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Assessing Ecological Resilience to Human Induced Environmental Change in Shallow Lakes



THE UNIVERSITY
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Declaration

The candidate confirms that the work submitted is his own, except where work which forms part of jointly-authored publications has been included. The thesis contains three chapters which are intended for publication in peer-reviewed journals. Details of each publication are given below. The candidate confirms that appropriate credit has been given within the thesis where reference has been made to the work of others. No part of this work has been submitted for any other degree or professional qualification.

Lay summary

Shallow lakes are one of the most common ecosystems on Earth and often represent the main source of water and food for humans, as well as providing areas for recreation and income from tourism. Environmental changes such as pollution from industry and farming, as well as changes to temperature and rain patterns, can cause shallow lakes to suddenly change from clear water with plenty of aquatic plants to a state where the water turns green with algae and most of the aquatic plants disappear. Once this change occurs, the lake is likely to remain in this state unless steps are taken to reverse the process. The consequences of this transformation can be severe, from water being no longer safe to drink and reduced availability of food. Understanding how, why and when these changes happen has been an area of intense research in recent decades. Tools expected to be capable of predicting these changes have been developed (early warning indicators (EWIs)) but have not been entirely successful. Furthermore, our understanding of this process, as well as interaction between the components of the lake involved in regulation of the changes, known as ecological resilience, is limited.

To better understand these changes and ways of predicting them, data were analysed from the Loch Leven Long-Term Monitoring Programme. Loch Leven is a large shallow lake in Scotland which has been studied for nearly 200 years. Monitoring data for different chemicals, animals and algae from the last 45 years was analysed to see if any sudden change had occurred. Changes were found amongst all these groups at different times over the last 45 years and EWIs were tested to determine if these changes can be predicted. Using EWIs in a group was found to lead to more accurate predictions. A more detailed analysis was conducted of a sudden change which occurred in 2007 as part of Loch Leven's recovery from nutrient pollution. Chemical, animal and algal components in the loch were all found to have changed in the same period, most of which happened suddenly.

A computer model capable of simulating Loch Leven was then used to measure its resilience using data from before the recovery and after the recovery. The results revealed low resilience in the loch, which means it is very vulnerable to any future environmental changes. To understand how Loch Leven would react to future changes the same computer model was used to test the effects of climate change predictions for temperature and rain for eastern Scotland. Wetter autumns and winters, leading to small increases in lake water depth and

addition of particles of mud, silt and sand from the surrounding landscape, were shown to pose the greatest risk to Loch Leven. These changes could lead to a turbid state with lots of algae, whereas higher temperatures combined with less rain in the summer can lead to the most intense algal blooms in the water.

It is thought that some kinds of shallow lakes are more at risk of change than others. Large lakes like Loch Leven, which is slightly deeper than most shallow lakes and has a few deep areas, are thought to be less resilient to change. Its depth means it is harder for aquatic plants to cover large areas which could help control algal growth. Because of this, maintaining good water conditions is more reliant on small animals, called water fleas, which graze on the algae. It was found that in Loch Leven and other lakes like it, water fleas are a key factor in maintaining the clear state. Understanding these processes and testing tools such as EWIs can help managers and scientists to target actions designed to both restore lakes to a clear state and prevent a sudden change to a turbid state. This understanding can help save money in water treatment costs in some areas as well as assist communities reliant on local shallow lakes for food and water to better manage a resource essential to their survival.

Abstract

Sudden unpredictable changes in ecosystems are an increasing source of concern because of their inherent unpredictability and the difficulties involved in restoration. Our understanding of the changes that occur across different trophic levels and the form of this change is lacking. This is especially true of large shallow lakes, where characteristics such as fetch and depth are close to theoretical boundary values for hysteretic behaviour. The development of reliable indicators capable of predicting these changes has been the focus of much research in recent years. The success of these early warning indicators (EWIs) has so far been mixed. There remain many unknowns about how they perform under a wide variety of conditions and parameters. Future climate change is predicted to have a wide range of impacts through the interaction of combined pressures, making the understanding of EWIs and the in-lake processes that occur during regime shifts imperative. Loch Leven, Scotland, UK, is a large shallow lake with a history of eutrophication, research and management and as such is an ideal study site to better understand resilience and regime shifts under a range of interacting stressors.

The objectives of this research are to: (1) analyse long term data to identify the occurrence of common tipping points within the chemical (water column nutrient concentrations) and biological (macrophytes, phytoplankton, zooplankton) components of the loch, then test these tipping points using five statistical early warning indicators (EWIs) across multiple rolling window sizes; and (2) quantify the changes in lake ecology using a before/after analysis and testing for non-linearity, combined with modelling using the aquatic ecosystem process model PCLake to determine the level of resilience following a regime shift during recovery from eutrophication; (3) using PCLake, examine the sensitivity of Loch Leven to regime shifts in the face of predicted environmental change (e.g. climate change, nutrient pollution).

Statistical analysis identified tipping points across all trophic levels included, from physical and chemical variables through to apex predators. The success of EWIs in predicting the tipping points was highly dependent on the number of EWIs used, with window size having a smaller impact. The 45% window size had the highest overall accuracy across all EWIs but only detected 16.5% more tipping points than the window size with the lowest overall accuracy. Differences between individual EWI performance and usage of them as a group

was substantial with a 29.7% increase between the two. In both individual and group use of EWIs, false positives (early warning without a tipping point) were more common than true positives (tipping point preceded by EWI), creating significant doubts about their reliability as management tools.

Significant change was seen across multiple variables and trophic levels in the before/after analysis following sudden recovery from eutrophication, with most variables also showing evidence of non-linear change. Modelling of responses to nutrient loading for chlorophyll, zooplankton and macrophytes, under states from before and after the shift, indicate hysteresis and thus the presence of feedback mechanisms. The modelling of responses to nutrient loading and predicted climate change in temperature and precipitation demonstrated that increases in temperature and decreases in summer precipitation individually had large impacts on chlorophyll and zooplankton at medium to high phosphorus (P) loads. However, modelling of the combined effects of these changes resulted in the highest lake chlorophyll concentrations of all tested scenarios. At low P loads higher temperatures and increased winter precipitation had the greatest impact on system resilience with a lower Critical Nutrient Load (CNL). The difference between chlorophyll and zooplankton as opposed to macrophytes was in the presence of a lower CNL for the increased winter precipitation-only scenarios which was not seen in the macrophytes. This highlights the potential role of high winter inputs potentially loaded with particulate matter in reducing resilience at lower P loads.

This research has highlighted the vulnerability and low resilience of Loch Leven to environmental change. The presence of multiple tipping points and high levels of EWI activity show a high level of flexibility in the system. Coupled with the occurrence of widespread trophic change during a sudden recovery and a small level of hysteresis and high levels of sensitivity to climate change, the low levels of resilience become clear. The impact of lake-specific characteristics such as moderate depth, large fetch and a heterogeneous bed morphology is particularly evident in the limitations on macrophyte cover and the reliance on zooplankton to determine the hysteresis offset (amount of phosphorus (P) loading between the two CNL). The presence of these characteristics can be used to identify other lakes vulnerable to change. Improving the predictive capabilities of resilience indicators such as EWIs, and better understanding of the ecological changes that occur during non-linear change in response to recovery and climate change, can help target relevant ecosystem

components for preventative management. These actions may become necessary under even the most conservative estimates of environmental change.

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Contents

Declaration	iii
Lay summary	v
Abstract	vii
Acknowledgements	xi
Contents	xiii
List of Tables	xvii
List of Figures	xix
Chapter 1 - Introduction	1
1.1 Regime shifts and resilience	3
1.2 Hysteresis and feedback mechanisms in lakes	3
1.3 Regime shifts and ecological reasons for sudden change	9
1.4 Erosion of resilience	12
1.4.1 Interacting stressors and resilience	13
1.4.2 Long-term impacts on resilience	14
1.5 Early warning indicators and the prediction of regime shifts	16
1.5.1 Resilience and variability across scales	18
1.6 Key Challenges identified from the literature	19
1.7 Research aims and objectives	20
1.8 Thesis structure	21
Chapter 2 – Methodology	23
2.1 Study site description	24
2.1.1 Loch Leven long term monitoring field methods	26
2.2 Zooplankton body size analysis	27
2.3 PCLake model setup	28
2.3.1 Derivation of Loch Leven nutrient loading for input to PCLake	30
2.3.2 PCLake Calibration and Validation	31
Chapter 3 - Assessing the use of statistical early warning indicators to predict ecological tipping points in a shallow lake, Loch Leven, U.K	39
3.1 Introduction	40
3.2 Methods	42
3.2.1 Study site	42

3.2.2 Data processing and analysis	42
3.2.3 Assessing optimum window size for EWIs.....	43
3.3 Results	44
3.3.1 Tipping point detection and coherence	44
3.3.2 Tipping point and EWI coherence across different window sizes	46
3.3.3 EWI Performance	47
3.4 Discussion	52
Chapter 4 - Assessing the occurrence of a regime shift in Loch Leven, UK: Ecological change and the presence of hysteresis.....	57
4.1 Introduction	58
4.2 Methods	60
4.2.1 Data Collection.....	60
4.2.2 Data Processing and Analysis	61
4.2.3 Process modelling using PCLake.....	62
4.3 Results	62
4.3.1 Before/After Analysis	62
4.3.2 Test for non-linear change	63
4.3.3 Process modelling of before and after states.....	66
4.4 Discussion	69
4.4.1 Ecological change across trophic levels	70
4.4.2 Impacts of climate on ecological change leading to a regime shift	71
4.4.3 Components of hysteresis and resilience in Loch Leven	71
4.4.4 Conclusions	73
Chapter 5 - Resilience of Loch Leven to Future Environmental Change	75
5.1 Introduction	76
5.2 Methods	78
5.3 Results	81
5.3.1 Chlorophyll responses	82
5.3.1.1 Low P loads	82
5.3.1.2 Low to medium P loads	82
5.3.1.3 Medium to high P loads.....	82
5.3.2 Macrophyte responses	83
5.3.3 Zooplankton responses	83
5.3.3.1 Low P loads	83
5.3.3.2 Medium to high P loads.....	83

5.4 Discussion	88
5.4.1 Responses to increased temperature and nutrient loading	88
5.4.2 Responses to changes in precipitation and nutrient loading	90
5.4.3 Temperature, precipitation and nutrient loading as interacting stressors	91
5.5 Conclusion	92
Chapter 6 – Overall discussion and conclusions.....	93
6.1 Interaction between non-linear change, early warning indicators and resilience ...	94
6.1.1 Detection of non-linear change in ecosystems and time series	94
6.1.2 Success rates of EWIs and problems with their use.....	95
6.1.3 Rolling window size and the occurrence of false positives	96
6.1.4 Capturing and understanding variability.....	98
6.2 Ecological change and stressor-response relationships: the dominant role of zooplankton.....	100
6.2.1 Hysteresis and the presence of feedback mechanisms	101
6.2.2 Resilience in Loch Leven and implications for management.....	103
6.3 Predicting resilience to climate change in large shallow lakes.....	105
6.3.1 Climate change, nutrients and resilience in Loch Leven	106
6.3.2 Evolution and the impact of parasites on lake resilience	108
6.4 Future research	110
6.4.1 Development of EWIs as predictive tools and ecological indicators.....	110
6.4.2 Interaction of stressors-response relationships with direction of impact	111
6.4.3 Landscape impacts on resilience: patterns of vulnerability in scale	111
6.5 Conclusions and wider implications	112
References	115
Appendix A	149
Appendix B.....	231
Appendix C.....	243

List of Tables

Table 1.1 Stabilising feedback mechanisms in shallow lakes.....	7
Table 1.2 Documented perturbations that led to a reported regime shifts in lakes. Switch type refers to direction of shift i.e. forward switch is a shift from a clear water state to a turbid water state and a reverse switch is a shift from a turbid water state to a clear water state.....	11
Table 2.1 List of datasets used for the tipping point/EWI analysis in Chapter 3.....	28
Table 2.2 List of PCLake variables changed during calibration to Loch Leven data. Sources of data are listed as LTMP (Loch Leven long term monitoring data), Met office (Met Office, 2019a, 2019b), Defew (Data gathered during 2005 Leven Loading survey (Defew, 2008)), Climate hydrology and ecology research support system (CHESS) (Robinson et al., 2016), Est. (Estimated due to lack of measured data).....	35
Table 3.1. Total number of tipping points considered at each window size along with the maximum number of true positives that could be detected along with results of the EWI analysis.....	45
Table. 3.2 EWI response for all window sizes for each individual tipping point by dataset. Numbers in bold show total responses for an individual EWI. Numbers in brackets differentiate different tipping points within the same time series. Blank cells represent no occurrences of that response type. Abbreviations for Trophic level are as follows: PP – Primary Producer, PC – Primary Consumer, SC- Secondary Consumer, AP – Apex Predator.....	50
Table 4.1 Statistical test results with the type of test performed for all tested variables within Loch Leven. Corrected P value column represents results subjected to Benjamini-Hochberg corrections for multiple tests. BDS P value column represents results for BDS tests performed on significant variables after correction. Values in bold represent significant results.....	61
Table 5.1 Overview of data used for climate change inputs to model runs (from UKCP09, 2009). Values with codes in brackets represent temperature/precipitation only runs. The worst-case scenario run values are market with *. Letters and numbers in brackets in emissions column and under probability headings represent scenario code.....	77

List of Figures

Fig. 1.1 Hypothetical stressor-response relationship showing differences in response to a pressure between a ‘clear’ water state and a ‘turbid’ water state in a hypothetical shallow lake.....	6
Fig. 1.2 Schematic diagram showing major feedback mechanisms in a shallow lake. Black frames boxes and arrows represent mechanisms that help stabilise a clear water state, red framed boxes and arrows represent mechanisms that help stabilise a turbid water state.....	8
Fig. 2.1 Bathymetric map of Loch Leven (Spears et al., 2012).....	27
Fig. 2.2 Model structure of PCLake (Janse et al., 2010).....	29
Fig. 2.3 Map of sampled streams (Gb, Gu – Gairney water, Sa – South Queich, Na – North Queich, Ca – Camel burn, Pb – Pow/Greens burn, Sl – Sluices/Outflow) during the 2005 nutrient loading survey of Loch Leven used in the calibration of PCLake.....	31
Fig. 2.4 PCLake comparison of observed values (circles) against modelled values (line) for Chlorophyll a.....	33
Fig. 2.5 PCLake comparison of observed values (circles) against modelled values (line) for NO ₃ -N.....	33
Fig. 2.6 PCLake comparison of observed values (circles) against modelled values (line) for Total Phosphorus.....	34
Fig. 2.7 PCLake comparison of observed values (circles) against modelled values (line) for Zooplankton Biomass.....	34
Fig. 3.1 Timeline of fishery and management events (top of graph) along with detected tipping points (bottom of graph) in Loch Leven.....	44
Fig. 3.2 Example graph showing detrended chlorophyll a time series in Loch Leven with the solid black line showing detrended raw data and the dashed black line showing raw EWI data. Changes of thickness of overlaid blue line show detected tipping points. Changes in overlaid red line show detected changes in the EWI at 15% window size. Other graphs from this analysis can be found in Appendix 1.....	45

Fig. 3.3 Number of datasets containing False Negatives (FN), False Positives (FP) and True Positives (TP) at different window sizes across all five EWIs.....	46
Fig. 3.4 Number of datasets containing False Negatives (FN), False Positives (FP) and True Positives (TP) across five different EWI over all window sizes.....	47
Fig. 3.5 Number of true positives for EWIs individually and as a group (All) as a percentage of the total number of true positive possible.....	48
Fig. 3.6 Number of different response types (False Negatives (FN), False Positives (FP) and True Positives (TP)) across all trophic levels (Primary Producers (PP), Primary Consumers (PC), Secondary Consumers (SC) and Apex Predators (AP)).....	49
Fig. 4.1 Before/After results for named variables within Loch Leven. Before results represent processed data for 2000-2006, after results represent processed data for 2007-2013.....	63
Fig. 4.2 Count of helmet presence in individual <i>Daphnia</i> specimens measured for body size. Before and after results represent the same number of individuals sampled.....	64
Fig. 4.3 Stressor-Response relationship between chlorophyll and phosphorus load in two states in Loch Leven modelled in PCLake. The before state is represented using data from 200-2005 and the after state is represented using 2008-2013 data. Critical nutrient loads (CNL) are calculated as the point directly after its sudden rise. CNL are: Before - $1.325 \text{ mg m}^{-2} \text{ day}^{-1}$, After - $1.815 \text{ mg m}^{-2} \text{ day}^{-1}$	65
Fig. 4.4 Stressor-Response relationship between zooplankton biomass and phosphorus load in two states in Loch Leven modelled in PCLake. The before state is represented using data from 200-2005 and the after state is represented using 2008-2013 data. Critical nutrient loads (CNL) are calculated as the point directly after its sudden rise. CNL are: Before - $1.325 \text{ mg m}^{-2} \text{ day}^{-1}$, the after state does not have a CNL as it rises in 3 steps before reaching the same level as the before state. These steps are at $1.08 \text{ mg m}^{-2} \text{ day}^{-1}$, $1.325 \text{ mg m}^{-2} \text{ day}^{-1}$ and $1.57 \text{ mg m}^{-2} \text{ day}^{-1}$	66
Fig. 4.5 Stressor-Response relationship between macrophyte percentage cover and phosphorus load in two states in Loch Leven modelled in PCLake. The before state is represented using data from 200-2005 and the after state is represented using 2008-2013 data. Critical nutrient loads (CNL) are calculated as the point directly after its sudden rise. CNL are: Before - $1.325 \text{ mg m}^{-2} \text{ day}^{-1}$, After - $1.815 \text{ mg m}^{-2} \text{ day}^{-1}$	67

Fig. 5.1 Example experimental layout of a single tier. An example run could include a value from low emissions precipitation and medium emissions temperature for each of the probability levels.....78

Fig. 5.2 Responses of chlorophyll a to varying levels of P loading under a range of temperature and precipitation scenarios. Low, high and medium emissions scenario groupings are for precipitation with Misc showing control, single pressure and worst-case scenarios.....82

Fig. 5.3 Responses of macrophyte % cover to varying levels of P loading under a range of temperature and precipitation scenarios. Low, high and medium emissions scenario groupings are for precipitation with Misc showing control, single pressure and worst-case scenarios. Arrows describe groupings due to label grouping.....83

Fig. 5.4 Responses of zooplankton biomass to varying levels of P loading under a range of temperature and precipitation scenarios. Low, high and medium emissions scenario groupings are for precipitation with Misc showing control, single pressure and worst-case scenarios.....84

Chapter 1 - Introduction



Our ecosystems are facing a period of unprecedented environmental change due to anomalous weather patterns associated with climate change, the ingress of non-native invasive species, agricultural and industrial pollution, and overexploitation of ecosystem services and resources (Millenium Ecosystem Assessment, 2005). Ecosystem responses to environmental change have long been assumed to respond in a smooth, gradual and reversible way. In recent decades it has become increasingly apparent that ecosystems and communities can appear healthy and stable in the face of different pressures then suddenly shift into an entirely different state which has been termed a 'regime shift' (Andersen et al., 2009), with examples observed in lakes (Ibelings et al., 2007; Jackson, 2003; Moss et al., 1996; Rip, 2007; Scheffer and Carpenter, 2003), oceans (Done, 1992; Steele, 1998), forests (Hirota et al., 2011) and savannah (Kéfi et al., 2007).

