for example, Hirsch et al., 1982; Hirsch and Slack, 1984). Such tests, however, assume monotonic trends. This paper highlights the extra information that can be gained from allowing greater flexibility in statistical models using additive and nonparametric regression models with correlated errors incorporated where necessary.

The following three models can be used to explore trends and seasonality fully for each of the variables of interest:

$$y = \mu + m_1(\text{year}) + m_2(\text{month}) + \varepsilon, \quad \varepsilon \sim N(0, V\sigma^2) \tag{1}$$

$$y = \mu + m(\text{year}_\text{s}) + \varepsilon, \quad \varepsilon \sim N(0, \sigma^2) \tag{2}$$

$$y = \mu + m(\text{year}, \text{month}) + \varepsilon, \quad \varepsilon \sim N(0, V\sigma^2) \tag{3}$$

Model (1) is used to consider the trend, $m_1(\text{year})$, and seasonality, $m_2(\text{month})$, over time for each response variable, for example log SRP, and model (2) is used to consider seasonal trends, $m(\text{year}_\text{s})$. In the latter case, the response contains seasonal means for a variable of interest, for example air temperature in spring. Model (3) is used to consider how the seasonal pattern across months, within each year, changes over the time period. In models (1) and (3) an AR(1) correlation structure is assumed for the errors. Therefore, each model is fitted initially assuming independent errors to estimate the lag 1 correlation of the residuals, $\hat{\rho}$. The matrix V is then constructed using $V_{ij} = \hat{\rho}^{|i-j|}$.

Model Fitting

Model (2) is a nonparametric regression model with independent errors (see, for example, Bowman and Azzalini, 1997). The local linear method of smoothing, Cleveland (1979), is used to fit the smooth function, $\hat{m}(\mathrm{year_s})$ and a normal kernel density is used for the weights, with mean zero and standard deviation h. The smooth function $\hat{m}(\mathrm{year_s})$ can be expressed as Sy and the smoothing parameter, h, is determined by setting the degrees of freedom $(df) = tr(S) = 5$. The value of the degrees of freedom needs to be set to define the complexity of the model. This choice, of $df = 5$, allows a moderate degree of non-linearity, however results are not very sensitive to different values.

For more than one covariate, nonparametric regression can be extended to an additive model , Hastie and Tibshirani (1990), e.g. model (1). Correlated errors are incorporated for model (1), which is fitted using the backfitting algorithm. A normal kernel density is used to construct the weights for the year component. However, for cyclic terms, such as month, a smooth function can be obtained using local constant regression with a circular smoother used for the weights, for full details see Ferguson et al. (2007) and Giannitrapani et al. (2005). Smooth functions, $\hat{m}_j(x_j) = S_j y$, can be obtained for each of the components $j = 1, 2$ in the model and for each component $df = tr(S_j) - 1 = 4$ to reflect the fact that each term is constrained to have mean zero eliminating one degree of freedom.

Model (3) is an extension of (2) to two dimensions. In this case the formulation of the bivariate smooth component is similar to that used for the year component in the additive model with a product of weight functions formed using a normal kernel density for year and a circular smoother for month. The function $\hat{m}(\mathrm{year}, \mathrm{month})$ can be expressed as Sy and the smoothing parameters are determined by setting

$df = tr(S) = 10$.

For each variable, three time periods have been considered to explore the system. These are 1968 to 2002, 1971 to 2002 (excludes the first three years when *Daphnia* were absent as a result of probable pesticide pollution) and 1988 to 2002 (recent period with continuous monitoring).

For each of the variables of interest, plots are produced for each of the covariates in the additive models. On each plot the fitted values are displayed along with a shaded band indicating $\pm$ 2 standard errors from these estimates. Details of the standard error calculations are provided in Giannitrapani et al. (2005) and Ferguson et al. (2007). For nonparametric regression, seasonal figures are provided with a reference band for 'no effect' displayed on each plot; for details see Bowman and Azzalini (1997).

Model Testing

An approximate F-test (Hastie and Tibshirani, 1990) is used to test hypotheses concerning model components. However, the construction of the residual sums of squares for models (1) and (3) is modified to incorporate correlation, Giannitrapani et al. (2005). For both models being compared the correlation matrices and smoothing parameters are equal.

For the additive models it is of interest to test whether components are significant in addition to one another i.e. testing the hypotheses of 'no effect vs effect' (4), and whether the nonparametric effect is necessary or a linear component is adequate i.e. testing the hypotheses of 'linear vs nonparametric effect' (5). The month term is not tested for a linear effect since it is a cyclic component.