Regime shifts can have an array of impacts on both the ecosystems and the societies that rely on those systems. Examples of losses of ecosystem services can be seen in a number of systems, such as the shift from savannah to desert or scrub wood (Kéfi et al., 2007). This can remove grazing habitat for wild and domesticated animals resulting in losses for societies that rely on this grazing for livestock (Anderies et al., 2002). Another example of losses of ecosystem services can be seen in shallow lakes when they experience a shift from a clear water to a turbid water regime. These ecosystems can provide many services to local communities such as drinking water, recreation and food, all of which can be negatively impacted by this regime shift. High phytoplankton densities can increase the cost of water treatment, and cause health risks to humans when in contact with bloom - containing water (van Dolah et al., 2001). Waterfowl populations reliant on macrophytes for food can disappear altogether on severely impacted lakes reducing their conservation and recreational value (Jupp and Spence, 1977). Severe algal blooms can also result in anoxic conditions and lead to fish kills, reducing revenue for the local economy and recreational value for anglers (Folke et al., 2004b). Through this small number of examples, it is possible to see the harmful effects regime shifts in lakes can have on society. However, our capacity to predict such events is currently limited by a lack of process understanding of the factors acting to drive sudden large-scale ecological change. This knowledge gap hampers management and demonstrates the urgent need for better detection, attribution, and prediction of such events and this thesis sets out to demonstrate approaches for addressing this knowledge gap in Loch Leven, a large shallow lake in the UK.

1.1 Regime shifts and resilience

The basic idea behind regime shifts is simple and can be likened to a canoe on water. If a person leaned over to one side in a canoe, the angle would shift relatively little until a critical threshold is reached beyond which the canoe will suddenly tip over completely. The key is the threshold; just before this threshold you could lean back and easily return to an upright position. Once this point is reached however, the canoe will shift to an alternate regime (also referred to as an alternate stable state, stability domain or basin of attraction (Scheffer et al. 2009)) of being upside down, and the canoeist will get wet. In shallow lake ecosystem this analogy can be represented by two alternate regimes, one characterised by clear water and abundant macrophytes and the other by turbid water and phytoplankton dominance. The mechanisms are more complex, but the basic idea is similar in that shifts in variables (such as nutrient concentrations, temperature, zooplankton abundance) can lead to a shift from one regime to the other (Scheffer et al. 1993). In theoretical terms a regime has been termed a basin of attraction which implies that if the governing variables of an ecosystem enter into one of these basins it will accelerate towards the regime of that attractor (Scheffer et al., 2009), showing the kind of dynamics described in the canoe analogy above.

The term resilience was first defined in ecological terms by Holling (1973) and refined by Walker et al. (2004) and Folke et al. (2004) as “the capacity of a system to absorb disturbance and reorganise while undergoing change so as to retain essentially the same function, structure, identity and feedbacks”. Other simpler definitions of resilience have been proposed most of which use ‘engineering resilience’ defined as the rate of return to an equilibrium following a perturbation (Folke et al., 2004b). This definition takes no account of alternate regimes and so is less applicable to ecosystems with complex non-linear dynamics (Strange, 2007). The resilience of an ecological system such as a lake is has been shown to be determined by a complex set of interacting variables that regulate stabilising feedback mechanisms, which range from physical structure (e.g. fetch) through to community composition (e.g. *Daphnia* abundance/planktivorous fish abundance (Folke et al., 2004b; Scheffer et al., 1993).

1.2 Hysteresis and feedback mechanisms in lakes

The feedback mechanisms described for both the clear water and turbid water regimes act to stabilise them, causing hysteresis (Table 1.1). Shifts in variables (e.g. phosphorus (P)

concentrations, zooplankton abundance) need to be much greater than those that caused the shift in the first place to effect a change in regime and in many cases a further 'shock' to the ecosystem is needed to force a regime shift (see Fig. 1.1). This behaviour is due to feedback mechanisms which stabilise their respective regimes (Scheffer et al., 1993) (see Fig. 1.2). For the clear water state macrophytes stabilise sediment, limiting the extent it can mix into the water column, with some species oxidising the sediment surface, reducing the amount of nutrients released into the water column from bed sediments (Sondergaard et al., 2003). This keeps phytoplankton biomass in check and limits turbidity (Carpenter et al., 1983). Macrophytes also absorb nutrients directly from the water limiting their availability for phytoplankton (Carignan and Kalff, 1980; Lürling et al., 2006) and have been shown to release allelopathic substances that negatively affect the growth of phytoplankton (Hilt and Gross, 2008). Macrophyte beds provide essential refuges for zooplankton and macroinvertebrates from predation, allowing higher population densities and so greater herbivory on phytoplankton and periphyton (Jones and Sayer, 2003; Lauridsen et al., 1996; van Donk and van de Bund, 2002). Macrophyte beds alter fish community dynamics as they buffer the sediment from mixing by cyprinids (Engel, 1988) and act as greater obstacles to cyprinids than to species such as perch, thus changing competitive dynamics (Diehl, 1988). Also predatory fish, such as pike, benefit from the increased habitat complexity offered by macrophytes, increasing their effectiveness as predators and so limiting populations of cyprinids and planktivorous fish (Eklov and Hamrin, 1989).

In the turbid regime similar feedback mechanisms exist. Growth of dense phytoplankton blooms increases turbidity and, when combined with increased likelihood of disturbance of bed sediment in the absence of stabilising structures, such as macrophytes, the amount of light and CO₂ available for macrophyte growth is limited (Moss, 1990). In the absence of macrophytes, the unstructured sediment can, itself, limit the reestablishment of macrophytes (Schiemer and Prosser, 1976). The increased mixing of sediment can result in increased nutrient concentrations in the water column both from the mixed sediment (Spears and Jones, 2010) and also from reducing bed sediment zones (Carpenter et al., 1983). The increased particle density of sediment in the water column can also reduce the filtering efficiency of zooplankton reducing their effectiveness as herbivores (van Donk et al., 1990) as well as creating further shading (Ask et al., 2009). The loss of macrophytes results in refuge loss for many species of zooplankton and macroinvertebrates allowing greater predation pressure by fish so negatively affecting herbivory rates on phytoplankton (Jeppesen et al.,

1998). The fish community is also affected and changes in competitive ability can alter community composition. Cyprinids such as carp and roach rely on tactile orientation methods and so are less affected by turbid water and can outcompete species reliant on vision (Diehl, 1988). These species are also less vulnerable to predation in turbid states due to reduced visual capability and numbers of predatory fish (Lammens et al., 1990). The increased abundance of cyprinids leads to increased sediment re-suspension as their feeding and searching behaviour stirs up sediment and reduces zooplankton numbers through predation (Andersson et al., 1988; Blindow et al., 1993; Meijer et al., 1990). Another consequence of increased cyprinid populations can be that species such as bream can uproot macrophytes and so negatively impact on re-colonisation (Ten Winkel and Meulemans, 1984).

Characterising ecological change throughout a system is an important part of deciphering if a regime shift has taken place. From a management perspective this is particularly important as this can give an indication of how difficult the system would be to restore or how resilient a system is to future environmental change. Despite the benefits of characterising and quantifying the ecological change during a shift it can be a difficult and expensive thing to achieve not least because it requires data from many variables from before, during and after the shift has taken place. These feedback mechanisms demonstrate the presence of hysteresis which as a theoretical construct, helps to simplify the complex and numerous ecological interactions discussed above into something easier to grasp and yet still powerful enough to help understand the presence of alternate states. Recent research has highlighted the use of stressor-response relationships as a way of understanding the form of change that has occurred (Larned and Schallenberg, 2018; Litzow and Hunsicker, 2016). Demonstrating hysteresis using stressor-response relationships involves the plotting of a stressor against a response (e.g. P loading against chlorophyll) (see Fig. 1.1)). What this tells us is that two distinct levels of the response variable can exist at the same level of the stressor variable, which is also comparable to demonstrating the presence of bistability (Andersen et al., 2009). Despite the usefulness of stressor-response relationships in understanding hysteresis they have still proven difficult to produce using observational data (Faassen et al., 2015). In some cases statistical tests such as detrended correspondence analysis (DCA) have been used to generate phase-space plots which can give an indication of bistability and so provide some evidence for the presence of hysteresis (Wang et al., 2012a). Other studies have also shown how different measures of stressor-response relationships can provide strong evidence for

the presence of hysteresis with simpler data and analyses (Bestelmeyer et al., 2011). Through the use of stressor-response relationships we can gain insight into the range of the stressor in which we are likely to see a shift, this range called the hysteresis offset, has the potential to be a useful tool in the management of systems prone to these forms of changes (Larned and Schallenberg, 2018). Combined with our understanding of the feedback mechanisms present in lakes and monitoring of carefully selected variables, there is great potential to learn about different forms of responses to different pressures in a wide range of systems. Combining this understanding with knowledge of system specific characteristics is a clear knowledge gap with which the relative impact on resilience of particular stressors can be quantified.

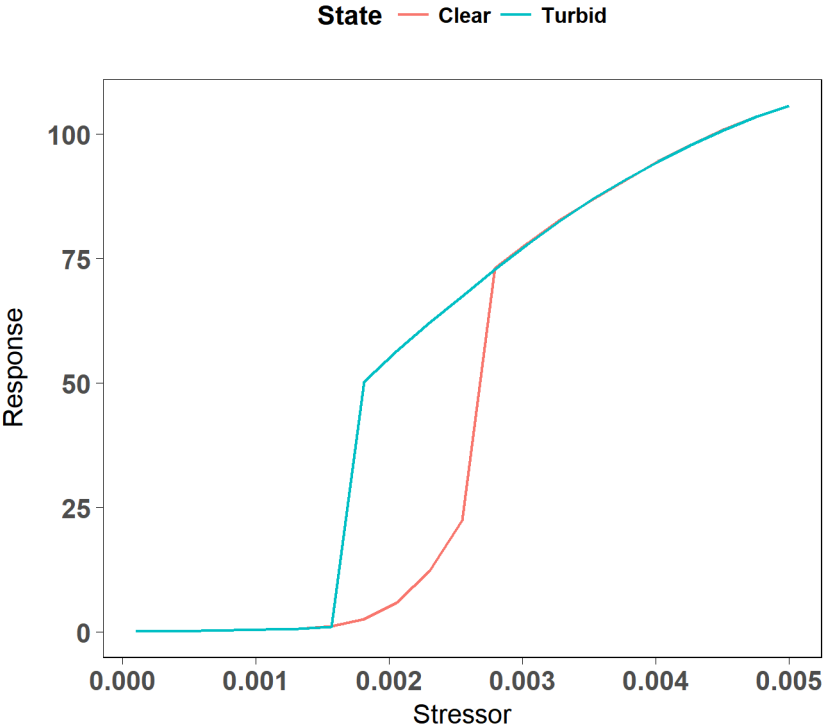


Fig. 1.1 Hypothetical stressor-response relationship showing differences in response to a pressure between a ‘clear’ water state and a ‘turbid’ water state in a hypothetical shallow lake.

Table 1.1 Stabilising feedback mechanisms

Regime	Functional Group	Action	Feedback Mechanism(s)	References
Clear	Macrophytes	Stabilise sediment	Reduces sediment mixing, turbidity, internal loading	Blindow et al., 1993; Engel, 1988
		Refuge for zooplankton	Reduces predation of zooplankton by planktivorous fish allowing higher abundances, increasing phytoplankton grazing rates	Lauridsen et al., 1996; Van Donk and Van de Bund, 2002
		Absorb nutrients	Limits nutrient availability for phytoplankton limiting growth	Carignan and Kalff, 1980; Lürling et al., 2006
		Release allelopathic chemicals	Negatively affect phytoplankton growth	Hilt and Gross, 2008
Turbid	Phytoplankton	Increase environment heterogeneity	Alter fish community dynamics, benefiting piscivorous fish over planktivorous and benthic feeding fish	Diehl, 1988; Eklov and Hamrin, 1989
		Light attenuation	Shade macrophytes limiting growth	Moss, 1990
		Removal of zooplankton refuge	Increased predation by planktivorous fish reducing densities	Jeppesen et al., 1998
		Destabilise sediment through macrophyte loss	Increases turbidity and internal loading of nutrients through wave induced mixing and redox conditions	Carpenter et al., 1983; Spears and Jones, 2010
		Increased particle density in water column	Reduced filtering efficiency of zooplankton decreasing grazing rates, increased shading	Van Donk et al., 1990
		Increase environment homogeneity	Alter fish community dynamics, benefiting benthic and planktivorous fish over piscivorous fish	Lammens et al., 1990
		Increased benthic fish densities	Increased sediment mixing and removal of macrophytes before establishment, increased predation on macroinvertebrates	Andersson et al., 1988; Meijer et al., 1990; Ten Winkel and Meulemans, 1984

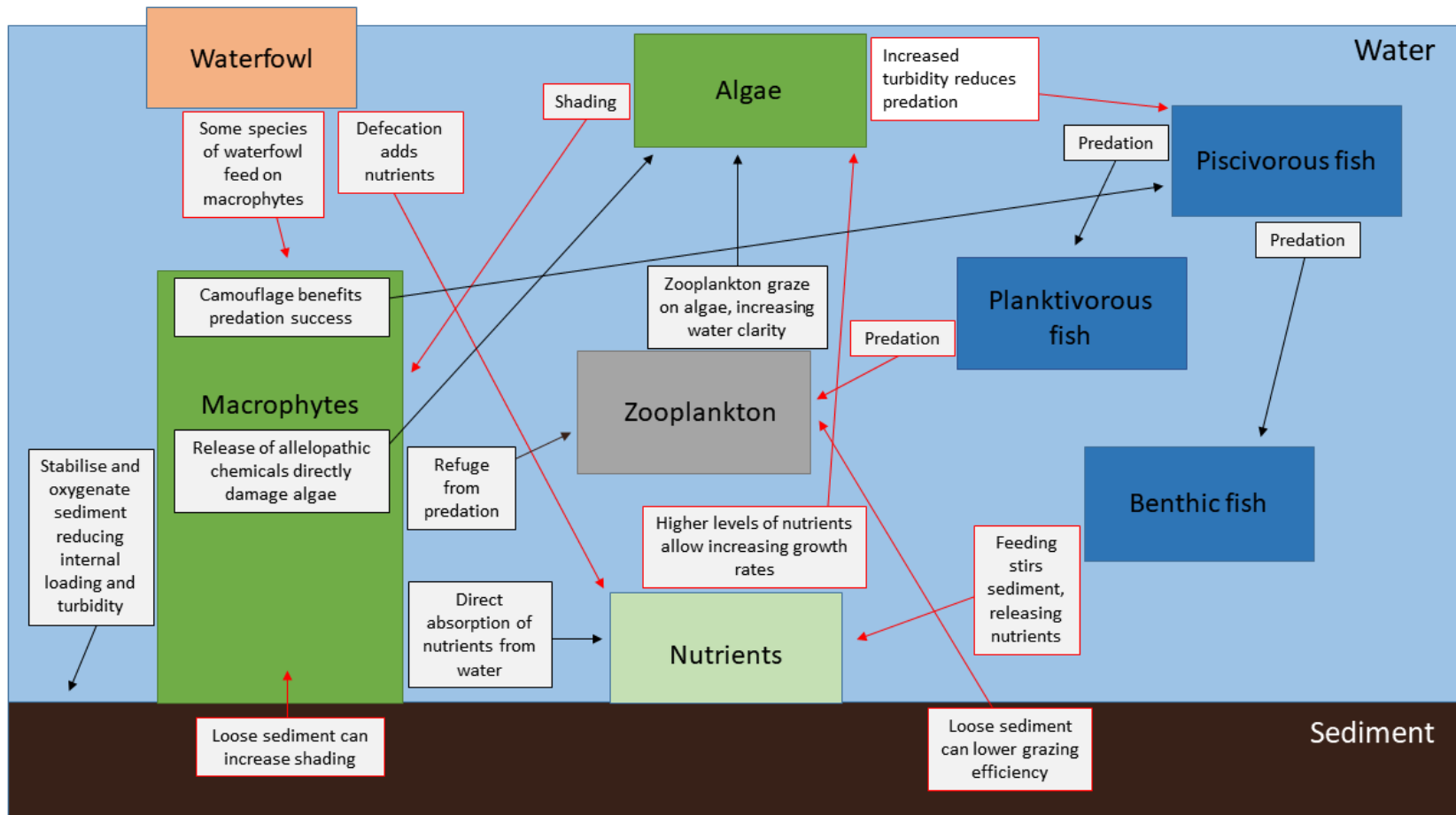


Fig. 1.2 Schematic diagram showing major feedback mechanisms in a shallow lake. Black frames boxes and arrows represent mechanisms that help stabilise a clear water state, red framed boxes and arrows represent mechanisms that help stabilise a turbid water state.

1.3 Regime shifts and ecological reasons for sudden change

Regime shifts between clear water and turbid water regimes can be thought of as forward switches with shifts from turbid water to clear water regimes known as reverse switches. A number of mechanisms have been shown to cause both forward and reverse switches and are summarised in Table 1.2. Although these perturbations have been linked with regime shifts, the conditions within a lake need to be able to support the new regime for it to persist. For instance, if nutrient levels (e.g. nitrogen (N) and P) are low then a turbid water regime is less likely to happen or persist as phytoplankton will not be able to exploit nutrients sufficiently to achieve high growth rates in the face of zooplankton herbivory. If sediment has a chance to settle, enough light should penetrate to allow macrophytes to grow. Although the response is situation dependant, in general these kinds of variables contribute to, or erode, ecological resilience to environmental change and perturbations in shallow lakes.

During a regime shift, different elements of the lake ecosystem can act in different ways. How dominant species react within functional groups such as phytoplankton grazers could be particularly important in understanding the dynamic behaviour seen during a regime shift. Field studies (Mills et al., 1987), enclosure experiments (McQueen and Post, 1988) and simple food chain models of fish-*Daphnia*-phytoplankton dynamics (Scheffer et al., 2000) showed that *Daphnia* populations crashed rather than declining gradually, in response to increased predation. This collapse has been attributed to food limitation rather than direct predation pressure (De Stasio et al., 1995; Luecke et al., 1990). Further studies identified that ingestion of gelatinous capsules produced by *Microcystis* species can lead to increased mortality through increased energy expenditure and reduced ingestion as they can be difficult to expel once ingested (Trabeau et al., 2004). This, when combined with predation pressure could lead to population collapse. A long-term study on Lake Oneida showed that when the density of the primary predatory fish (yellow perch in its first year) exceeded 14,000 individuals ha⁻¹ the *Daphnia* populations crashed. Early studies attributed this to poor quality food with inedible species dominating the phytoplankton (Lampert et al., 1986), however increases in predation in late spring/early summer are linked to the continued reduced *Daphnia* populations (Mills and Forney, 1983). A possibility is that *Daphnia* respond to increased predation by morphological change (neck spines, helmet development) (Repka et al., 1995; Tollrian, 1990), increased reproductive effort (Spitze et al., 1991) or by initiating diapause

(Ślusarczyk, 1995). Morphological change and increased reproductive effort may compensate for the increased predation for a short time but with food limitation, a particular level of a pressure may be reached where food resources are no longer sufficient to compensate, leading to population collapse. Diapause has been shown not only to react to predator kairomones (Pijanowska and Stolpe, 1996; Ślusarczyk, 1995) but also to food stress (reduced quantity and/or quality) (Taylor, 1985) and so this reaction could account to some degree for perceived population crashes. How factors such as compensation in ecological communities determines the level of resilience is currently unknown but the dynamics of adaptations such as those discussed above are likely to have a substantial impact on ecosystem resilience. The non-linear collapse in zooplankton populations following compensation against pressures could be a primary factor in non-linear ecosystem scale behaviour, particularly if such behaviour cascades to other trophic levels. In lake specific terms these interacting factors can have a large impact on resilience, as *Daphnia* are one of the most efficient grazers of phytoplankton in temperate lakes and so represent the main (but not the only) top down mechanism for phytoplankton control (Cottingham and Schindler, 2000).

Table 1.2 Examples of documented perturbations and components of restoration programmes that contributed to possible regime shifts in lakes. Switch type refers to direction of shift i.e. forward switch is a shift from a clear to a turbid water state and a reverse switch is a shift from a turbid to a clear water state.

Switch Type	Perturbation/Action	Apparent Switch Mechanism	Lake Name/Region	References
Forward	Fish addition	Increased zooplankton predation	Peter and Paul lakes, Michigan, USA	Carpenter et al., 2011
	Predatory fish kills	Decreased predation on planktivorous fish - increased zooplankton predation	Wintergreen lake, Michigan, USA	Hall and Ehlinger, 1989
	High winds	Damage to macrophytes and mixing of sediment	Lake Apopka, Florida, USA	Bengtsson and Hellström, 1992; Schelske et al., 1995
	Increased water level	Light limitation of macrophytes	Lake Tamnaren, Sweden	Wallsten and Forsgren, 1989
	Pesticide addition	Damage to zooplankton community	Norfolk Broads, UK	Stansfield et al., 1989
	Invasive species introduction	Crayfish cutting macrophytes loose - decreasing coverage	Lake Chozas, Spain	Rodriguez et al., 2003
	Periphyton growth	Epiphytic growth on macrophytes - light limitation	Lake Almind, Denmark	Sand-jensen and Borum, 1984
	Waterfowl grazing	Reduction of macrophyte biomass	Lake Zwemlust, Netherlands	van Donk and Otte, 1996
Reverse	Fish removal	Decreased zooplankton predation	Lake Zwemlust, Lake Noordiep, Netherlands, Lake Vaeng, Denmark	Meijer et al., 1994
	Increased flushing rate	Removal of phytoplankton and nutrient rich water - increased clarity	Lake Veluwe, Netherlands	Ibelings et al., 2007
	Zebra mussel introduction	Filter feeding of phytoplankton	Lake St Clair, Ontario, Canada/Michigan, USA	Griffiths, 1992
	Decreased water level	Increase light availability for macrophytes	Lake Takern, Lake Krankesjon, Sweden	Blindow et al., 1993

1.4 Erosion of resilience

Gradual environmental change such as climate change or increasing nutrient levels/pollution can slowly erode the resilience of a lake ecosystem. In the case of increasing P concentration, due to feedback mechanisms the structure and function of the lake may seem stable (Scheffer et al., 1993). However, as P levels rise, the ecosystem resilience in response to perturbations decreases. This happens as the disturbance disrupts the feedback mechanisms, destabilising the regime, allowing the phytoplankton to exploit the increased P levels and so form its own feedback mechanisms, stabilising the lake into the new regime (Janse et al., 2008; Jeppesen et al., 1990; Scheffer et al., 1993).

When thinking along these lines, it raises the question of how past changes in pressures such as climate change impacted on relatively 'pristine' states. Some palaeolimnological studies have shown substantial, ecosystem level changes to recent climate warming in remote, arctic lakes (Smol et al., 2005). Many of these changes seem to result from increased productivity associated with warming, and whilst these high latitude lakes are likely to be particularly sensitive to increasing temperatures, this demonstrates the possibility that the long term historical state of lakes may not have been as stable as was once believed. Over longer periods of time some lakes have demonstrated high nutrients during periods of colder temperatures. For instance, Sacrower see, a lake in north eastern Germany, experienced a shift from eutrophic to meso/oligotrophic conditions at the end of the last ice age. The presence of longer ice cover and more intense stratification led to anoxic conditions near the sediment, resulting in increased internal loading which ceased when temperatures warmed (Kirilova et al., 2009). In areas of relatively high natural productivity such as grazing lands for large populations of wild herbivores, the idea of a stable, pristine state may be even less likely to have existed (Moss, 2015). It is currently unclear what these findings mean for long-term ecological resilience in lakes but it seems possible that the threat presented by climate change to the resilience of lakes may have been underestimated. The long term nature of past climate change may play a part in how they have impacted on the state of lakes but it may also be possible that the ability of resilience processes to counteract and withstand climate change are lower than believed. This makes it all the more important to understand how climate change, along with other pressures, impacts on ecosystem resilience.

1.4.1 Interacting stressors and resilience

A hypothetical example of this can be seen between the interacting pressures of rising temperature and P inputs. Increased temperature leads to increased organic P release into sediment pore water and then to bottom water as well as increased microbial activity, which in turn, can lead to release of iron (Fe) bound P from the sediment due to reduction of Fe oxides in more reducing conditions and release of adsorbed P (Sondergaard et al., 2001; Spears et al., 2007). Hence increased temperature can increase TP levels through internal loading (Jensen and Andersen, 1992) and if there are external P inputs as well this can result in particularly high TP levels. These conditions would benefit certain species of phytoplankton which have shown increased growth rates at higher temperatures (Robarts and Zohary, 1987a; Shatwell et al., 2014; UWRRAA, 1995) combined with elevated TP levels. As well as the positive effects on phytoplankton growth, increased temperatures can lead to reduced body size of zooplankton, which can have adverse effects on grazing rates (Moore and Felt, 1993) limiting their ability to control phytoplankton populations. Changes in seasonal precipitation patterns have also been predicted and the way these changes occur can impact lakes in varying ways. For instance, decreases in summer precipitation can result in longer water retention times, leading to higher densities of phytoplankton (Gomes and Miranda, 2001; Lee et al., 2012; Mooij et al., 2009; Søballe and Kimmel, 1987). Alternatively, increases in precipitation have the potential to reduce chlorophyll concentrations and improve water clarity if it occurs during the summer (Carvalho et al., 2012) but if it occurs during the winter it can increase external P loading due to agricultural runoff (Jeppesen et al., 2009) and increase the input of particulate matter which has been shown to reduce resilience in clear water states (Lischke et al., 2014).

Combine these conditions with an additional shock perturbation such as summer storms, where high winds can stir up the sediment, (Douglas and Rippey, 2000) this can lead to increases in both turbidity and P concentrations (Ogilvie and Mitchell, 1998). Large shallow lakes have a large fetch and shallow depth (little to no stratification), increasing their vulnerability to wind induced wave mixing in the sediment (Janse et al., 2008; Spears and Jones, 2010), making lakes with these characteristics inherently less resilient to these types of pressure scenarios due to the increased probability of increased particulate matter and nutrients in the water column. Along with the increase in temperature and TP levels mentioned earlier (Rinke et al., 2010) and predicted precipitation changes, this will likely

increase the probability of a regime shift to a turbid state. The impact of lake specific characteristics has been shown to affect how multiple stressors impact on cyanobacterial abundance (Richardson et al., 2018). Factors such as alkalinity, mixing regime and colour (presence of humic substances) interacted strongly with retention time but other interactions were significantly more complex with no 'one size fits all' approach available. Better understanding of how these pressures interact and impact on the resilience of shallow lakes with characteristics thought to increase vulnerability, such as moderate depth and large size, is a key knowledge gap in our current understanding and can help improve our understanding of how process dominance (e.g. macrophyte nutrient absorption at shallow depths to zooplankton herbivory at moderate depths) can shift depending on lake characteristics.

1.4.2 Long-term impacts on resilience

Gradual change in ecological communities can be a sign that resilience is being eroded as well as a linear response to changes in external drivers. For instance, sediment cores from a shallow lake showed decreasing species richness in the macrophyte community over many decades (Sayer et al., 2010a). This reduction in richness was found to mirror a shift from slower growing species present throughout the growing season to shorter lived species capable of completing their lifecycle in a much shorter time (Hilt et al., 2018; Sayer et al., 2010a, 2010b). The loss of summer macrophyte coverage can then lead to increased internal loading due to looser sediment and less oxidation (Jensen and Andersen, 1992). As well as this, fast growing species tend to be more susceptible to herbivory due to having less time to allocate resources to defence (Elger and Willby, 2003; Mattson, 1980) which can lead to greater vulnerability to light competition and herbivory. This makes the community in this state less resilient to the effects of competition from phytoplankton, periphyton and herbivory (Hidding et al., 2016; Hilt et al., 2018; Jones and Sayer, 2003).

The resilience of ecosystems can also be eroded in less obvious ways through effects on populations. An example of this can be seen in genetic erosion which acts to degrade the genetic diversity of a population increasing their vulnerability to a variety of pressures (e.g. disease, pollution). The main mechanisms are through increased mortality and reproductive impairment, which can lead to a selective population bottleneck (Carpenter et al., 2011; Coors et al., 2009; Johnson et al., 2010). Lopes et al. (2009) subjected clones of *Daphnia longispina* to combinations of non-selective predation and doses of pollutants (in this case

toxic heavy metals taken from mine water) which resulted in some clones becoming extinct under specific pressure scenarios. The result was a population more resistant to these contaminants but less diverse overall. Thus, if for example a different pollutant or disease should enter the system, then the population is less likely to be able to resist it (Altizer et al., 2003). The genetic diversity present within a population can also impact on how pressures such as disease and parasitism affect them. This is particularly important as these types of pressures have been predicted to become more prevalent in response to climate change with warmer winters removing a major source of pathogen mortality (Harvell et al., 2002). The evolutionary response of species and populations to these and other forms of perturbations can have substantial impacts on ecosystem resilience. For instance, in a recent study, a model showed that fish species recovering from a population crash led to decreased size at maturity and earlier reproduction (Audzijonyte and Kuparinen, 2016). Coupled with the predicted impacts of warming on fish, such as switching to dominance by species with a wide temperature tolerance and general reductions in body size (Jeppesen et al., 2012), these could alter fish-zooplankton dynamics.

How evolution impacts on the range of traits within a population could also impact on a species or populations ability to respond to environmental changes. Having a larger diversity of traits within a population increases the number potential responses to a stressor, which is generally thought to increase resilience (Dakos et al., 2019). Changes in the abundance and diversity of traits and species could affect a range of trophic levels in lakes, potentially making communities more vulnerable through the loss of species. Communities with low levels of redundancy (i.e. small number of species sharing the same functional trait) and diversity are less likely to absorb and recover following perturbations (Yachi and Loreau, 1999), so contributing to the erosion of resilience. An example can be seen in the experimental manipulation of lakes subjected to acidification where a range of changes across the system were seen. Changes such as loss of larger crustacean zooplankton species shifting to dominance by rotifers (small bodied species), increases in filamentous phytoplankton and decreases in larger bodied fish with overall species diversity reduced at all trophic levels (Schindler, 1990). It is easy to see how a system subject to this stress would have lower resilience to other perturbations such as nutrient inputs. At a population level, the effect of within-population diversity can reduce population variability. For instance, in the metapopulation of sockeye salmon (*Oncorhynchus nerka*) in Bristol Bay, Alaska, fishery closures due to low numbers of spawning fish are predicted to occur ten times more

frequently under conditions involving a single large homogenous population. The current levels of population diversity give an overall reduction in variability of 2.2 times in comparison (Schindler et al., 2010). The direct impact of population diversity on stability is clear from this study and although the link between the various forms of diversity and redundancy (functional, species and genetic) and ecosystem resilience is in most cases an unknown it is likely to be a very important factor in understanding and managing ecosystem resilience in the face of environmental change.

1.5 Early warning indicators and the prediction of regime shifts

Although there have been a few success stories in lake restoration such as Lake Veluwe (The Netherlands) (Ibelings et al., 2007) and Lake Krankesjön (Sweden) (Blindow et al., 2002), the general success rate of restoration measures has been less than 50% over the short term and even lower when viewed over a 10-15 year time scale in a study of ~70 restoration studies in Denmark and The Netherlands (Søndergaard et al., 2007). Short term improvements were widespread in many important variables (e.g. Chlorophyll, TP, Secchi depth) but the spread of macrophyte coverage was much slower. The need to further reduce external nutrient inputs as well as control internal nutrient loading have been noted as major causes of failures and that in some cases regular manipulations will be needed to maintain a clear state (Søndergaard et al., 2007). Given the difficulties and high costs associated with reversing regime shifts and lake restoration in general after they have occurred it is not surprising that a great deal of research has gone into finding methods capable of predicting them. A range of different methods have been proposed, ranging from so called 'generic' indicators based on relatively simple statistical measures of variability (Scheffer et al., 2009) to complex model based indicators (Dakos et al., 2012a; Taranu et al., 2018). The theory behind these methods is based on phenomena known as critical slowing down (CSD) and flickering. CSD is a measure of change in a variable's return to equilibrium following a perturbation, then as a transition or tipping point is approached, this return rate becomes slower (Wissel, 1984). This can be detected through increases in temporal autocorrelation and measures of variance (Dakos et al., 2012a). Flickering is different in that it measures the increasing rate of short term fluctuations between two alternate states in highly stochastic systems which can be detected in similar indicators despite the difference in underlying dynamics (Dakos et al., 2013). The assumption with flickering is that strong external events regularly force the system from one state to another (such as short term changes in water level induced through management

and low rainfall (Wang et al., 2012b)), removing any possibility of detecting a gradual approach to a threshold through the breakdown of feedback mechanisms (Dakos et al., 2013; Wang et al., 2012b). A number of tests of these indicators have been run to detect various forms of non-linear change in simple models (Carpenter et al., 2008; Carpenter and Brock, 2006), laboratory populations (Dai et al., 2012; Ghadami et al., 2018), climatic variables (Lenton et al., 2012), population genetics (Aguirre and Manrubia, 2015), a whole-lake (Carpenter et al., 2011; Seekell et al., 2011; Wilkinson et al., 2018), palaeolimnology (Bunting et al., 2016; Taranu et al., 2018; Wang et al., 2012a) and real-world monitoring data (Burthe et al., 2016; Gsell et al., 2016). Many of the early tests involving simplified models, single populations and experiments were considered successful but as methods were extended to less controlled environments more prone to natural and unexplained variability, the success rate of these early warning indicators (EWIs) became much lower. This has raised questions as to their applicability for use by managers in real-world systems with the reasons behind these failures in natural ecosystems likely to be many and complex.

One factor that could impact the perceived success rate of EWIs may involve the 'tipping points' or 'non-linear events' against which the EWIs were tested. The use of methods such as piecewise linear regression, Pettit and STARS analysis (Gsell et al., 2016) and generalized additive models (GAM) (Burthe et al., 2016) test time series data for statistical properties such as step-wise changes in means and significant breaks in linear trends. These forms of statistical tests do not provide any information on the perturbations that caused the transitions or tipping points and so there is no information as to whether CSD or flickering has occurred. Another factor is a lack of consideration of past and baseline variability to better understand the probability of being able to detect a tipping point (Spears et al., 2017).
The

Real-world monitoring data is generally relatively low frequency (biweekly to monthly) and so may be unable to capture the dynamics of species and variables with high turnover rates, which has the potential to mask some variability that may otherwise have been captured had high frequency data (hours to days) been available (Dakos et al., 2012a; Scheffer et al., 2009). A test comparing modelled data and experimental data with data frequency reductions showed high correlation between detection and high data frequency in the modelled data but not in the experimental data (Clements et al., 2015) which suggests that other factors such as a high signal-to-noise ratio, present in some natural populations, can cause problems

with EWI usage (Krkošek and Drake, 2014). Whilst the use of high frequency data has shown high levels of success in the US experimental lakes (e.g. Carpenter et al., 2011; Seekell et al., 2011; Wilkinson et al., 2018) the results shown by Clements et al., (2015) suggest that results from a wider range of lake and ecosystem types may be more mixed. The effects of increased data frequency on the occurrence of false positives is a further unknown and in real-world systems, subject to large amounts of ‘noise’, this has potential to raise significant issues. However, without further testing it is impossible to know how impactful high frequency data could be, and considering how important theory suggests it could be, along with its potential in other areas of research (LaDeau et al., 2017), it remains a high priority in EWI research.

Recent research has also highlighted that prediction can be substantially improved when transitions are tested against their form in a stressor-response relationship (e.g. forms demonstrating hysteresis found to be more reliable) (Litzow and Hunsicker, 2016). Another factor to consider is that our current understanding of how patterns of variability in ecosystems and their component parts respond to different types of perturbations is poor and remains a significant knowledge gap. The way different forms of EWIs capture variability has some potential to capture these differences and could serve as an interim until we can better understand how stressors, perturbations and EWIs interact. With our ever-increasing knowledge of how EWIs work and their success rate under particular conditions, there is potential to adapt some aspects of long-term monitoring to improve the chances of success if EWIs are used. For instance, greater use instruments to collect ultra-high frequency data is an obvious improvement for variables such as nutrients, algae and zooplankton. Perhaps more valuable would be careful consideration of which measurable aspects of different ecosystem processes may best be utilised by EWIs. The addition of these variables to monitoring programmes could provide valuable new avenues for scientific exploration and effective monitoring, improving the detection of impending regime shifts and our system understanding.

1.5.1 Resilience and variability across scales

Ecological understanding of resilience processes is critical to being able to detect regime shifts and manipulate changes in resilience, but it can be difficult to obtain general patterns across multiple lake and ecosystem types. The use of conceptual models to understand resilience in a less system-specific way can be a useful tool when trying to understand environmental impacts across multiple scales in space and time. Discontinuity theory is a

concept that describes the organisation and structure of ecosystems by a few dominant processes that result in discontinuities (gaps) and aggregations at particular spatial or temporal scales (Holling, 1992). An example of this can be seen in the distribution of body size in biological organisms, for instance, in two experimental lakes similar numbers of discontinuities were found despite very different chemical conditions and species compositions before and after manipulation (Havlicek and Carpenter, 2001). This suggests that common processes operate in these systems and that these processes vary at the different size scales (Allen et al., 2005). Despite the similarities in the number of discontinuities in these lakes, the 'densities' or size of aggregations of species around particular body sizes were different, which could be a measure of resilience (Allen et al., 2005). It is thought that the presence of these aggregations and discontinuities is due to differences in the spatial and temporal distribution of resources and functions (Holling, 1992; Peterson et al., 1998) and that species capable of contributing to function across scales contribute to resilience (e.g. zooplankton with wide thermal range able to graze on phytoplankton over a larger portion of the year) (Allen et al., 2005; Angeler et al., 2013). The discontinuities or 'troughs' are thought to represent gaps, containing less resources or structure and so are generally populated by fewer species (Angeler et al., 2016). Over the last decade research has highlighted that the positioning of a species or population along a discontinuity gradient within a trough or towards the edge of an aggregation leads to an increased risk of extinction and high variability in abundance (Bouska, 2018; Spanbauer et al., 2016; Wardwell and Allen, 2009). As discussed above, variability in ecosystems is also thought to represent proximity to a transition or regime shift (Scheffer et al., 2009). Understanding where along a discontinuity gradient a species lies, along with its distance to the centre of an aggregation, could give an indication as to its likely variability and so its use as an EWI. In large, spatially connected systems (e.g. multi-lake catchment) combining approaches such as the discontinuity analysis used in a 1300 km river system (Bouska, 2018) with new approaches measuring large scale resilience to smaller scale, local pressures (van de Leemput et al., 2018) has potential to not only provide much better predictive capabilities but unlock our understanding of resilience over much larger scales.

1.6 Key Challenges identified from the literature

It is clear from this literature review that the existing knowledge base surrounding resilience and regime shifts in shallow lakes is extensive, however much of what is known is derived

from isolated studies and there is a need to consolidate across multiple studies as well as high detail case-studies. Particularly when considering how the separate functional aspects of an ecosystem will interact to regulate resilience to changes in multiple stressors. In this respect Loch Leven is a particularly useful case study as it is the source of an extensive knowledge base of lake structure and function. Its long and diverse history of management and use by society provides a range of scenarios to be tested through field studies, statistical analysis and computer modelling. Combined with knowledge of Loch Leven's site-specific characteristics this allows us to begin untangling the complexity surrounding their effects on resilience. Overall this allows a powerful and wide-ranging base from which to assess this site's resilience to pressure changes and to provide further insight into the forms of responses expected in large shallow lakes.

1.7 Research aims and objectives

Based around knowledge gaps in our understanding of how ecological resilience, regime shifts, and ecosystem variability interact with environmental change in large shallow lakes, identified from the literature review, this thesis aims to assess how past and future changes in a large shallow lake (Loch Leven, Kinross, UK) interact with each other and its site-specific characteristics to determine its variability and resilience to regime shifts and non-linear change. To address this aim three main objectives were investigated in chapters 3-5:

- (1) Analyse the Loch Leven long term data to identify the occurrence of common tipping points within the physical (water clarity) chemical (water column nutrient concentrations) and biological (phytoplankton, zooplankton) components of the loch and to determine whether they could have been detected using statistical early warning indicators.
- (2) Quantify ecological change across trophic levels during a potential regime shift, coupled with an assessment of non-linearity within those same variables. Using the computer model PCLake we then determined the stressor-response relationship present for dominant process variables.
- (3) Using PCLake, examine the sensitivity of Loch Leven to regime shifts in the face of predicted environmental change (e.g. climate change, nutrient pollution).