Model (2) has been tested in terms of the hypotheses 'no effect vs effect' in order to investigate if seasonal trends are significant (6) and the hypotheses in (7) are compared to investigate if the seasonal pattern across the year changes significantly over the time period considered. In order to allow comparison between the bivariate and additive model (7) the smoothing parameters have to be equal. As a compromise the geometric mean of the univariate and bivariate smoothing parameters has been calculated for each model component and these new smoothing parameters are used for both models in the testing procedure.

$$\begin{aligned} H_0 : \mathbb{E}\{y\} &= \mu + m_1(\text{year}) \\ H_1 : \mathbb{E}\{y\} &= \mu + m_1(\text{year}) + m_2(\text{month}) \end{aligned} \tag{4}$$

$$\begin{aligned} H_0 : \mathbb{E}\{y\} &= \mu + \beta\text{year} + m_2(\text{month}) \\ H_1 : \mathbb{E}\{y\} &= \mu + m_1(\text{year}) + m_2(\text{month}) \end{aligned} \tag{5}$$

$$\begin{aligned} H_0 : \mathbb{E}\{y\} &= \mu \\ H_1 : \mathbb{E}\{y\} &= \mu + m(\text{year}_\text{s}) \end{aligned} \tag{6}$$

$$\begin{aligned} H_0 : \mathbb{E}\{y\} &= \mu + m_1(\text{year}) + m_2(\text{month}) \\ H_1 : \mathbb{E}\{y\} &= \mu + m(\text{year}, \text{month}) \end{aligned} \tag{7}$$

Results

Exploring Trends and Seasonality

Figure 1 illustrates generally decreasing availability for SRP. However, a slight increase is evident in the late 1980's and early '90's. There are significant decreasing annual trends for all time periods considered (Table 1) and strong seasonality. Table 2 highlights that trends can be considered linear, although the whole time period (1968-2002) is borderline nonparametric.

For nitrate, Figure 2, there are significant annual trends for all time periods considered, Table 1, and these are generally increasing. However, the greatest increase appears to be from the mid 1990's onwards. There is also strong seasonality and Table 1 and Table 2 highlight that there is evidence of a nonparametric trend in each time period.

While a slight increasing trend and strong seasonality are evident in Figure 3 for mean air temperature, the annual trends in all time periods are not significant. Table 2 highlights that it is reasonable to assume that trends are linear and this is also true for cumulative rainfall. A general increase in rainfall (Figure 4) is evident over the whole time period. However, the trend in the latter period (1988-2002) is not significant, Table 1.

Following re-establishment of *Daphnia* grazers in the loch in 1971, there have been no significant trends in annual mean grazer densities, p-value $= 0.529$ (1971-2002). There is significant seasonality in *Daphnia* densities, with peaks in late spring and early summer (Table 1, Figure 5). Table 2 highlights that over the whole period (1968-2002) the trend appears nonparametric. Discounting the early years, however, the trend could be considered linear (p-value $= 0.728$, 1971-2002).

For chlorophyll$_a$, additive models indicate significant nonparametric declining trends and strong seasonality (Table 1, Figure 6) for the whole time period, 1968-2002. However, for the period 1988-2002, while seasonality is still strong the annual nonparametric trend is not significant and Table 2 highlights that it is highly likely to be linear.

Exploring Seasonal Trends

The main decrease for SRP was in summer, autumn and winter (Figure 7) over the whole time period. However, trends in the latter period are not significant with the exception of a borderline p-value for Autumn, Table 3.

For mean air temperatures, however, while annual trends were not significant, a borderline significant, generally increasing trend is highlighted for spring temperatures over the whole period (1968-2002), but not for the latter years (1988-2002), Table 3 and Figure 8. There also appears to be a generally increasing trend in winter. However, this nonparametric trend is not significant. Results are more significant when water temperature (p-value = 0.021, spring 1968-2002) is considered as opposed to mean air temperature.

For cumulative rainfall, there is a significant, generally increasing, trend for winter (1968-2002), Figure 9 and Table 3. Spring and summer are generally wetter too, but trends are not statistically significant over the whole time period, Table 3.

For *Daphnia*, in the period 1971-2002, summer densities are the only season to show significant changes (p-value = 0.025) with a decreasing trend evident until the early 1990s, followed by an increasing trend to 2002, Figure 10. However, for the later period no seasonal trends were apparent. This is also true for chlorophyll$_a$. However, there were significant reductions in spring and summer for the whole time period due to big reductions early on in the first three years, Figure 11 and Table

3, for chlorophyll$_a$.

Exploring Changes in Seasonality

Only log chlorophyll$_a$ shows any clear change in seasonality over the whole time period with a significant p-value of 0.009 (Table 4, Figure 12 left). A much reduced and earlier spring peak (from April to February) is highlighted along with a more prominent "clear-water" period in late Spring / early summer (May/June). The seasonal patterns for the other variables under consideration have generally remained the same from 1968-2002 (Table 4). However, as illustrated in Figure 12 (right) there is evidence of a slight change in the seasonality of SRP, although this is not significant.

Discussion

Freshwater communities with their short generation times allow exploration of impacts of environmental change on ecosystem structure and functioning.

The abundance of phytoplankton in particular is a key indicator of water quality and ecological status, recognised in recent European legislation (European Parliament, 2001). Chlorophyll$_a$ concentration in the water column is a widely recognised simple measure of phytoplankton abundance, and so of particular interest in any assessment of the impacts of environmental change in freshwaters. This study aimed to examine trends and seasonality in chlorophyll$_a$, as well as the main potential drivers of change in the phytoplankton community, notably temperature and rainfall, nutrients (SRP and nitrate availability) and dominant grazer (*Daphnia*) densities. Nonparametric regression and additive models have been used to assess whether trends in these key ecological variables are significant, linear or non-monotonic and whether there have been any changes in seasonality.

Annual trends

The clearest annual trend in the dataset is the significant reduction in SRP concentrations, a key nutrient often limiting phytoplankton crops. In particular, trend analysis over the last 15 years indicated significant reductions, highlighting the success of more recent management to reduce point-source inputs from sewage works in the catchment. There is also growing evidence that internal loads from the sediments have been decreasing since the late 1990s (Carvalho and Kirika, 2002). Conversely, nitrate concentrations appear to be increasing in recent years, particularly since the mid-1990s. This nutrient is largely derived from diffuse agricultural sources in the catchment (Bailey-Watts and Kirika, 1999) and may, therefore, be increasing largely in response to enhanced run-off associated with the increasing rainfall trend (Heathwaite and Johnes, 1996). The non-monotonic trends observed for both chlorophyll$_a$ and *Daphnia* were well described by the nonparametric additive modelling approach. The models highlighted that significant reductions in chlorophyll$_a$ concentrations were only apparent early on in the time series, largely following the re-establishment of *Daphnia* populations. For the most recent period (1988-2002) no significant trends were apparent for either chlorophyll$_a$ or *Daphnia*. The lack of chlorophyll$_a$ response to the more recent phosphorus reductions suggests that phosphorus may no longer be limiting phytoplankton over this period. In terms of an annual chlorophyll$_a$ response, increases in nitrate availability may have off-set phosphorus reductions, or, limitation by grazers may be more important.

Seasonal trends

Annual trends do not, however, reflect changes in the seasonal processes occurring in a lake, it may be that phosphorus or nitrogen availability or grazer densities show more distinct seasonal trends.

As expected, trends were much more apparent when seasons were examined separately. In terms of climatic changes, the trend to warmer springs as observed here has also been observed in many other studies and potentially has direct physiological effects (e.g. enhanced growth rates) on plankton communities (Anderson, 2000; Petchey et al., 1999) as well as effects on phenology (the timing of the spring blooms and clear water phases) and, therefore, changing relationships between predators, *Daphnia*, and prey, phytoplankton, (Anneville et al., 2004; Winder and Schindler, 2004).

The fact that chlorophyll$_a$ also showed significant declining trends, particularly in spring, suggests it could be an indirect response to the warmer spring temperatures (a direct response is generally assumed to result in an increase in chlorophyll$_a$). The seasonal breakdown of chlorophyll$_a$ trends does also appear to show a further recent recovery in spring and summer chlorophyll$_a$ since 2000, although, as for temperature, these trends were not significant if the last 15 years were considered (1988-2002). It is not immediately obvious, however, how warmer springs would result in reduced algal biomass. Other than temperature, potential drivers of the spring chlorophyll$_a$ reductions could be reduced SRP availability or increased *Daphnia* densities. There is not a lot of evidence for the former, as spring SRP concentrations generally increased from 1968-1975 (the period over which greatest reductions in chlorophyll$_a$ occurred) and have remained more or less unchanged since 1995 (the later period of further chlorophyll$_a$ reductions). Summer SRP concentrations have declined since

1995 and may, therefore, be responsible for some of the reductions observed in summer chlorophyll$_a$ since 1995. There is, however, much more supporting evidence for the role of *Daphnia* in limiting the spring phytoplankton, as the big decline in chlorophyll$_a$ concentrations in the early 1970s is consistent with the re-appearance of *Daphnia* in the loch. This followed several years absence, thought to be due to regular pesticide pollution from industry in the catchment. There is also evidence for increased spring *Daphnia* densities since 2000 which could be responsible for the reductions in chlorophyll$_a$ observed over these recent years.

The effects of pesticides were most likely responsible for the changes observed in *Daphnia* densities before 1971. Some studies have shown the positive effect of increasing spring temperatures on *Daphnia* abundance, thought to be associated with enhanced growth and reproductive rates. In the example of Loch Leven, however, there is no clear evidence to suggest that temperature changes were responsible for determining spring *Daphnia* densities although previous analysis, Ferguson et al. (2007), showed significant positive relationships between late winter/early spring temperatures and spring *Daphnia* densities.

In contrast to changes in spring, winter chlorophyll$_a$ concentrations appear to show an increasing trend from the early 1980s. This may possibly be associated with enhanced growth rates associated with the slightly warmer winters observed, although neither trends were significant when the last 15 years were considered (1988-2002). Rainfall also showed a generally increasing statistically significant trend in winter. This may have resulted in enhanced loading of nutrients that are predominantly from diffuse-sources, such as nitrate (Heathwaite and Johnes, 1996), which could have also helped support increased phytoplankton productivity. However, increased rainfall also results in an increased flushing rate and potentially, therefore, enhanced losses of phytoplankton from the lake (Bailey-Watts et al., 1990).

The differing chlorophyll$_a$ trends in winter and spring highlight the importance of examining seasonal trends. It is possible that reductions in spring phytoplankton are offset by increases in winter crops, resulting in no clear changes if examined as an annual measure.

Seasonality

All variables showed significant seasonality, represented well by the smooth function of month in the additive models. The seasonality of SRP shows clear minima in spring to levels close to the limit of detection, while nitrate remains high. In summer the opposite is true, with nitrate declining to undetectable levels while SRP concentrations increase. There is clearly a switch from a more P-limited system in spring to a more N-limited system in summer, which has implications for catchment management of both nitrogen and phosphorus sources, particularly diffuse sources of nitrogen in summer.