1.8 Thesis structure

The thesis is structured around 3 paper-like chapters (chapter 3-5) with a preceding methods chapter (chapter 2) which outlines the history and characteristics of Loch Leven as a study site as well as field and laboratory methods used for the collection of the Loch Leven long-term dataset and zooplankton body size data used in chapter 4 and the validation of PCLake. Further information is provided about the structure of PCLake, the methods used to gather nutrient loading data and other methods used during validation to the Loch Leven data.

Chapter 3 focuses on detection of statistically defined tipping points in a number of long-term datasets from across trophic levels in Loch Leven. These were assessed for coherence in time and then the same datasets were tested by five different EWIs across a range of window sizes. Determining if these EWIs predicted the previously detected tipping points and how window size impacted on their efficacy was followed by a further assessment of how the success of detection was impacted by considering EWIs together rather than individually. This was conducted to better understand how differences in how EWIs detect variability can be exploited to capture a wider range of signals prior to tipping points.

Chapter 4 describes ecological change around a single specific event thought to represent a possible regime shift in Loch Leven. Use of a before/after analysis followed by testing for non-linear behaviour allowed me to determine significance and form of change across multiple trophic levels. This was followed by a bifurcation analysis within PCLake to determine the shape of the stressor-response relationship for dominant process variables such as chlorophyll a, zooplankton and macrophytes. Using these steps allowed an assessment of the presence of regime shift dynamics within Loch Leven and to understand the level of resilience it has to future regime shifts.

Chapter 5 uses PCLake to test major response variables (chlorophyll a, zooplankton and macrophytes) to predicted levels of environmental change in multiple stressor variables (P loading, temperature and precipitation). These are assessed in multiple combinations both based on real predictions and alone to better understand how they interact. The generation of critical nutrient loads (CNL) for each scenario allow the assessment of resilience against these stressor combinations.

Chapter 6 brings the findings from the three data chapters together and discusses them in the context of the wider literature on ecosystem resilience and the overall research aims.

Possibilities for future research within the field are then identified, followed by some concluding remarks.

Chapter 2 – Methodology



This chapter provides an overview of the study site, Loch Leven, Perth and Kinross, UK, and its history of research and management. It also contains a short description of field methods used for the Loch Leven Long-Term Monitoring Programme (LTMP) and the laboratory methods used to generate the zooplankton body size data presented in Chapter 4. An overview of the model PCLake is included along with the methods used to obtain nutrient loading, flow and state data used in model calibration. Further information on specific methods can be found in Chapters 3-5.

2.1 Study site description

Loch Leven is a shallow lake situated in the Scottish Lowlands, UK (56°10'N; 3°30'W) at approximately 107 m above sea level. It has a surface area of 13.3 km², a mean depth of 3.9 m, a median depth of 3.17 m and a maximum depth of 25.5 m (Kirby, 1974). It drains a catchment area of c.145 km², the mean height of which is 179.93 m (CEH, 2018). The majority of the catchment is farmland, dominated by arable land closer to the loch (Castle et al., 1999) with livestock mostly in the upland areas, the highest point of which is approximately 490m. Approximately 11% of the catchment is covered by woodland, with a further 2% covered by urban areas and human habitation (May and Spears, 2012). The loch itself has several conservation classifications (Site of Special Scientific Interest (SSSI), Ramsar site, Special Area of Conservation (SAC), Natura 2000) showing its importance as a habitat for a range of species. It is also the site of an internationally renowned trout fishery (May and Spears, 2012).

The loch has a long history of management, spanning at least 150 years, with many attempts to improve the extent to which the loch provides a range of ecosystem services. One of the most profound changes was the lowering of the water level and the installation of sluice gates at the outflow which was primarily implemented to control the supply of water for downstream industry with the objective of producing a greater extent of farm land (Munro, 1994). The works began in 1831 with levels dropping 1.5 m by 1850 (Morgan, 1970). The water levels are managed to maintain an even flow through the summer months by gradually building the levels up during the autumn and winter months (May and Spears, 2012). Loch Leven is currently managed by Scottish Natural Heritage (SNH) as a National Nature Reserve and has a detailed catchment management plan through collaboration between Perth and Kinross council, SNH, Scottish Environmental Protection Agency (SEPA) and Scottish Water

(Reid et al., 2016). This management plan is broken down into two main areas management for natural heritage and management for people. Each of these has 5 main objectives and I will briefly cover those focused on natural heritage as they are most relevant.

- **Objective 1 – Maintain and enhance the loch and its surroundings for birds, particularly waterfowl.** This objective will focus on maintenance of wetland and breeding habitat on the reserve with some view to extending wetland habitats and introducing artificial nesting habitat.
- **Objective 2 – Restoration of water quality and ecological condition to those seen in 1910.** This objective will focus on the improvement of water quality through continued monitoring and work to control nutrient inputs with a view to improve the abundance and distribution of macrophytes. Manipulation of water levels and work to control invasive species are also a priority.
- **Objective 3 – Maintain, extend and enhance habitats around the loch.** This objective focuses on maintaining and extending the nature reserve which includes the potential incorporation of other, smaller surrounding reserves to improve habitat connectivity.
- **Objective 4 – Maintain, extend and enhance notable species on the reserve.** Manage predatory species that could be a threat to ground nesting birds, such as mink and grey squirrel. Manage terrestrial habitats to promote red squirrels and provide nesting habitat for sand martin.
- **Objective 5 – Demonstrate good practice and innovative conservation and visitor management.** Review and promote access guidance to balance the needs of visitors with those of the reserve itself.

Fishery management has been ongoing at Loch Leven since at least the mid-1800s with approximately 60,000 brown trout (*Salmo trutta*) fry and 4000 two year old fish stocked per year by 1882, increasing to 300,000 fry by the early 1930s (Winfield et al., 2012). This stocking ceased in the late 1930s but restarted in 1983 following poor angler return, with 4000 fish stocked per year rising to 166,000 by 1988. Stocking levels remained similar (>100,000 per year) until 2004 when they dropped to 5000 and ceased completely in 2006. Along with the

native brown trout, between 1993-2004, 30,000 rainbow trout (*Oncorhynchus mykiss*) were stocked with all stocking ceased in 2006 due to lack of economic improvement in the fishery (May and Spears, 2012; Winfield et al., 2012).

As well as the long history and variety of management measures implemented in the loch, scientific research has a long history at Loch Leven, dating back to 1710 (Sibbald, 1710). Perhaps the most intense period of scientific research was from 1966-1973 during the International Biological Programme (IBP) as part of a wider international effort (May and Spears, 2012), which documented a wide range of physical, chemical and biological processes within the Loch. This period marked the start of the Loch Leven LTMP that has continued to this day.

2.1.1 Loch Leven long term monitoring field methods

Field sampling for the Loch Leven LTMP is conducted every two weeks at two separate sites on the lake: “reed bower”, a mid-basin point, and “sluices”, in front of the outflow (see Fig. 2.1). Conductivity, pH, and dissolved oxygen are measured in surface waters at both sites using HACH HQ40d probes calibrated to industry standards before every field sampling day with three separate readings taken per probe, from which the arithmetic mean is then calculated. Secchi depth (water clarity) is measured using a Secchi disc at reed bower. Zooplankton is sampled at reed bower by drawing a plankton net (mesh size 120 µm, net mouth diameter 20 cm) along a diagonal 4 m net tow to the surface, then at sluices by collecting surface water with a bucket then pouring 30 L through the same net. Both samples are preserved on-site with 4% formaldehyde. Water chemistry samples are obtained from an integrated water column sample at reed bower using a weighted polythene tube starting at approximately 0.25 m above the sediment to the surface. At sluices samples are taken directly from the surface. Phytoplankton samples are subsampled from integrated samples taken at reed bower. Bird count data was supplied by SNH with support from the Royal Society for the Protection of Birds (RSPB) who conduct monthly point counts across sections covering the whole of the loch according to Wetland Bird Survey methods (Austin et al., 2008).

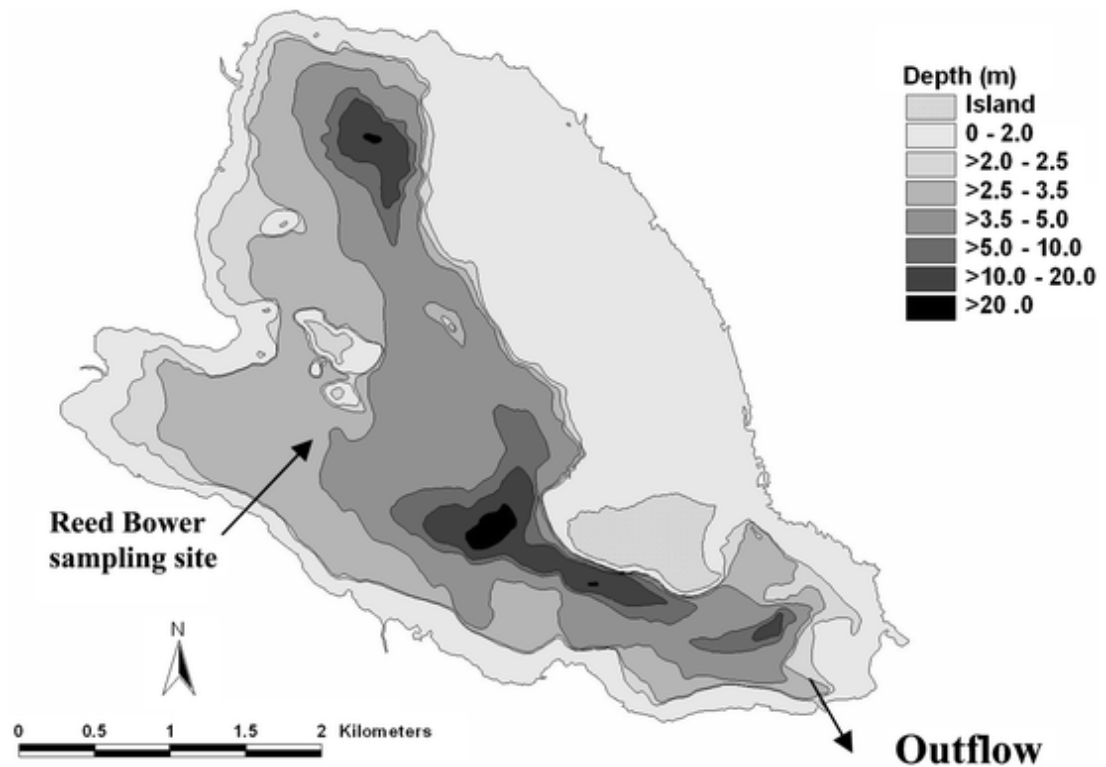


Fig. 2.1 Bathymetric map of Loch Leven (Spears et al., 2012).

2.2 Zooplankton body size analysis

Sub-samples for zooplankton body size determination were collected from archived zooplankton samples collected during routine sampling for the years 2000-2013. This gives a balanced number of years before and after the target tipping point in 2007 analysed in chapter 4. Archived samples were suspended in 250 mL solution of tap water then sub-sampled with a Stempel pipette (volume 5 mL). Sub-samples were placed in a long trough for examination under a low power Nacet binocular microscope. Three individuals were selected at random for each species from each sub-sample. Measurements were conducted using a graticule eyepiece with measurements taken from the centre of the eye to the point of insertion of the tail spine for *Daphnia hyalina*. For the three copepod species found in Loch Leven (*Cyclops abyssorum*, *Cyclops vicinus* and *Eudiaptomus gracilis*) measurements were taken from the tip of the head to the tip of the furcal rami (distal) as this was the most easily defined point for all species on preserved samples. For *Daphnia*, the presence or absence of helmet spikes was recorded as a proxy for predation pressure by planktivorous fish (Boersma et al., 1998; Dodson, 1989).

Table 2.1 List of datasets used for the tipping point/EWI analysis in Chapter 3. Trophic level abbreviations used: PP - Primary Producers, PC - Primary Consumers, SC - Secondary consumers, AP – Apex Predators, Chem – Chemical, Phy – Physical. Datasets recorded as annual in frequency represent annual maxima of bird numbers. Datasets with * denotes data which I have helped collect in the field during this PhD.

Dataset	Frequency	Length (Years)	Trophic Level
Chlorophyll *	Biweekly	45	PP
<i>Asterionella</i> *	Biweekly	45	PP
<i>Aulacoseira</i> *	Biweekly	45	PP
Unicellular Algae *	Biweekly	45	PP
<i>Diatoma</i> *	Biweekly	45	PP
<i>Cyclops vicinus</i> *	Biweekly	42	PC
<i>Cyclops abyssorum</i> *	Biweekly	42	PC
<i>Eudiaptomus gracillis</i> *	Biweekly	42	PC
<i>Eudiaptomus nauplii</i> *	Biweekly	42	PC
<i>Daphnia</i> *	Biweekly	42	PC
Greylag Geese	Annual	45	SC
Pochard	Annual	45	SC
Mute Swan	Annual	45	SC
Pinkfooted Geese	Annual	45	SC
Mallard	Annual	45	SC
Teal	Annual	45	SC
Great Crested Grebe	Annual	45	SC
Coot	Annual	45	SC
Tufted Duck	Annual	45	SC
Cormorant	Annual	45	AP
Total Phosphorus *	Biweekly	45	Chem
NO ₃ -N *	Biweekly	45	Chem
Secchi Depth *	Biweekly	45	Phy
Soluble Reactive Phosphorus *	Biweekly	45	Chem
Silica *	Biweekly	45	Chem
Water temperature *	Biweekly	45	Phy

2.3 PCLake model setup

To better understand the ecological interactions and in lake responses considered in Loch Leven we used the well-established ecosystem model PCLake. An overview of the model is given below. An in-depth description is provided by the model developer in Janse (2005). PCLake uses a set of modules to simulate the pelagic zone of a well-mixed water column

along with the sediment top layer and a set of inputs and outputs (see Fig. 2.1). The two main modules focus on the main components of the food webs, nutrients and matter. The model has no depth profile or spatial heterogeneity. Stocks and fluxes are quantified as dry weights per m² or m³ for total mass and for phosphorus and nitrogen components, and where applicable, silica, allowing them to be manipulated.

The biological components of the model are combined into functional groups, such as zooplankton which act as the main top down control on the phytoplankton groups and as a source of food for planktivorous fish, adult and juvenile planktivorous/benthic fish, and piscivorous fish. Phytoplankton are split into three major groups - green algae, cyanobacteria and diatoms - with differences in nutrient uptake and light requirements for specific growth rates. Macrophytes are included as a functional group and act in direct competition with phytoplankton for nutrients and light. Along with the main interacting components, a wide array of parameters influence how these interactions play out. Some components can be input as a time series, such as wind, light, water temperature, evaporation, inflow/outflow rates and nutrient loadings (see Table 2.2). Others allow the manipulation of group-specific parameters, such as growth rates, assimilation rates and nutrient absorption.

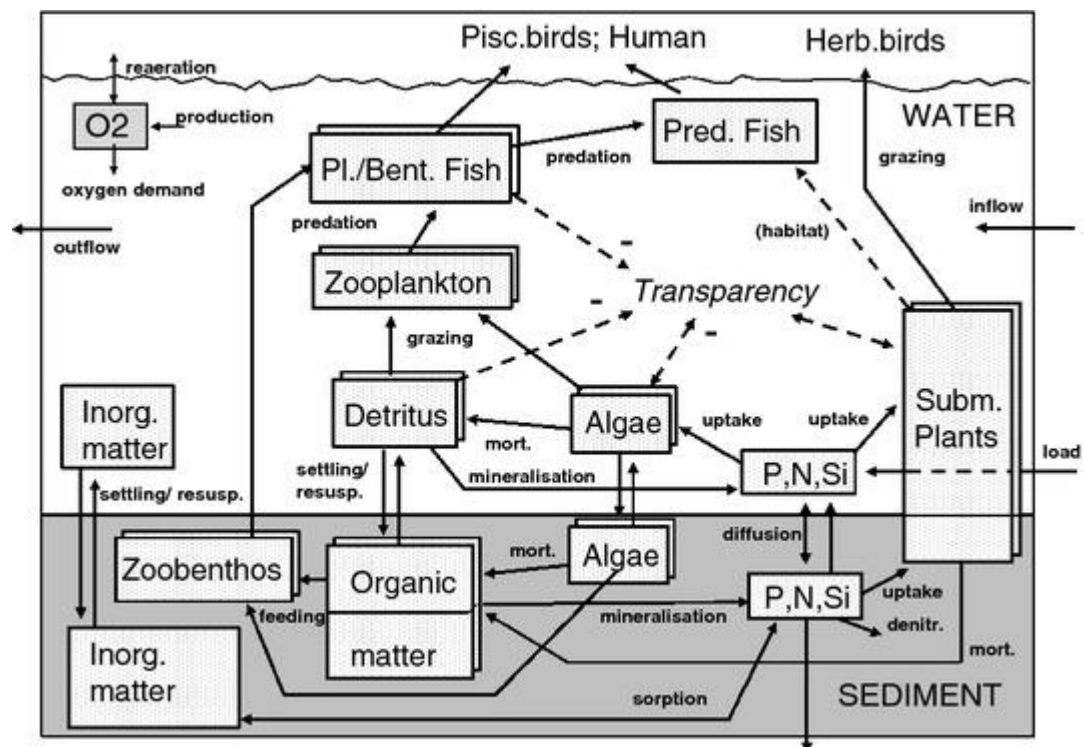


Fig. 2.2 Model structure of PCLake (Janse et al., 2010)

2.3.1 Derivation of Loch Leven nutrient loading for input to PCLake

Over the last 40 years extensive Loch Leven nutrient loading surveys have been conducted every 10 years, occurring in 1985, 1995, 2005 and 2015/16 (Bailey-Watts, 1996; Bailey-Watts and Kirika, 1987; Defew, 2008). For the purposes of this project, the data from the 2005 survey were used as it comprised the most recent, single complete year which is needed to properly fit the model. The survey methods are outlined below, with full details available in Defew (2008).

During the 2005 survey, a total of 6 inflows (see Fig. 2.2) and one outflow were sampled for nutrient concentration analysis every 8 days over the entire year. Continuous flow data for the 3 largest inflows (South Queich, North Queich and Pow burn) were provided by the Scottish Environment Protection Agency (SEPA) who maintain permanent flow gauges for these inflows. For the remaining inflows, 8-day flows were estimated using stage boards on sampling days and creating rating curves (stage-flow relationships) derived from flow measurements made at selected stream heights. Continuous flow data for 8-day sampled inflows were generated using regression relationships with flows from continuously gauged inflows. To account for flows from the small areas of the catchment not covered by the 2005 survey, a flow/catchment area relationship was used (Equation 2.1).

Equation 2.1

$$Q_{ug} = \left(\frac{Q_g}{CA_g} \right) * CA_{ug}$$

Where:

Q_{ug} = stream flow of ungauged catchment ($m^3 s^{-1}$)

Q_g = stream flow of gauged catchment ($m^3 s^{-1}$)

CA_{ug} = Catchment area of ungauged catchment (km^2)

CA_g = Catchment area of gauged catchment (km^2)

Having spot measurements of nutrient concentrations at 8-day intervals combined with continuous flow measurements means a method to account for potential gaps in nutrient measurements is needed. Following Stevens & Smith (1978), $\log_{10} - \log_{10}$ concentration-flow

regression relationships were constructed and used to calculate continuous nutrient concentrations.