One major innovation of the statistical models outlined is that they allow analysis of changes in seasonality. This is only apparent for chlorophyll$_a$ with earlier (but much reduced) peaks in late winter/early spring (February/March) and more obvious minima in late spring/early summer (May/June). The earlier peak may be a response to slightly warmer winter and spring months and the clearer minima could also be an indirect response to temperature via increased grazers over these later months. The chlorophyll$_a$ minima certainly occurs concurrently with the *Daphnia* maxima over these two months. A previous analysis of relationships between ecological responses and environmental drivers, Ferguson et al. (2007), highlighted a significant positive relationship between spring water temperatures and spring *Daphnia*, providing supporting evidence for a climatic effect on chlorophyll$_a$ seasonality.

Assessing ecological responses to environmental change

The statistical modelling of the Loch Leven datasets illustrates a number of advantages for assessing environmental changes in ecological datasets. Firstly, although many physical or chemical drivers of change may show more or less linear trends (e.g. temperature and phosphorus changes at Loch Leven), biological responses (e.g. chlorophyll$_a$ and *Daphnia*) often show more complex, non-linear trends. For this reason nonparametric models are required to assess non-monotonic patterns over time and throughout the year. Autocorrelation is also common in ecological datasets and these models present methods for incorporating correlated errors where necessary. Cyclic components, such as month of the year, can also be included using a circular smoother, to enable investigation of seasonal patterns across the months of the year, in addition to trends.

Because of strong seasonality, environmental changes in freshwater ecosystems are often assessed using annual measures of nutrients or chlorophyll$_a$ (e.g. Organisation for Economic Cooperation and Development OECD, 1982). This may, however, mask important seasonal trends. The analysis at Loch Leven highlights the greater scope for identifying, or at least implicating, the drivers or processes responsible for the changes without constraining trends to be linear. Clearly cause and effect cannot be identified, but at least strong and significant relationships between variables can be used to infer possible hypotheses for further investigation.

While these models provide an extremely valuable exploratory view of the patterns within variables over time, relationships between variables and the effect of covariates on responses in the system are not considered. Ferguson et al. (2007) use extensions of these models with covariates incorporated in the modelling along with terms for trend and seasonality and consider both contemporaneous and lagged relationships between system responses and covariates. Ferguson et al. (2007, 2006) also highlight that univariate and multivariate varying-coefficient models are an effective way to illustrate how relationships between variables change throughout the year. Both modelling approaches are an aid to disentangling the effects of nutrient and climate variables on water quality and grazers and help to provide insight into the different effects of climate change and eutrophication.

The analysis also highlighted the great value of long-term ecological research (LTER) monitoring sites. Ecosystems are rarely affected by only a single pressure; it is much more likely that sites are affected by multiple pressures with synergistic or opposing effects, such as eutrophication and climate change. To be able to disentangle the effects of these pressures requires many decades of data. The trend analysis of the shorter 15 year period illustrated this well, with very few variables showing statistically significant trends that were distinguishable from natural ecosystem variability.

With climate change being a major political issue, it is likely to become increasingly important to demonstrate convincing, statistically-supported, evidence of ecological impacts. The study illustrated the application of the models for assessing changing patterns in seasonality through the use of bivariate nonparametric regression. Such models can be used to explore significant shifts in the phenology of seasonal events (e.g. spring clear-water phase, flowering etc.) and also changing seasonality of processes (e.g. predator-prey relationships). As such, they are likely to prove extremely valuable with regards to highlighting the ecological impacts of climate change.

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Tables

Table 1: Additive model test results for 'no effect' - Approximate F-Test

	p-values for testing for 'no effect vs effect'					
variables	SRP	$N0_3$-N	air temp	rain	*Daphnia*	chlorophyll$_a$
year(68-02)	1.00×10^{-4}	0.011	0.175	4.00×10^{-4}	<0.001	<0.001
month(68-02)	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
year(88-02)	0.026	3.00×10^{-4}	0.458	0.166	0.698	0.838
month(88-02)	<0.001	<0.001	<0.001	<0.001	<0.001	2.00×10^{-4}

Table 2: Additive model test results for 'linearity'- Approximate F-Test

p-values for testing for 'linear vs nonparametric effect'						
variables	SRP	$N0_3$-N	air temp	rain	*Daphnia*	chlorophyll_a
year(68-02)	0.057	0.005	0.754	0.169	<0.001	2.00×10^{-4}
year(88-02)	0.319	0.004	0.401	0.222	0.562	0.725

Table 3: Nonparametric regression test results for 'no effect' - Approximate F-Test

p-values for testing for 'no effect vs effect' for 1968-2002						
season	SRP	$N0_3$-N	air temp	rain	*Daphnia*	chlorophyll$_a$
spring	0.048	0.136	0.057	0.098	<0.001	2.00×10^{-4}
summer	0.038	0.051	0.903	0.162	<0.001	0.003
autumn	0.092	0.650	0.153	0.156	0.036	0.321
winter	0.050	0.369	0.142	0.022	0.004	0.021

p-values for testing for 'no effect vs effect' for 1988-2002						
season	SRP	$N0_3$-N	air temp	rain	*Daphnia*	chlorophyll$_a$
spring	0.611	0.138	0.328	0.215	0.365	0.627
summer	0.137	0.071	0.461	0.035	0.566	0.225
autumn	0.050	0.527	0.269	0.510	0.794	0.366
winter	0.104	0.079	0.562	0.857	0.595	0.539

Table 4: Testing for 'changes in seasonality' - Approximate F-test

	p-values for testing for 'changes in seasonality'					
variables	SRP	$N0_3$-N	air temp	rain	*Daphnia*	chlorophyll$_a$
yr,month	0.113	0.204	0.870	0.340	0.224	0.009

Figures

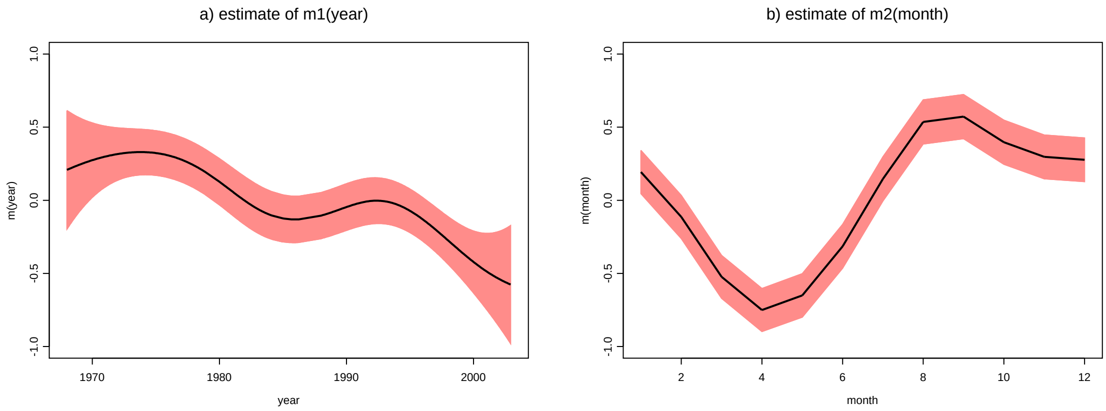


Figure 1: For log SRP as a response from January 1968 to December 2002. Separate component plots for year and month with shaded regions to identify ± 2 standard errors from the estimate. The lag 1 correlation of the residuals is 0.36.

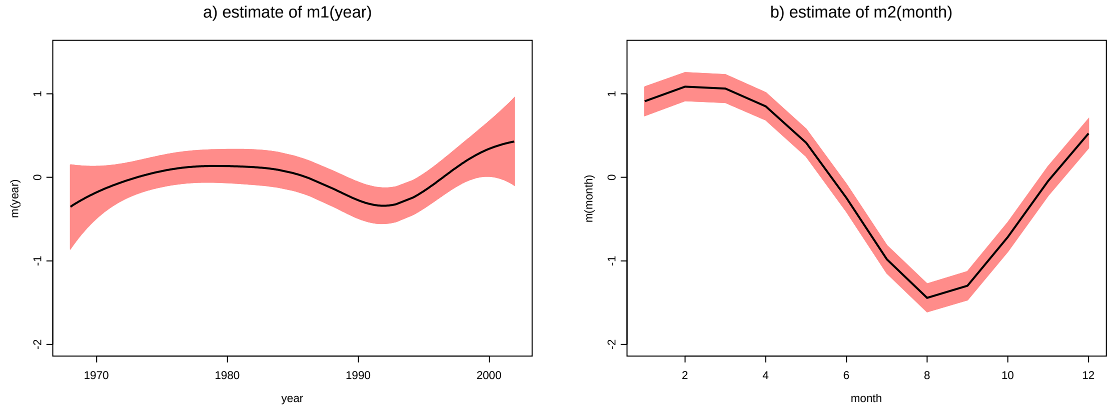


Figure 2: For log NO_3-N as a response from January 1968 to December 2002. Separate component plots for year and month with shaded regions to identify $\pm$ 2 standard errors from the estimate. The lag 1 correlation of the residuals is 0.52.

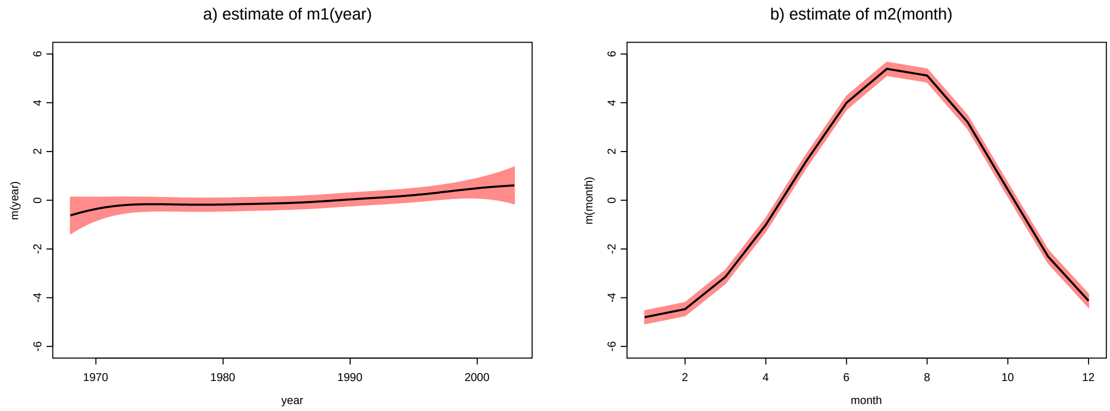


Figure 3: For mean air temperature as a response from January 1968 to December 2002. Separate component plots for year and month with shaded regions to identify $\pm$ 2 standard errors from the estimate. The lag 1 correlation of the residuals is 0.34.