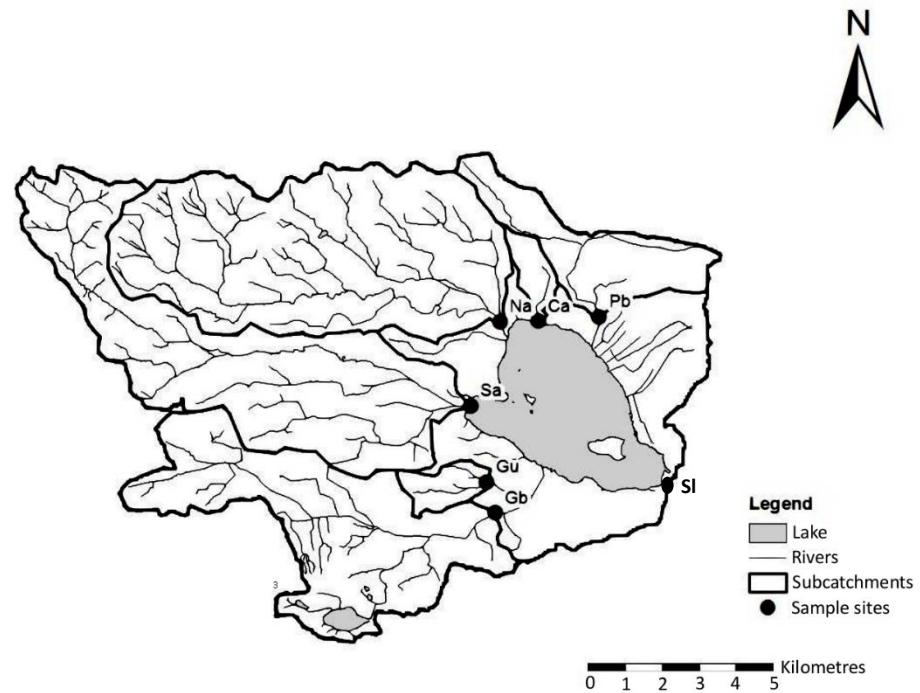


Fig. 2.3 Map of sampled streams (Gb, Gu – Gairney water, Sa – South Queich, Na – North Queich, Ca – Camel burn, Pb – Pow/Greens burn, Sl – Sluices/Outflow) during the 2005 nutrient loading survey of Loch Leven used in the calibration of PCLake.

2.3.2 PCLake Calibration and Validation

Following input of the data outlined above and in Table 2.2, sensitive parameters were identified from previous studies and sensitivity analyses (Janse, 2005; Janse et al., 2010; Nielsen et al., 2014) and adjusted and tested against observed data. The default values for PCLake were calibrated to a collection of 20 lakes from the Netherlands to simulate a ‘typical’ lake for this region (Janse, 2005). Adjusting the model to better simulate a lake under very different conditions such as those seen in Loch Leven was difficult to achieve. PCLake has a large number of other inputs that can be utilised during the calibration process (see Table 2.2 for a summary of all input variables altered to reach the final model fit shown in Figs 2.4 to 2.7). Some of the most important are available as time series inputs and were obtained either directly through the Loch Leven LTMP or through external sources such as the Met office. In the case of evaporation data, this was sourced from a modelled dataset (Robinson et al., 2016) for land based evaporation then converted to better represent open water

evaporation using a monthly conversion factor (Finch and Hall, 2001). In some cases a specific paper was used in finding an input value for particular parameters. The value in these cases was rarely a direct transfer from the paper to the model but is more used as a guide. For instance, in finding a value for the optimum temperature for diatoms a paper was found discussing values for some dominant species groups which are also present in Loch Leven, whilst other species groups are not included and so a direct transfer would not have been applicable. In a few cases relevant values could not be found either in the Loch Leven data or in the literature, in these cases the original values were altered in ways that made sense ecologically, based on differences in regional geology and climate between eastern Scotland and the Netherlands and helped improve the model fit to the real data. Effort was also made to minimise the size of the change of any individual parameter to keep model interactions similar to those established during the extensive building and testing of the model (e.g. Janse, 2005; Janse et al., 2008; Janssen et al., 2014; Mooij et al., 2007; Nielsen et al., 2014).

Reasonable fit was found for chlorophyll with most of the major changes captured by the model with minimal differences in timing (see Fig. 2.4). Similar levels of fit were also achieved for nitrate (see Fig. 2.5) and total phosphorus (see Fig. 2.6) showing reasonable agreement for the major nutrient dynamics. Zooplankton was more difficult to fit (see Fig. 2.7) but some of this difficulty may have come from the relatively small sample size used for body size measurements, the use of regression equations to estimate biomass from this and the fact that nauplii (first larval stage of crustaceans) were excluded from the body size measurements. Most importantly the dynamics of the spring zooplankton increase were captured if somewhat overestimated by the model. This gave reasonable confidence that the major processes and interactions were being captured and presented, although due to the equifinality theory and the complexity of the model (Beven, 2006) it is impossible to be absolutely sure the dynamics exactly mirror those seen in the real lake. When using any model, such as PCLake there is always a degree of trepidation about its ability to accurately represent a real lake, in this PhD the focus is on discovering broad scale ecological patterns (e.g. which combination of pressures results in a lower critical nutrient load) which are less likely to be misrepresented in the model than for instance the exact increase in chlorophyll that would be expected under a given temperature increase.

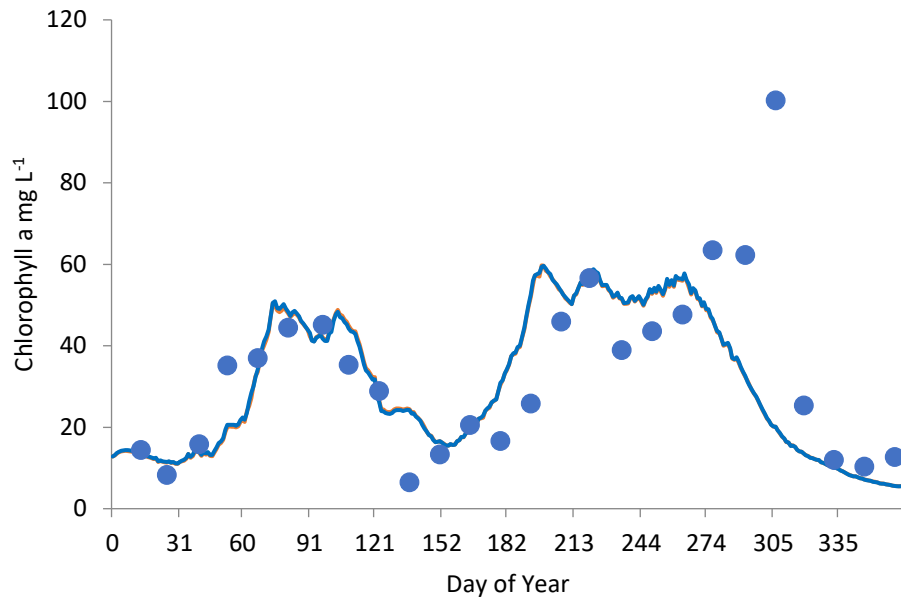


Fig. 2.4 PCLake comparison of observed values (circles) against modelled values (line) for Chlorophyll a

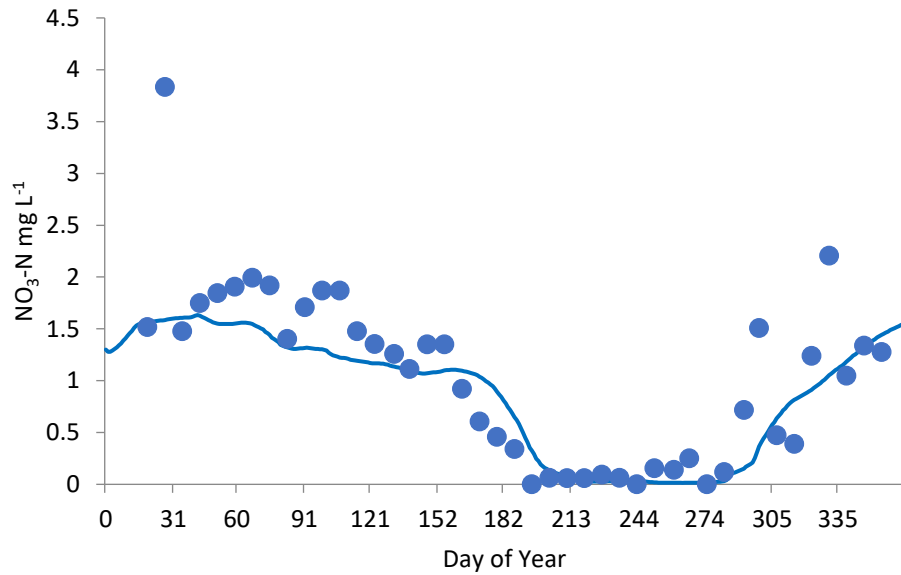


Fig. 2.5 PCLake comparison of observed values (circles) against modelled values (line) for NO₃-N

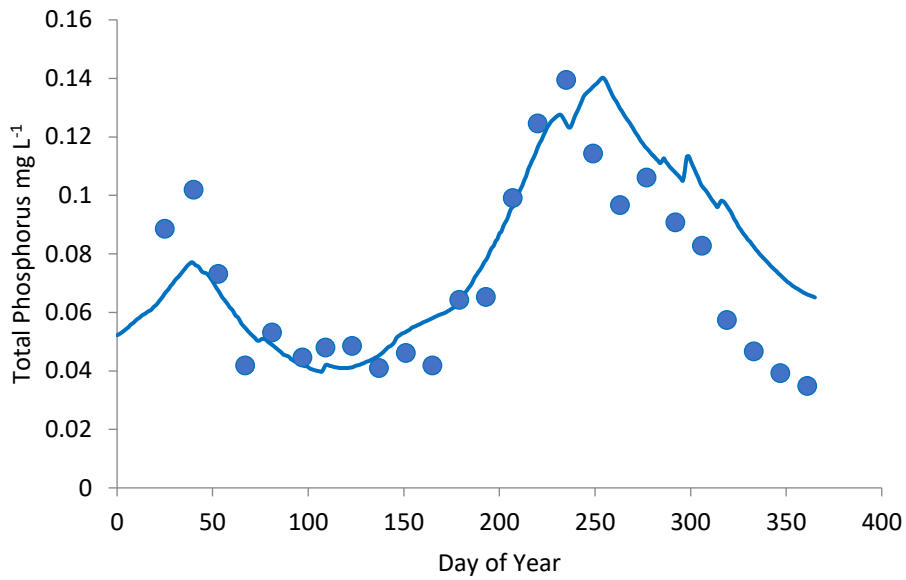


Fig. 2.6 PCLake comparison of observed values (circles) against modelled values (line) for Total Phosphorus

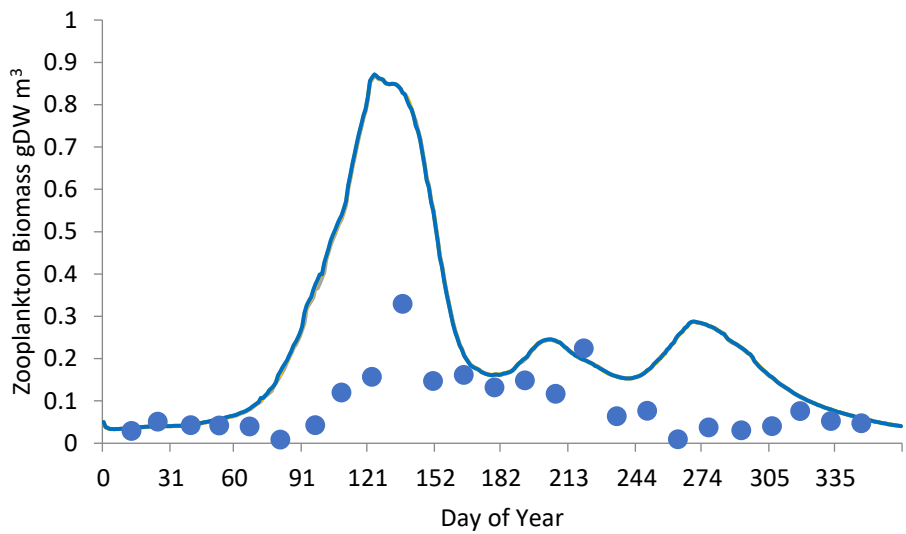


Fig. 2.7 PCLake comparison of observed values (circles) against modelled values (line) for Zooplankton Biomass

Table 2.2 List of PCLake variables changed during calibration to Loch Leven data. Sources of data are listed as LTMP (Loch Leven long term monitoring programme data), LTMP Est (values estimated based on indirect data from the Loch Leven LTMP), Met office (Met Office, 2019a, 2019c), Defew (Data gathered during 2005 Leven Loading survey (Defew, 2008)), Climate hydrology and ecology research support system (CHESS) (Robinson et al., 2016), Specific citation for values derived from the literature, Est. (Estimated due to lack of measured data). Units are those used by the model and were converted to these formats where necessary.

Parameter	Short name	Type	Unit	Original Value	New Value	Source
Depth	_sDepthW_	State	m	2	3.17	LTMP
NO3 in lake water	_sNO3W_	State	g N m3	0.1	2.1	LTMP
PO4 in lake water	_sPO4W_	State	g P m3	1	0.035	LTMP
Dissolved Silica in lake water	_sSiO2W_	State	g Si m3	3	6	LTMP
Oxygen in lake water	_sO2W_	State	g O2 m3	10	8	LTMP
Diatoms DW in lake water	_sDDiatW_	State	gDW m3	0.5	1	LTMP Est
Green algae DW in lake water	_sDGrenW_	State	gDW m3	0.5	0.2	LTMP Est
Vegetation DW in lake water	_sDVeg_	State	gDW m2	1	0.1	LTMP Est
Water temperature	_mTemp_	Time series	oC			LTMP
Light	_mLOut_	Time series	W m2			Met Office
Wind	_mVWind_	Time series	m s			Met Office
Inflow	_mQIn_	Time series	mm day			Defew
Outflow	_mQOut_	Time series	mm day			LTMP
Evaporation	_mQEv_	Time series	mm day			CHESS
P loading	_mPLoad_	Time series	g P m2 day			Defew
N loading	_mNLoad_	Time series	g N m2 day			Defew

Parameter	Short name	Type	Unit	Original Value	New Value	Source
Fetch	_cFetch_	Parameter	m	1000	5900	LTMP
Resuspension by adult fish browsing	_kTurbFish_	Parameter	g g_fish day	1	0.5	Est.
Daily grazing of birds	_cDGrazPerBird_	Parameter	gDW coot day	45	80	Cramp et al., 1986
Specific cover	_cCovSpVeg_	Parameter	%cover gDW m2	0.5	0.2	LTMP Est
Quadratic half-saturation NO3 concentration for denitrification	_hNO3Denit_	Parameter	mgN l	2	1	Est.
mol_O2_formed_per_mol_NO3-ammonified	_O2PerNO3_	Parameter	-	1.5	1	Est.
Optimum temperature for grazing	_cTmOptLoss_	Parameter	oC	25	20	Est. Grover and Chrzanowski, 2006
Optimum temperature diatoms	_cTmOptDiat_	Parameter	oC	18	15	Chrzanowski, 2006
Maximum P uptake capacity of diatoms	_cVPUptMaxDiat_	Parameter	mg P mgDW day	0.01	0.04	Est.
Optimum temperature green algae	_cTmOptGren_	Parameter	oC	25	20	Est.
Maximum P uptake capacity of greens	_cVPUptMaxGren_	Parameter	mg P mgDW day	0.01	0.03	Est.
Maximum N uptake capacity of greens	_cVNUptMaxGren_	Parameter	mg N mgDW day	0.07	0.1	Est.
Maximum P uptake capacity of bluegreens	_cVPUptMaxBlue_	Parameter	mg P mgDW day	0.04	0.08	Est.
Maximum N uptake capacity of bluegreens	_cVNUptMaxBlue_	Parameter	mg N mgDW day	0.07	0.11	Est.

Parameter	Short name	Type	Unit	Original Value	New Value	Source
Maximum filtering rate zooplankton	_cFiltMax_	Parameter	ltr mgDW day	4.5	4.6	May and Jones, 1989
Selection factor for diatoms	_cPrefDiat_	Parameter	-	0.75	0.8	Est.
Maintenance respiration constant zooplankton	_kDRespZoo_	Parameter	day-1	0.15	0.18	Est.
Optimum temperature zooplankton	_cTmOptZoo_	Parameter	oC	25	24	Clare, 2002
Optimum temperature of fish	_cTmOptFish_	Parameter	oC	25	15	Solomon and Lightfoot, 2008

Chapter 3 - Assessing the use of statistical early warning indicators to predict ecological tipping points in a shallow lake, Loch Leven, U.K

Ives, S. C. Burthe, S. Henrys, P. May, L. Woods, H. Gunn, I. D. M. Heal, K. V. Spears, B.M

The candidate, as lead author, performed all statistical analysis, writing and production of graphics. Data were collated by the candidate with help from L. May, H. Woods and I. D. M. Gunn. Statistical tools were developed by P. Henrys and were taught to the candidate with help from S. Burthe. Co-authors contributed to the editing of the manuscript.



3.1 Introduction

Sudden non-linear change in populations and across whole ecosystems can lead to extreme deterioration in ecological structure and function, loss of ecosystem services and local extinction of species (Brock and Carpenter, 2010; Carpenter et al., 2011; Folke et al., 2004). These changes can be caused by changes in extrinsic drivers, for example, the oft-cited regime shift between phytoplankton and macrophyte dominance in shallow lakes, driven by phosphorus (P) loading (Scheffer et al., 2001, 1993; Scheffer and Jeppesen, 2007). This behaviour is thought to be caused by the breakdown of stabilising feedback mechanisms, resulting in hysteresis and 'critical transitions' (Scheffer et al., 2001).

The suddenness, characteristic of these changes makes managing these events particularly difficult. Although the shift from macrophyte to phytoplankton dominance is often sudden, some studies have shown that changes within the macrophyte community can begin much earlier, sometimes decades to centuries in advance (Davidson et al., 2005; Sayer et al., 2010a). This can give advance warning of when the macrophyte community is at its most vulnerable. Despite this, being able to predict the shift between a degraded macrophyte community and phytoplankton dominated state as well as other forms of non-linear change could allow managers to act to prevent ecological degradation before a regime shift occurs and maintain good ecological conditions (Pace et al., 2016). In recent years, methods have been proposed to predict particular types of sudden ecological change. Although a variety of these methods exist, the majority are based on one of two phenomena: critical slowing down (CSD) (Wissel, 1984) or flickering (Dakos et al., 2012a). CSD and flickering represent quantifiable aspects of ecological stability, which theoretically should respond under certain conditions when approaching a shift. CSD should be measurable in the increasing time to recovery following small perturbations as a shift approaches (Scheffer et al., 2009). Flickering is the response of a system where perturbations cause shifts backwards and forwards between regimes (Dakos et al., 2012a). These phenomena can theoretically be measured within time series, through a number of indicators such as increasing antecedent variance and autocorrelation (Dakos et al., 2012b).

Early work using laboratory experiments (Drake and Griffen, 2010), ecosystem scale experiments (Carpenter et al., 2011) and simulated data sets (Cottingham et al., 2000)

purported to demonstrate that EWIs could be used successfully to predict various forms of ecological transition. For instance, Carpenter and Brock (2006) simulated phosphorus flows in water, soil and sediment in a lake that experienced a transition. Using the outputs from this model, variance measured as standard deviation (SD) predicted the simulated shift years in advance. Using laboratory populations of *Daphnia magna*, Drake and Griffen (2010) manipulated food provision to induce population collapse in some replicates. Four candidate EWIs (coefficient of variation, autocorrelation, skewness and spatial correlation) were then tested and reported to successfully predict the collapse. Carpenter et al. (2011) took this one step further by experimentally inducing a regime shift in a lake through the addition of top predators. Their characterisation of a regime shift is based on a selection of changes, including statistically defined non-linear change in select variables, combined with planktivorous fish distribution in a manipulated vs a control lake. In real life systems without controls, the situation is much more complex, with extensive and interacting pressures potentially impacting the systems and no fore-knowledge of the mechanisms behind changes.