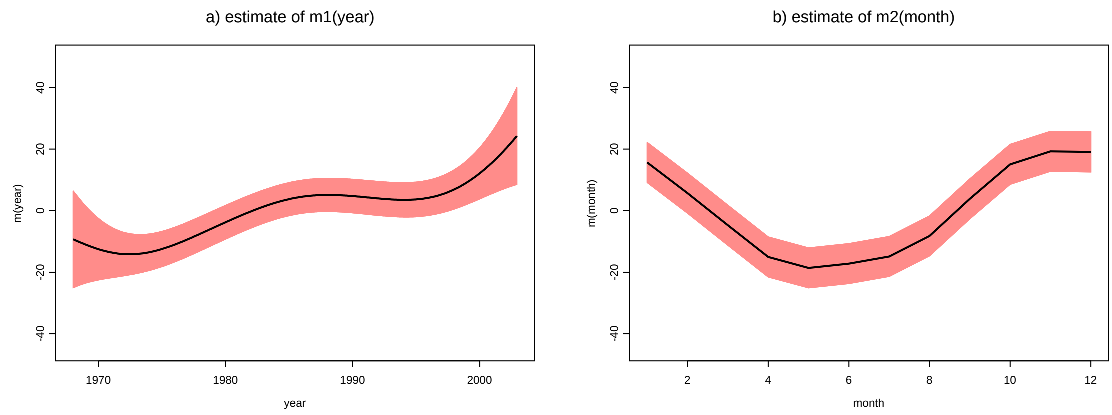


Figure 4: For cumulative monthly rainfall as a response from January 1968 to December 2002. Separate component plots for year and month with shaded regions to identify $\pm$ 2 standard errors from the estimate. The lag 1 correlation of the residuals is 0.03.

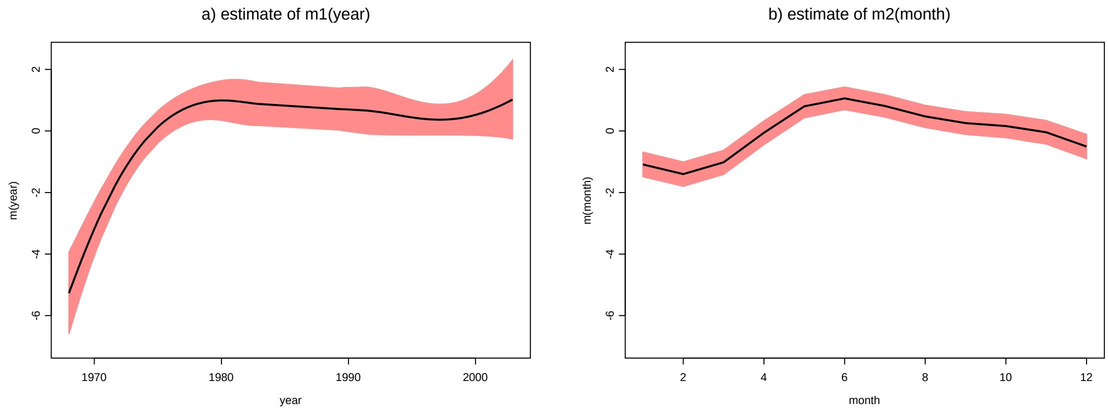


Figure 5: For log *Daphnia* as a response from January 1968 to December 2002. Separate component plots for year and month with shaded regions to identify $\pm$ 2 standard errors from the estimate. The lag 1 correlation of the residuals is 0.68.

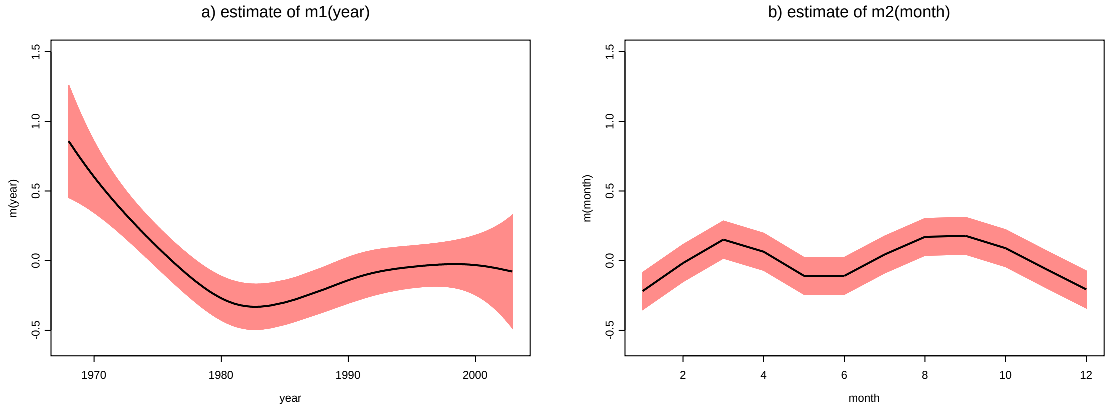


Figure 6: For log chlorophyll$_a$ as a response from January 1968 to December 2002. Separate component plots for year and month with shaded regions to identify $\pm$ 2 standard errors from the estimate. The lag 1 correlation of the residuals is 0.49.