Burthe et al. (2016) tested EWIs on contemporary long-term monitoring data across multiple lakes and one marine system. This study involved a more systematic testing of EWI responses to a particular type of statistically defined non-linear change across a large array of datasets and ecosystems and indicated low levels of agreement between tipping points and EWIs across multiple trophic levels. Gsell et al. (2016) conducted a similar assessment against another kind of statistically defined transition in lakes but focused on variables expected to respond to CSD. Despite this, they also reported low levels of agreement between EWIs and transitions. This suggests that either the shifts/transitions detected in these studies are not of the type usually detected by EWIs (i.e. they are not subject to CSD or flickering) (Boettiger et al., 2013; Dakos et al., 2015), some aspect of the methodology employed when using EWIs (e.g. data frequency) is insufficient/incorrect or the reliability of EWIs is low.

Many EWIs are calculated using a rolling window across a time series, within which the indicator is calculated across said window at a given time step. The selection of window size may be important in determining the sensitivity of EWIs, given that larger window sizes dampen the signal and shorter ones are subject to small scale noise (Lenton et al., 2012; Spears et al., 2017). It is therefore important to examine the effects of rolling window size on accuracy. This can be conducted using a systematic approach and by conducting a

sensitivity analysis (Dakos et al., 2012a) to test for the most appropriate window size, a parameter of the EWI calculation.

Here we address these knowledge gaps using the long-term time series data from Loch Leven, Scotland, to test the following hypotheses: (1) that multiple tipping points have occurred in Loch Leven and that these are consistent across trophic levels, (2) where these tipping points occur, they will be preceded by an EWI, (3) the accuracy of EWIs will vary with window size, and (4) using EWIs in tandem will result in increased accuracy of predictions.

3.2 Methods

3.2.1 Study site

Loch Leven is a large shallow lake in east central Scotland (56°10'N, 3°30' W). It has a catchment area of 145 km², a surface area of 13.3 km², a mean depth of 3.9 m and a maximum depth of 25.5 m. The lake has a long history of nutrient pollution and management and has been the site of a long-term monitoring programme including data from ~150 limnological variables, many dating back to 1968 (May and Spears, 2012).

3.2.2 Data processing and analysis

Twenty-six time-series of species and chemical data from the Loch Leven Long-Term Monitoring Programme (see Table 2.1) were analysed to identify common tipping points across trophic levels. These datasets were selected due to a mixture of factors such as their importance in lake ecological function, a spread across different trophic levels as well as length and data frequency of the datasets. Prior to analysis each dataset underwent standardised processing and detrending to account for seasonal changes and differences in sampling frequency. Day of year was used as a covariate to account for any seasonal effects and is applied as a Generalised Additive Model (GAM, (Hastie and Tibshirani, 1990)) using the *mgcv* package (version 1.8-3; (Wood, 2011)) in R (R Core Team, 2018). Estimates of the model will then be removed from the time series to provide data free of seasonal influence.

Prior to EWI analysis, the data were assessed for the presence of tipping points. Following Burthe *et al.* (2016), this involved the fitting of a GAM with smoothly varying function of time as a covariate, allowing the detection (through the use of thin-plate regression splines (Wood, 2003)) and characterisation of tipping points. Three states will characterise the trend

and hence any tipping points; increasing trend, stationary and decreasing trend. The first derivative of the smoothing function will then be used to calculate 95% point-wise confidence intervals, which allows the assessment of whether the gradient is significantly different from zero. Non-significant tests will be classified as stationary with significant increasing or decreasing trends classified accordingly. Following this step, variance calculated as standard deviation, autocorrelation at lag-1, skewness, kurtosis and return rate will be calculated using window sizes ranging from 15% of the time series length to 65% using the early warnings package (version 1.0.59) in R following the methodology from Burthe *et al.* (2016) and Dakos *et al.* (2012a). These derived time series will then be analysed using the same methods outlined above.

3.2.3 Assessing optimum window size for EWIs

The GAM classifies tipping points according to the trend preceding the tipping point and the direction of the tipping point as used in Burthe *et al.* (2016). The classifications are as follows:

- Stationary to Positive
- Stationary to Negative
- Positive to Stationary
- Negative to Stationary

To correctly assess EWI accuracy, only particular classifications of tipping points for both the raw data and EWIs were used. EWIs were only tested against tipping points that are classified as either stationary to negative or stationary to positive. To be classed as an 'Early Warning', EWIs were classed as stationary to positive apart from return rate which was classified as stationary to negative as it is expected to decrease prior to a shift. EWIs occurring within a 10-year window of the end of a time series are discounted, as it is impossible to determine if that tipping point occurred within the defined window. Due to the nature of the analysis, some tipping points occur prior to the beginning of EWI time series because of the window size; these have been ignored to prevent bias. To classify the coherence of EWIs and tipping points we used the terminology from Scheffer *et al.* (2009) defined as follows:

- True Positive – Tipping point preceded by an EWI
- False Positive – EWI occurrence but no corresponding tipping point
- False Negative – Tipping point occurrence but no preceding EWI

Using these definitions we can assess the frequency of these events, which gives us a measure of the accuracy and reliability of EWI assessment.

One tipping point was not included in any analysis due to its date being too close to the beginning of the time series for any of the window sizes to detect. Any tipping points detected by some window sizes but not by others due to being 'missed' by the rolling window were excluded from any summary statistics. Rolling window sizes ranging from 15% of the time series length to 65% were analysed for all time-series containing tipping points. The analysis was stopped at 65% as the number of tipping points that could be included became too small.

3.3 Results

3.3.1 Tipping point detection and coherence

Twenty-six time series were tested for tipping points with a total of ten tipping points detected across eight of these time series (30.7% of times series) (see Fig. 3.1) with one tipping point excluded due to its position very early in the time series, making it unsuitable for use with EWIs. Tipping points were detected across multiple trophic levels ranging from primary producers through to apex predators (see Table 2.1). Five datasets had a single detected tipping point with two datasets having two tipping points detected (e.g. chlorophyll a (see Fig. 3.2)), giving a total of nine tipping points used for this analysis. There were three years in which two tipping points occurred: 1981 with two bird species (cormorant, greylag geese), 1999 with two zooplankton species (*Cyclops abyssorum* and *Eudiaptomus gracilis*) and 2004 with chlorophyll a and greylag geese (see Fig. 3.1).

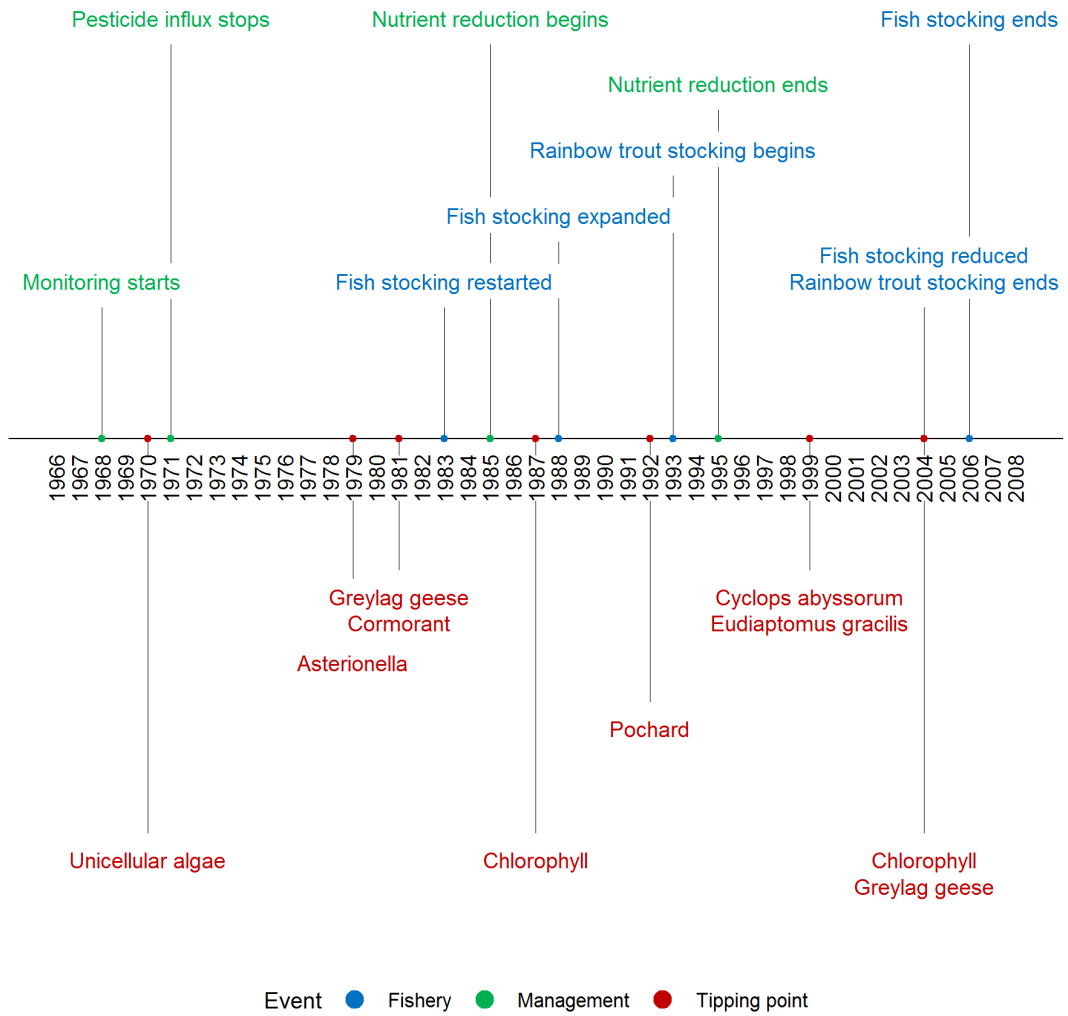


Fig. 3.1 Timeline of fishery and management events (top of graph) along with detected tipping points (bottom of graph) in Loch Leven (see also Table 3.2).

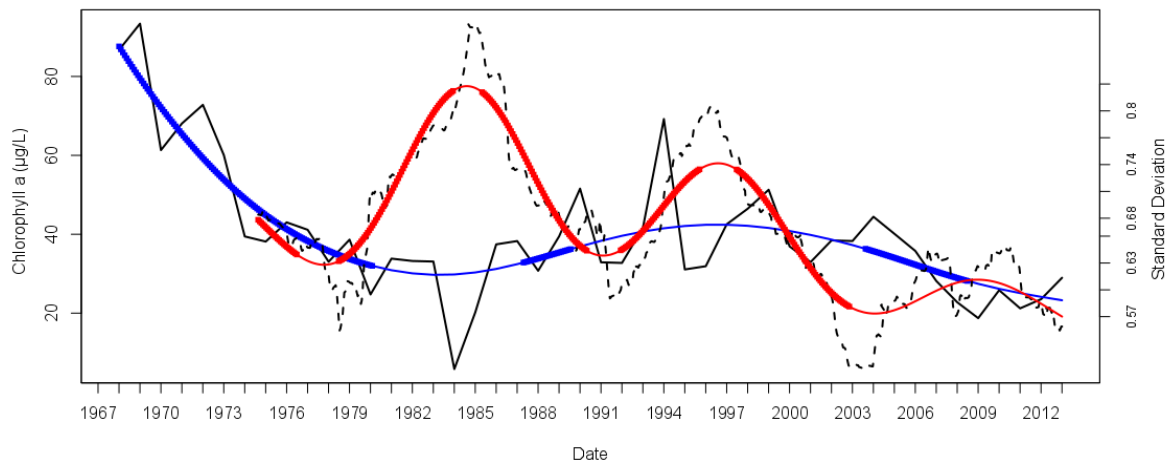


Fig. 3.2 Example graph showing detrended chlorophyll a time series in Loch Leven with the solid black line showing detrended raw data and the dashed black line showing raw EWI data. Changes of thickness of overlaid blue line show detected tipping points. Changes in overlaid red line show detected changes in the EWI at 15% window size. Other graphs from this analysis can be found in Appendix 1.

Table 3.1. Total number of tipping points considered at each window size along with the maximum number of true positives that could be detected along with results of the EWI analysis.

Rolling window size %	Tipping points	Max Possible True positives	False Negatives	False Positives	True Positives
15	9	45	33	11	12
25	9	45	38	14	7
35	6	30	22	10	8
45	5	25	17	6	8
55	4	20	15	2	5
65	4	20	15	4	5

3.3.2 Tipping point and EWI coherence across different window sizes

Each time series containing a tipping point was analysed with all five EWIs, across six different window sizes. Overall, 45 true positives were detected (25%) across all EWIs and all window sizes. The highest accuracy was found in the 45% window size with eight true positives detected (32.0%) from a possible 25, 12 (26.7%) true positives were found at 15% WS, seven (15.6%) at 25% WS, eight (26.7%) at 35% WS, five (25%) at 55%WS and (25%) 65% WS (See Fig. 3.3). Total spread between highest and lowest accuracy amongst window sizes was 16.4%. In all cases false negatives were the most numerous of all available outcomes (see

Fig. 3.3 and Table 3.1) and totalled 140 occurrences of a possible 185 (75.6%). The amount of false negatives was directly proportional to the number of true positives and so represents the remaining percentage in all cases. The WS with the highest true positive percentage was the 45% WS which had 32%, the percentage of false negatives for this WS was 68% with a total of 17 from a possible 25. The 15% WS had 33 false negatives (73.3%), the 25% WS had 38 (84.4%), 35% WS had 22 (73.3%), 55% WS had 15 (75%) and 65% WS had 15 (75%).

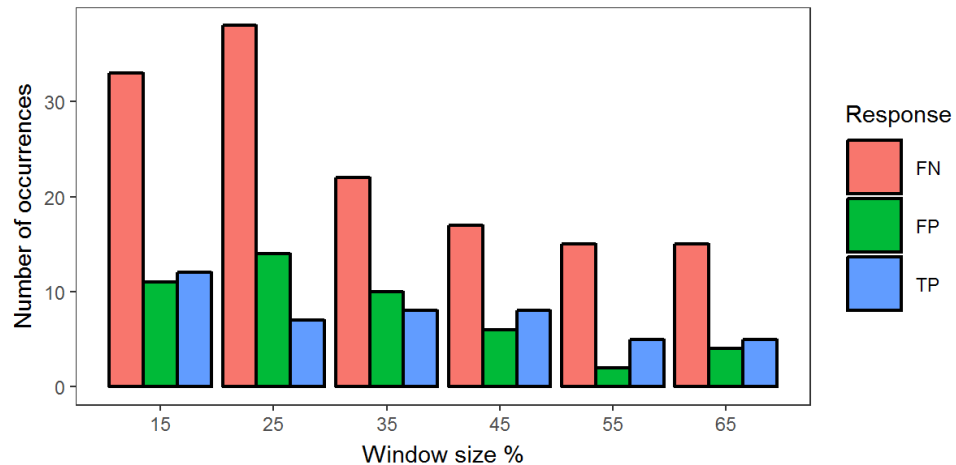


Fig. 3.3 Number of datasets containing False Negatives (FN), False Positives (FP) and True Positives (TP) at different window sizes across all five EWIs.

As well as being able to successfully predict tipping points another aspect of EWI usage is false predictions (false positives). In total 47 false positives were found across all EWIs, slightly more than the number of true positives (104% of the number of true positives). The 25% window size had the highest number with 14 false positives, followed by 15% WS with 11, 35% with 10, 45% with 6, 65% with 4 and 55% with 2 (Fig. 3.3).

3.3.3 EWI Performance

Of the five EWIs tested, standard deviation had the highest number of true positives at 15 of a possible 37 (40.5%) but also had the joint highest number of false positives (13). Kurtosis had 10 true positives (27%) and 12 false positives, Skewness had 9 true positives (24.3%) and 13 false positives, Autocorrelation had 8 true positives (21.6%) and 4 false positives and Return rate had 3 true positives (8%) and 5 false positives (See Fig. 3.4). As with the window size analysis, false negatives represented the most numerous outcome in all cases. Return rate had the highest number of false negatives with 34 (91.9%) followed by autocorrelation

with 29 (78.4%), skewness with 28 (75.7%), kurtosis with 27 (73%) and standard deviation with 22 (59.5%) (see Fig. 3.4).

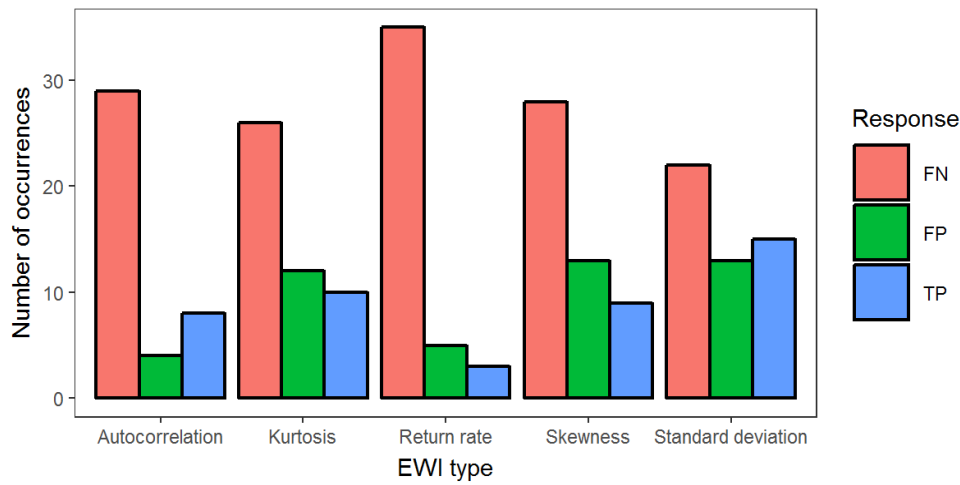


Fig. 3.4 Number of datasets containing False Negatives (FN), False Positives (FP) and True Positives (TP) across five different EWIs over all window sizes.

Using five EWIs allowed us to not only test their accuracy independently, but also to assess how they performed as a group. Standard deviation performed best in terms of overall accuracy across all window sizes and was one of only two EWIs with more true positives than false positives, the other being autocorrelation. Looking at all window sizes, the use of multiple EWIs substantially increased accuracy from 40.5%, when considered individually, to 70.2% when considered as a group (see Fig. 3.5). From this, the majority of tipping points were only detected by a single EWI, the type of which varied substantially (see Table 3.2). Across all window sizes 37 tipping points can be considered, of which 26 (70.2%) were predicted by at least one EWI. Of these, 12 tipping points were predicted by a single EWI (32.4%), 10 were predicted by two EWIs (27%), three were predicted by three EWIs (8%), one was predicted by four EWIs (2.7%) and zero by all five. The use of EWIs as a group was the only circumstance where true positives outweighed the false negatives where for all 5 EWIs there were 11 false negatives (29.8%) from a possible 37. The number of false negatives for those detected by a single EWI was 25 (67.6%), for two EWIs 27 (73%), for three EWIs 34 (92%), for four EWIs 36 (97.3%) and none for all five.

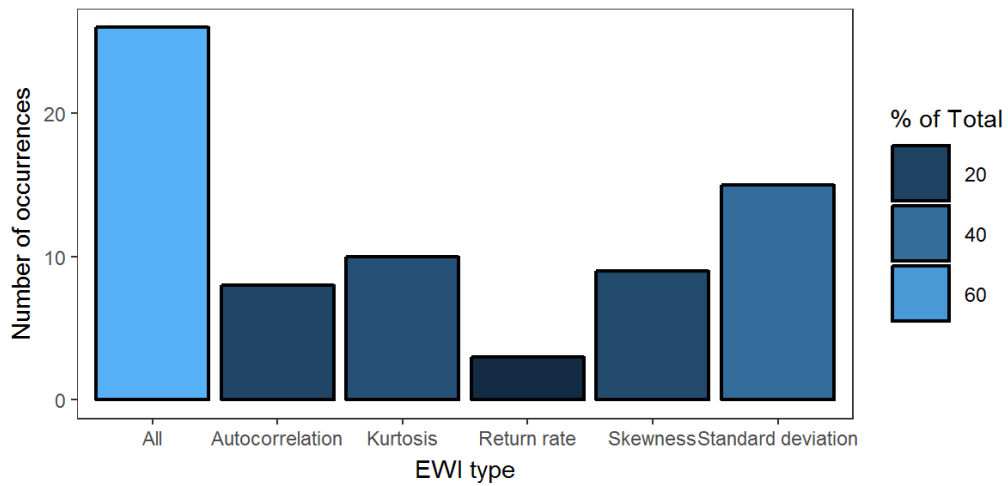


Fig. 3.5 Number of true positives for EWIs individually and as a group (All) as a percentage of the total number of true positive possible.

When classified by trophic level, three tipping points were detected in Primary Producers (PP), two in Primary Consumers (PC), three in Secondary Consumers (SC) and one in Apex Predators (AP). Overall PP had the highest success rate with 19 true positives from a possible 55 (34.5%), 16 false positives and 36 false negatives (65.5%), PC had the second highest success rate with 14 true positives from a possible 60 (23.3%), 22 false positives and 46 false negatives (76.7%), SC had 12 true positives from a possible 60 (20%), 8 false positives and 48 false negatives (80%) and AP had 0 true positives from a possible 10, 1 false positive and 10 false negatives (see Table 3.2 and Fig. 3.6). These results show two main patterns, lower trophic levels show slightly higher number of true positives and lower numbers of false negatives with false positives showing a more mixed pattern. Also, both PP and PC have higher true positives and false positives than either the SC or AP. PP and PC both feature biweekly data whereas SC and AP have annual data, showing differences in the ability of EWIs to function at different data frequencies.

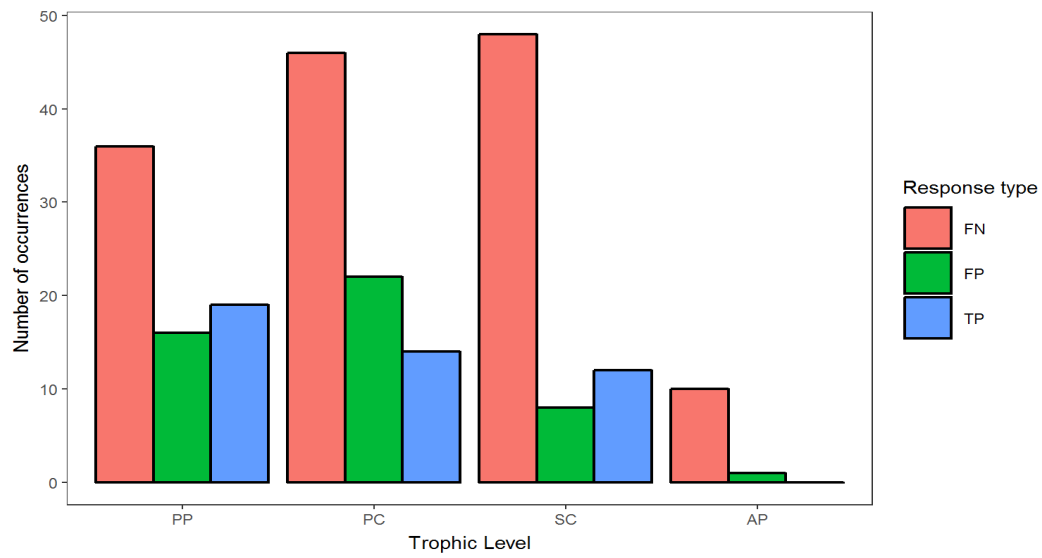


Fig. 3.6 Number of different response types (False Negatives (FN), False Positives (FP) and True Positives (TP)) across all trophic levels (Primary Producers (PP), Primary Consumers (PC), Secondary Consumers (SC) and Apex Predators (AP)).

Table. 3.2 EWI response for all window sizes for each individual tipping point by dataset. Numbers in bold show total responses for an individual EWI. Numbers in brackets differentiate different tipping points within the same time series. Blank cells represent no occurrences of that response type. Abbreviations for Trophic level are as follows: PP – Primary Producer, PC – Primary Consumer, SC- Secondary Consumer, AP – Apex Predator.

EWI/Response type	Chlorophyll (1)	Chlorophyll (2)	Cormorant	Cyclops	Eudiaptomus	Greylag (1)	Greylag (2)	Pochard	Asterionella	
Trophic Level	PP	PP	AP	PC	PC	SC	SC	SC	PP	
Autocorrelation		3	6	2	6	6	2	7	7	2
FN		2	3	2	5	5	2	6	2	2
FP								1	3	
TP		1	3		1	1			2	
Kurtosis		4	7	2	9	9	2	7	4	4
FN		2	1	2	5	6	2	3	3	2
FP		2	1		3	3		1		2
TP			5		1			3	1	
Return rate		4	8	3	8	6	2	6	4	2
FN		4	5	2	5	6	2	5	4	2
FP			2	1	2					
TP			1		1			1		
Standard deviation		3	9	2	8	11	3	6	4	4
FN		1	5	2	2	2	1	3	4	2
FP			3		2	5	1			2
TP		2	1		4	4	1	3		
Skewness		4	8	2	8	11	2	7	5	3
FN		1	2	2	5	5	2	5	4	2
FP		1	2		2	5		1	1	1
TP		2	4		1	1		1		

3.4 Discussion

Tipping points were found in 30.7% of the variables tested, across four trophic levels. No sign of coherence was found between tipping points across trophic levels pointing to system-wide non-linear change, although there were three years in which two tipping points were detected. Overall EWI performance in predicting detected tipping points was low, with differences between different window sizes being minimal (total spread of 16.4%), showing that in this instance varying window size has minimal impact on overall accuracy but did change which tipping points were predicted by EWIs. On an individual level each EWI was generally unreliable across all datasets and window sizes, but when considered as a group, accuracy was substantially higher. Across all forms of analysis, false negatives represented the most common and numerous response, with a single exception when EWIs were used as a group.

Similar to Burthe et al. (2016), we assumed detected tipping points to represent generic non-linear change, rather than specific critical transitions or regime shifts. Unfortunately, like many other methods, this way of detecting tipping points gives us no information on whether they are subject to CSD and the likelihood is that at least some of them have been caused by external pressures or changes making the transition not subject to CSD such as a migratory bird species suffering due to conditions away from Loch Leven (Hastings and Wysham, 2010). However, they can inform us more generally about the behaviour of EWIs both individually and in-tandem, compared to statistically defined non-linear change under different window sizes. In other studies, variance (as standard deviation or coefficient of variation) and autocorrelation have been the most commonly used EWIs (Carpenter et al., 2008; Pace et al., 2013). Our results show that standard deviation had the highest number of true positives across all window sizes. Coupled with the joint highest number of false positives this demonstrates how sensitive it is to a wide range of ecological changes (Kéfi et al., 2013). Autocorrelation in general seems less sensitive due to a much lower number of true positives (second lowest overall), along with the lowest number of false positives but has been found to be one of the most robust EWIs in other studies (Clements et al., 2015). The different way changes in data affect autocorrelation compared to standard deviation (Dakos et al., 2012a) could explain these differences, not only between these but all of the EWIs tested here. When we see the small amount of overlap between the exact tipping points detected it shows the potential of EWIs to help us better understand ecosystem behaviour.

Changing the size of the rolling window, across which we calculate EWIs, can have a number of impacts. Smaller window sizes should allow greater sensitivity in EWIs, allowing shorter-term changes to have a greater impact on the signal. Larger window sizes should have a greater smoothing effect, only showing more sustained changes in the signal. Many of the impacts seen under different window sizes can vary depending on the length of the data set and the data frequency. Here we adopted a more systematic approach to changing window size, which showed a general increase in true positives at smaller window sizes. Despite the increased detection rate overall, the number of false positives found across the dataset exceeded the number of true positives and the number of false negatives was the most numerous response type of all. Whilst varying the window size had some impacts on the detection of true positives its impacts on false positives were comparable. In some cases, the window size would decrease the number of false positives but usually only at the expense of decreasing the detection rate of true positives at the same time. The occurrence of false positives is a common problem when using EWIs as a number of different forms of ecological change can display behaviour similar to that we would expect to see with CSD (Litzow et al., 2008; Schroder et al., 2005). Such factors present a major barrier to their potential application in management. Other studies have offered solutions to reduce the occurrence of false positives through the use of significance tests (Boettiger and Hastings, 2012; Seekell et al., 2012, 2011), Although the methods are different, significant false positives are still highly prevalent. In future work, the use of generic models (Lade and Gross, 2012) based on the basic structure of the dataset could potentially give a useful baseline in the absence of control sites.

Most other studies have assessed EWIs as independent measures, whilst recent work has assessed the ability of a composite EWI which was found to increase its predictive ability (Clements and Ozgul, 2018). Whilst our results show a significant increase in accuracy overall using a group approach, the largest percentage of tipping points was only detected by a single EWI. These results suggest that the number of EWIs could be increased even further to achieve an even higher level of accuracy. Careful analysis of how different EWIs behave under a variety of kinds of simulated transitions could help inform which would be most applicable to maximise chances of detecting the wide range of non-linear change which could occur. Whilst this represents a significant analytical challenge, decreasing the occurrence of false positives and properly accounting for them when they do occur perhaps represents one

of the most difficult challenges for future EWI research to overcome. Until that point, their potential use as management tools is limited.

When classified by trophic level the success rate of EWIs shows a minor but clear pattern. Lower trophic levels generally have a higher number of true positives and a lower number of false negatives compared to higher trophic levels whereas false positives show a mixed pattern. The lower two trophic levels (PP and PC) have a higher data frequency (biweekly) than the higher two trophic levels (SC and AP) (annual). The higher success rate may potentially be attributed to this, although it is impossible to say for sure and the difference is not particularly large (apart from AP). It is also possible that the organisms' measured in the lower trophic levels are more sensitive to perturbations and more subject to stochastic effects, although this would run counter to some previous studies looking at trophic level sensitivity to climate change (Voigt et al., 2003). Another interesting aspect to these results is the differences in false positives between the higher and lower frequency data types, which shows lower numbers of false positives in the lower frequency data trophic levels. It is possible that the lower number of false positives along with the lower number of true positives shows a general decline in the ability of EWIs to function at lower data frequencies which would fit with current theory (Dakos et al., 2012a; Perretti and Munch, 2012). Whilst thinking about trophic aspects of EWI usage, one potential, currently explored avenue, is the use of EWIs in some trophic levels being used to predict tipping points in others. For instance, the use of an apex predator time series to predict a tipping point in a primary producer. This has the potential to be high informative in terms of the direction of change and could provide useful management information much sooner than when using EWIs in a standard sense and can provide useful information about the expected lag between impacts at the top trophic levels cascading to the lower trophic levels.

Whilst EWI research is relatively young, its application to contemporary real-world data using statistical measures to identify tipping points has been less than successful. Despite this, the use of EWIs in a group substantially increased the detection rate of tipping points in this study, although the overall false positive and false negative rates were still high. In most cases the success rates of EWIs are framed in the form of the percentage of true positives such as standard deviation detecting 40.5% of all possible tipping points and the number of false negatives represents the remainder of this percentage (in this case 59.5%). In this study the only result that featured false negative results below 50% was that of all five EWIs as a group

(29.8%) and whilst presenting the results in this manner makes no difference statistically, it casts a very different light on the way they are viewed as potential management tools.

Although these results are discouraging, a number of caveats should be considered. The frequency of data used in this study and in others testing real world data is comparatively low compared to that offered by new and emerging technologies such as automated monitoring buoys and satellite imagery. The minor differences seen in the success rate of EWIs between different data frequencies in this study support this theory, however this came at the cost of increased false positives. However, as more high frequency data becomes available with longer time series from a variety of lakes and other ecosystems it will open opportunities for the research community to retest techniques already used, on improved data. Coupled with a wide range of experiments inducing different types of transitions and new statistical techniques, as well as extensive analysis of existing datasets to reciprocally test the ability of EWIs in different trophic levels to predict tipping points in others, this could allow us to objectively assess the effectiveness of EWIs to a range of transition types and greatly improve our understanding of fine-scale ecosystem behaviour.

Chapter 4 - Assessing the occurrence of a regime shift in Loch Leven, UK: Ecological change and the presence of hysteresis

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The candidate, as lead author, performed all statistical and modelling analysis, writing and production of graphics. Data was collated by the candidate with help from L. May, H. Woods and I. D. M. Gunn. PCLake was developed by W. M. Mooij and J. H. Janse and taught to the candidate by J. J. Kuiper and J. A. Elliott. Co-authors contributed to the editing of the manuscript.



4.1 Introduction

The threat of unpredictable and rapid ecosystem change has been intensely researched to identify methods of predicting occurrences of non-linear change (Burthe et al., 2016; Carpenter et al., 2011; Gsell et al., 2016; Scheffer et al., 2009; Seekell et al., 2011), as well as to understand the drivers of such events (Anttila et al., 2013; Genkai-Kato et al., 2012; Scheffer et al., 1993; Scheffer and Jeppesen, 2007). Systems that undergo threshold-like changes can seem unaffected, despite substantial changes in drivers over time (Strange, 2007). A wide range of ecosystems have been reported to undergo regime shifts (Folke et al., 2004a), in particular shallow lakes (Blindow et al., 1993; Ibelings et al., 2007; Moss et al., 1996). These transitions typically represent the change from a turbid water-phytoplankton dominated state to a clear water-macrophyte dominated state (or vice-versa). The existence of these states is dependent on feedback mechanisms which generate a hysteretic effect, wherein the system can exist in either state over an intermediate range of nutrient levels, with the likelihood of either state persisting increasing towards low and high nutrient levels respectively (Scheffer et al., 1993; Scheffer and Carpenter, 2003).

In a clear water state the presence of macrophytes stabilises the regime through a number of mechanisms including: stabilisation of sediments to prevent wind and fish mixing (Carpenter et al., 1983; Engel, 1988), direct absorption of nutrients from the water column (Carignan and Kalff, 1980; Lürling et al., 2006), release of allelopathic substances which directly limit phytoplankton growth (Hilt and Gross, 2008), provision of refuge for zooplankton and macroinvertebrates from fish predation (Lauridsen et al., 1996; van Donk and van de Bund, 2002) and camouflage provision for piscivorous fish (Diehl, 1988; Eklov and Hamrin, 1989). In the turbid water state similar and opposing feedback mechanisms exist including: increased phytoplankton growth and loose sediment leading to higher turbidity, making establishment of macrophyte communities more difficult (Moss, 1990; Schiemer and Prosser, 1976), increased amounts of particulate matter impairing zooplankton grazing efficiency (van Donk et al., 1990), removal of zooplankton refuges leading to increased predation (Jeppesen et al., 1998) and removal of camouflage for piscivorous fish leading to less top down control of planktivorous and benthic feeding fish (Lammens et al., 1990).

Much of this early knowledge comes from experiments conducted to restore lakes following eutrophication, which was a widespread problem in the latter half of the 20th century (Smith, 2003). High levels of nutrient loading, particularly in populated regions, led to widespread

phytoplankton blooms and, in the case of many shallow lakes, a persistent turbid state (Gulati and Van Donk, 2002). This led to a range of management measures with a major focus on reducing phosphorus (P) inputs from the catchment (Jeppesen et al., 2005). Despite large reductions, most lakes remained unresponsive for decades, mostly due to 'legacy phosphorus' accumulated in lake sediment (Sharpley et al., 2013). Many early successes in lake restoration involved food web manipulation in combination with nutrient loading reductions and provided much of the early practical understanding of alternative stable state theory (e.g. Jeppesen et al., 1990; Sondergaard et al., 1990; van Donk et al., 1990; Van Donk et al., 1990). In this context, the disruption of the feedback mechanism maintaining higher predation rates on zooplankton and/or removal of bottom feeding fish allows increased grazing on phytoplankton and less sediment disturbance (Blindow et al., 1993; Meijer et al., 1990).

Defining regime shifts has been a subject of widespread discussion, with some arguments requiring the presence of particular statistical properties such as non-linear change, hysteresis and bistability (Burthe et al., 2016; Carpenter et al., 2011; Gsell et al., 2016; Wang et al., 2012b). Other definitions include ecological prerequisites, such as change in physical, chemical and biological ecosystem components as well as changes across trophic levels (Lees et al., 2006). One of the major factors often omitted when considering the occurrence of a regime shift is the difference in form of the stressor-response relationship (Larned and Schallenberg, 2018). To some degree this can be estimated through the calculation of bistability, which demonstrates the possibility of different states under the same nutrient concentrations, representing an unstable equilibrium (Andersen et al., 2009). Ideally, data from both deterioration and recovery trajectories are required to properly assess the shape of stressor-response relationships. Since this is rarely available, a plausible alternative is the use of process models allowing the generation of these relationships after calibration to particular lakes or lake types (Spears et al., 2017). As with all complex models, process models with this capability (such as PCLake (Janse, 1997; Janse et al., 2008)) are subject to equifinality, where multiple parameter combinations can result in the same outcome (Beven, 2006). Despite this, they still represent one of the more reliable methods for better understanding the form of the change that has taken place when combined with real data.

Loch Leven, Scotland, UK, like many lakes, suffered high nutrient inputs and regular algal blooms in the mid-to-late 20th century. A long term plan to reduce external P loading was

enacted between 1985 and 1995 during which inputs were reduced from 20 t year⁻¹ to 8 t year⁻¹ (May and Spears, 2012b). Despite this, in lake P concentrations remained high for many years until a sudden decrease in 2007 (Spears et al., 2012). In this chapter the aim is to assess the form of the ecosystem change in 2007 within Loch Leven. Specifically, we are looking for change across multiple trophic levels, the presence of non-linear change and evidence of hysteresis. To do this, three steps will be taken:

1. Statistically quantify the changes of multiple variables across different trophic levels using a before/after analysis.
2. Test the variables showing significant change during the before/after analysis for the presence of non-linear change.
3. Use PCLake to test states using starting values from years 2005 (before the change) and 2008 (after the change) to test for differences in response to changes in external nutrient loading.

4.2 Methods

4.2.1 Data Collection

The majority of the data used in this chapter was collected as part of the Loch Leven Long Term Monitoring Programme (LTMP), described in section 2.1.1. Zooplankton body size data was characterised using archived weekly samples for the 14-year period covered by the before/after analysis, as explained in detail in section 2.2. Briefly, three individuals of each species were selected at random from each sample and measured under a binocular microscope. To calculate biomass, these measurements were combined with count data from the Loch Leven LTMP using a regression equation developed for each individual species from the River Thames, UK and Lake Donk, Belgium (Bottrell et al., 1976; McCauley, 1984). During zooplankton measurement the presence/absence of helmets in *Daphnia* specimens was recorded as these have been linked to predation pressure by fish through the presence of predator kairomones (Boersma et al., 1998; Tollrian, 1990) and small-scale water movement (Hrbáček, 1959).

4.2.2 Data Processing and Analysis

A before/after analysis was employed to test for significance in responses in the 14 year time series data, split into two seven year blocks of 'Before' and 'After' 2007. Given the data available at the time of analysis, a 14 year period was selected to provide a balanced analysis, running from 2000 until the end of 2013. The before period is classed as 2000 to the end of 2006 and the after data classed as 2007 to the end of 2013.

Data processing was conducted prior to the analysis by creating a separated data frame within R (R Core Team, 2018) consisting of every day of the year. This was matched to the empirical raw data prior to the interpolation between sample dates to provide daily time steps. The 15th of the month was selected as the sample date as actual sample dates varied substantially in each month across the sampling period. One value was extracted from each month for the whole 14-year period which allowed for the occasional missing value and so provide equal numbers of samples in both before and after periods. The high level of variability in the within-month sampling dates would lead to highly variable amounts of time between samples and so for consistency, a single sample per month from an interpolated dataset was chosen.

All time series datasets for the before/after analysis were analysed using the Wilcoxon signed rank test to account for the non-normal and non-independent nature of the data. The *Daphnia* helmet presence/absence data were analysed using a proportions test as part of the before/after analysis.