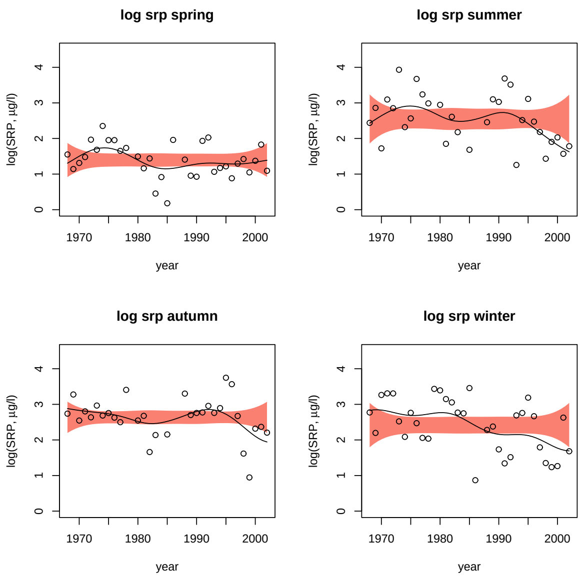
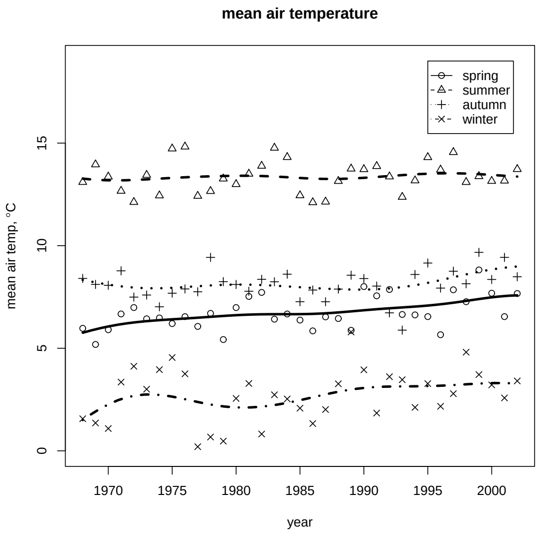


Figure 7: Scatterplots with nonparametric regression for log SRP seasonally from January 1968 - December 2002. A reference band for 'no effect' is also provided.



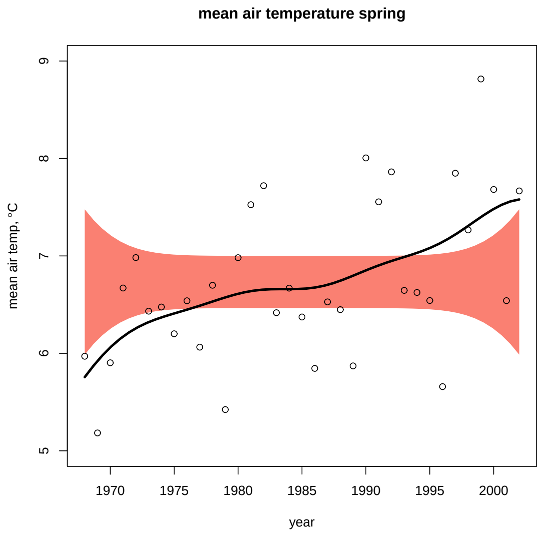


Figure 8: (Left) Scatterplot with nonparametric regression curves for mean air temperature seasonally from January 1968 - December 2002. (Right) Scatterplot with nonparametric regression for mean air temperature in spring from January 1968 - December 2002, a reference band for 'no effect' is also provided.

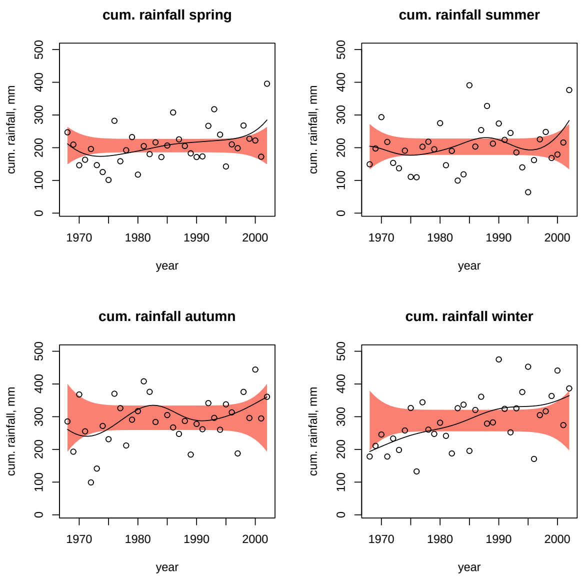


Figure 9: Scatterplots with nonparametric regression for cumulative seasonal rainfall from January 1968 - December 2002. A reference band for 'no effect' is also provided.

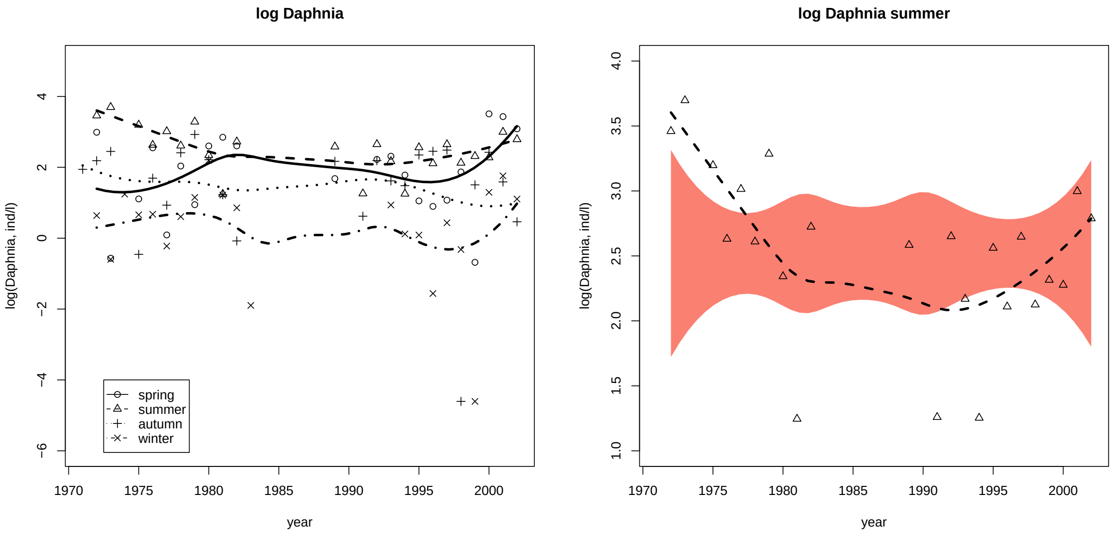


Figure 10: (Left) Scatterplot with nonparametric regression curves for log *Daphnia* seasonally from January 1971 - December 2002. (Right) Scatterplot with nonparametric regression for log *Daphnia* in Summer from January 1971 - December 2002, a reference band for 'no effect' is also provided.

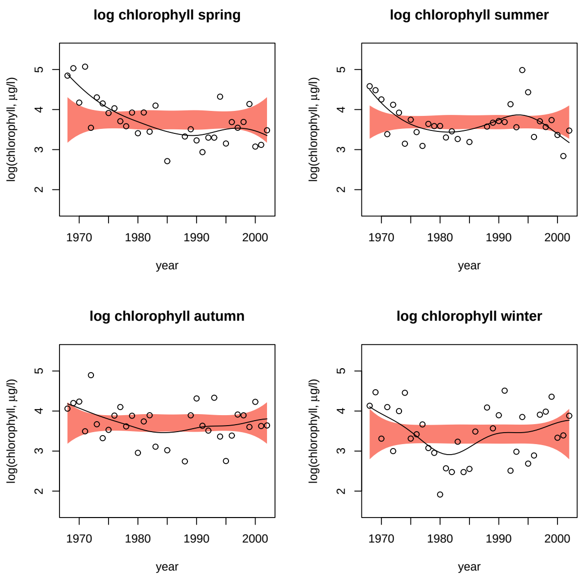
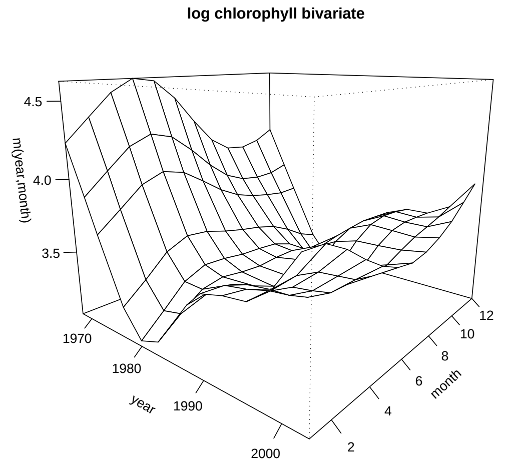


Figure 11: Scatterplots with nonparametric regression for log chlorophyll$_a$ seasonally from January 1968 - December 2002. A reference band for 'no effect' is also provided.



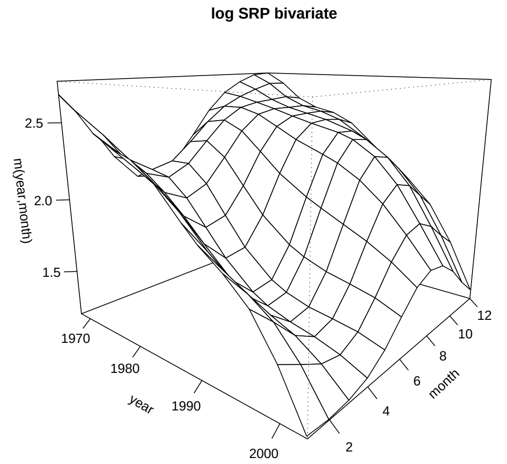


Figure 12: For log chlorophyll$_a$ (left) and log SRP (right) as a response with a bivariate term m(year,month). The lag 1 correlation of the residuals is 0.48 and 0.41 respectively.