Following the before/after analysis, all significant variables were further analysed to test for non-linearity through the use of the Brock-Dechert-Scheinkman (BDS) test which runs the time series data through Generalized Autoregressive Conditional Heteroscedasticity (GARCH) models, which predict the mean and variance of the time series based on the assumption that it is linear before removing the linear components, meaning what is left is non-linear (Hsieh et al., 2008). Following this procedure, any remaining structure in the residuals is likely to be non-linear. These are then tested under the assumption they are independent and identically distributed using the BDS test bootstrapping procedure with 10000 iterations (Brock et al., 1996; Dakos et al., 2012a).

4.2.3 Process modelling using PCLake

To test for the presence of hysteresis, a bifurcation analysis was conducted for chlorophyll, zooplankton biomass and macrophyte percentage cover in PCLake (see section 2.3 for a more detailed description of PCLake and the fitting process) with starting values taken from different variables in the Loch Leven dataset (see Table 2.2 in Chapter 2). This analysis can compare two different sets of state variables across P loads which were varied in the model between $0.1 \text{ mg m}^{-2} \text{ day}$ and $5 \text{ mg m}^{-2} \text{ day}$ at 21 intervals. To improve confidence in the presence of hysteresis both the before and after sets have been run using data from 6 separate years. One set will correspond to values taken from 2000-2005 Loch Leven data, and the other will contain values from the 2008-2013 Loch Leven data. Unfortunately, macrophyte percentage cover data is not available for Loch Leven but maximum growing depth (MGD) data are and so an estimation of the potential area of the Loch covered by macrophytes was generated based on loch depth profiles and how much of the surface area could be covered at 4.3 m as this was the MGD achieved for that year. This analysis allows us to test the shape of the stressor response relationship for chlorophyll under different nutrient loads which can indicate if the system is likely to exhibit hysteresis between the two sets of values.

4.3 Results

4.3.1 Before/After Analysis

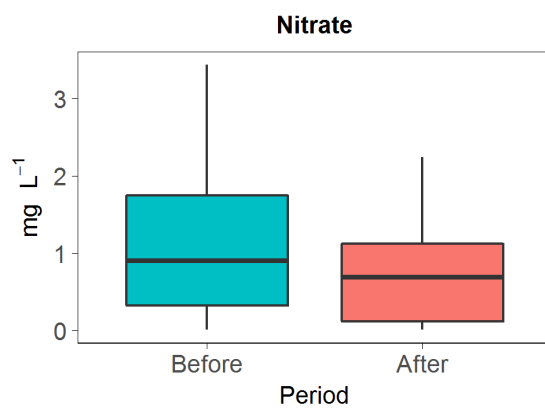
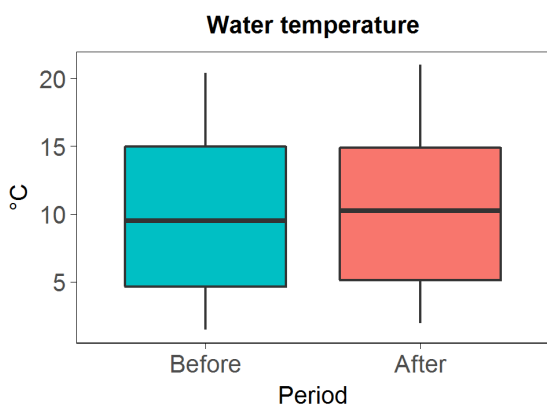
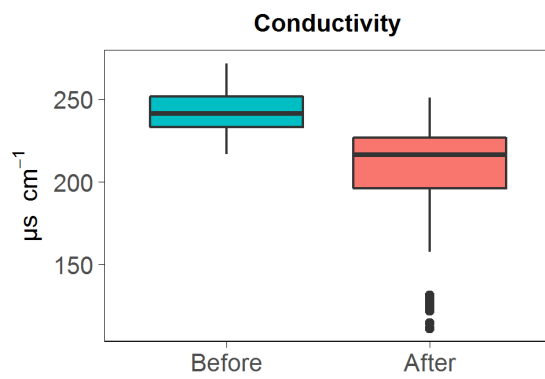
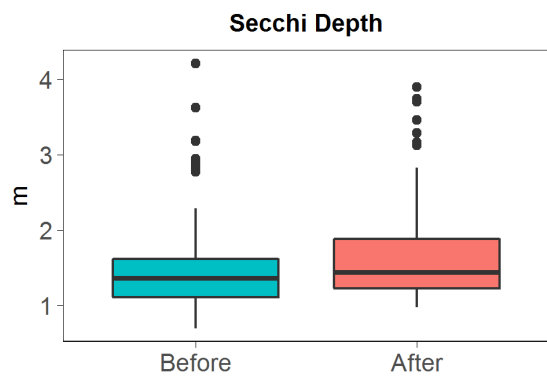
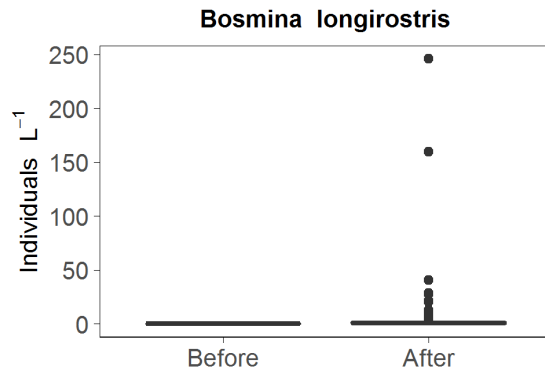
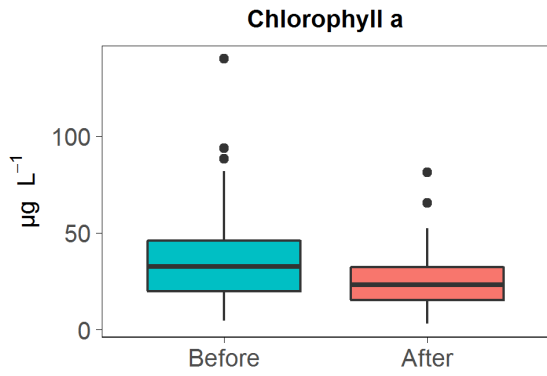
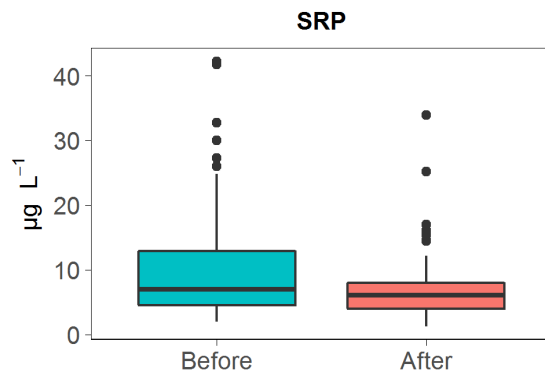
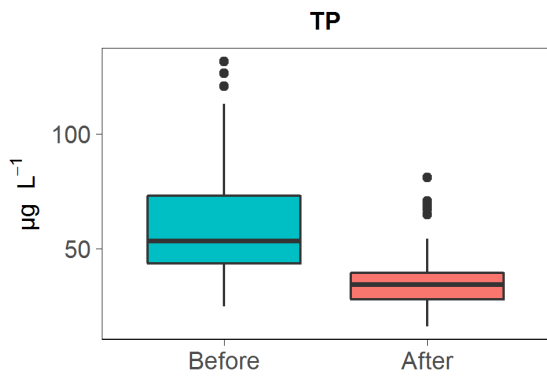
A total of 15 separate datasets were analysed representing physical, chemical and biological components across different trophic levels (physical, chemical, primary producers, primary consumers and a proxy for secondary consumers (*Daphnia* helmet presence)) of the Loch Leven ecosystem. Nine of the variables tested showed significant differences between before and after periods (see Table 4.1) which were spread across trophic levels. Total phosphorus (TP), nitrate, chlorophyll a, *Cyclops* abundance, body size and biomass and conductivity all decreased significantly following the shift (see Fig. 4.1). Soluble reactive phosphorus (SRP) was non-significant but decreased. *Daphnia* helmet presence also showed a significant decrease (see Fig. 4.2), with *Daphnia* body size being the only variable to increase significantly following the shift (see Fig. 4.1).

Table 4.1 Statistical test results of before and after 2007 states with the type of test performed for all tested variables within Loch Leven. Corrected p value column represents results subjected to Benjamini-Hochberg corrections for multiple tests. BDS p value column represents results for BDS tests for non-linearity performed on significant variables after correction. Values in bold represent significant results.

Variable	Statistical test	p value	Corrected p value	BDS p value
<i>Cyclops</i> sp.	Wilcoxon signed rank test	9.32E-11	6.52E-10	0.426
<i>Daphnia</i>	Wilcoxon signed rank test	0.6283	0.6766	
TP	Wilcoxon signed rank test	1.01E-07	4.71E-07	0.0123
Chlorophyll	Wilcoxon signed rank test	0.0011	0.0027	0.001
SRP	Wilcoxon signed rank test	0.0377	0.0586	
Secchi depth	Wilcoxon signed rank test	0.1057	0.1479	
Conductivity	Wilcoxon signed rank test	1.61E-12	2.25E-11	<0.0001
Silica	Wilcoxon signed rank test	0.4816	0.5618	
<i>Daphnia</i> body length	Wilcoxon signed rank test	0.0083	0.01460025	0.0419
<i>Cyclops</i> body length	Wilcoxon signed rank test	1.63E-07	5.71E-07	<0.0001
<i>Daphnia</i> biomass	Wilcoxon signed rank test	0.8183	0.8183	
<i>Cyclops</i> biomass	Wilcoxon signed rank test	2.78E-06	7.78E-06	0.002
Water temperature	Wilcoxon signed rank test	0.473	0.5012	
NO ₃ -N	Wilcoxon signed rank test	0.0039	0.0078	0.268
<i>Daphnia</i> helmet presence	Proportions test	0.0094	0.0154	

4.3.2 Test for non-linear change

Following the before/after analysis, significant variables were tested to assess linearity of time series around the 2007 shift, with the exception of *Daphnia* helmet presence which could not be assessed using this approach due to the categorical nature of the data. Six of the eight variables found to be significant following the before/after analysis were also found to exhibit non-linear trends, meaning the structure of the residuals cannot be explained by linear processes. These datasets were TP, chlorophyll, conductivity, *Daphnia* body size, *Cyclops* body size and *Cyclops* biomass (see Table 4.1).



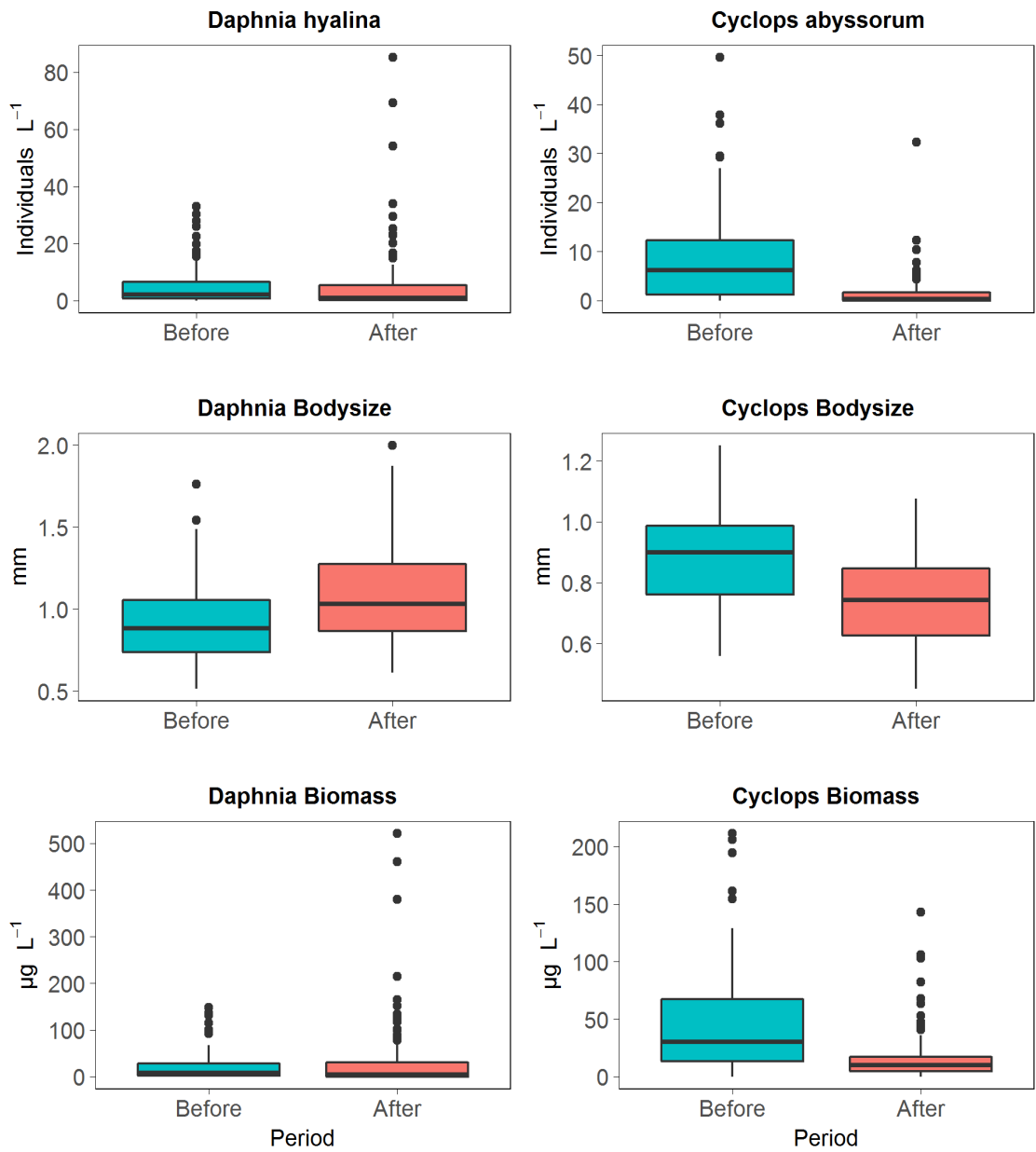


Fig. 4.1 Before/After results for named variables within Loch Leven. Before results represent processed data for 2000-2006, after results represent processed data for 2007-2013.

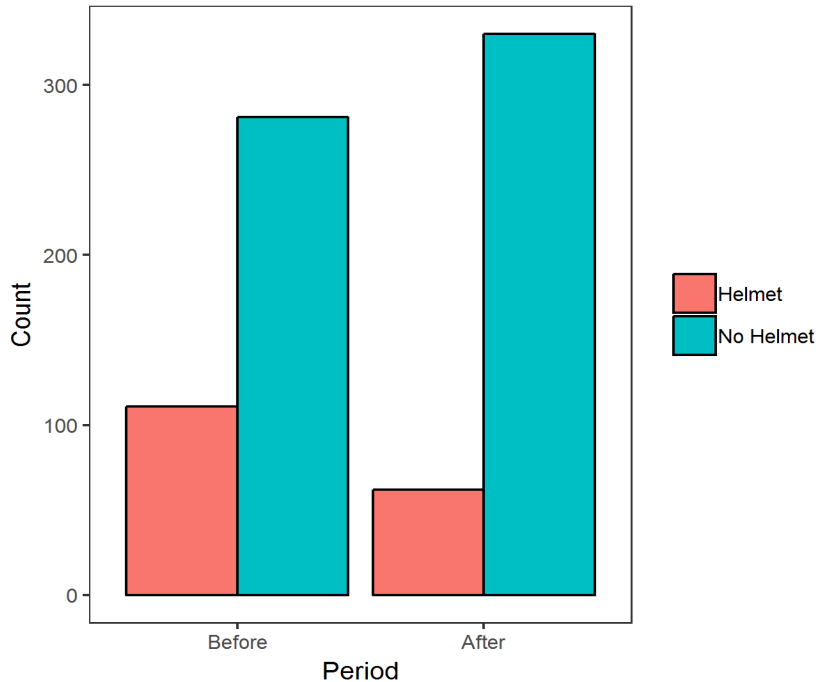


Fig. 4.2 Count of helmet presence in individual *Daphnia* specimens measured for body size. Before and after results represent the same number of individuals sampled.

4.3.3 Process modelling of before and after states

Modelling of the before and after states at multiple nutrient loads for chlorophyll showed an earlier critical nutrient load (CNL) in chlorophyll concentration of the before state at a P load of $1.325 \text{ mg m}^{-2} \text{ day}^{-1}$ with the after state having a CNL of $1.815 \text{ mg m}^{-2} \text{ day}^{-1}$. There was no variation in CNL between the 6 years in either the before and after sets with a maximum standard deviation of $\pm 0.594 \mu\text{g L}^{-1}$. At higher P loads both states follow an almost identical trajectory (see Fig. 4.3). Zooplankton showed a very different pattern with little obvious evidence of hysteresis. The CNL for the before state was $1.325 \text{ mg m}^{-2} \text{ day}^{-1}$, whereas the after state does not have a CNL as it rises in 3 steps before reaching the same level as the before state. These steps are at $1.08 \text{ mg m}^{-2} \text{ day}^{-1}$, $1.325 \text{ mg m}^{-2} \text{ day}^{-1}$ and $1.57 \text{ mg m}^{-2} \text{ day}^{-1}$. As with chlorophyll there was no difference between these values between the different sets in either before or after states with a maximum standard deviation of $\pm 0.0031 \text{ mg DW L}^{-1}$. The CNL for macrophyte percentage cover are the same as for chlorophyll with the after state reaching a slightly higher percentage cover of 11.8% compared to 11.1% for the before state.

As with chlorophyll and zooplankton there was no difference in CNL for any of the years in either the before or after sets with a maximum standard deviation of $\pm 0.016\%$.

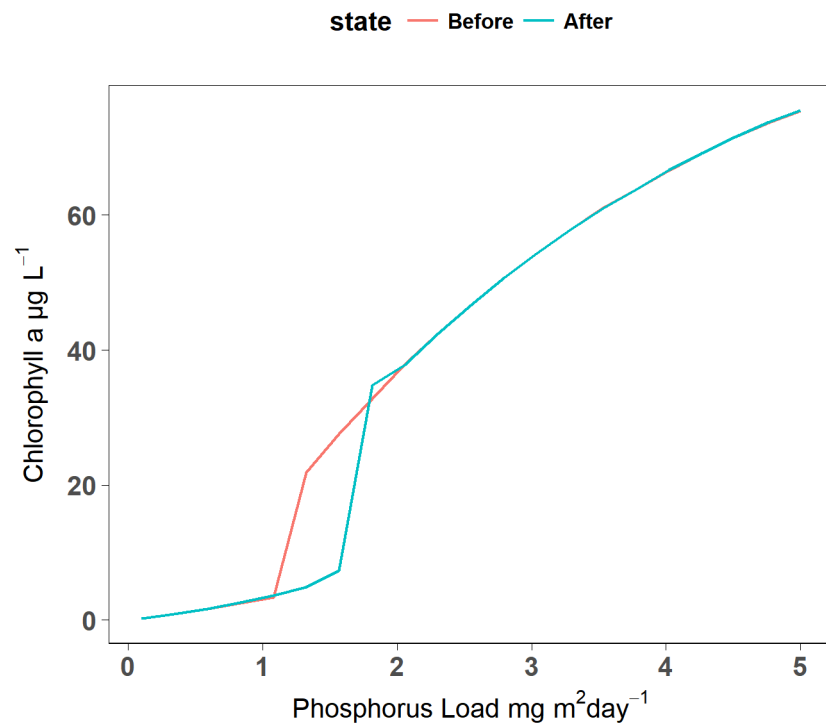


Fig. 4.3 Stressor-Response relationship between chlorophyll and phosphorus load in two states in Loch Leven modelled in PCLake. The before state is represented using data from 200-2005 and the after state is represented using 2008-2013 data. Critical nutrient loads (CNL) are calculated as the point directly after its sudden rise. CNL are: Before - $1.325 \text{ mg m}^{-2} \text{ day}^{-1}$, After - $1.815 \text{ mg m}^{-2} \text{ day}^{-1}$.

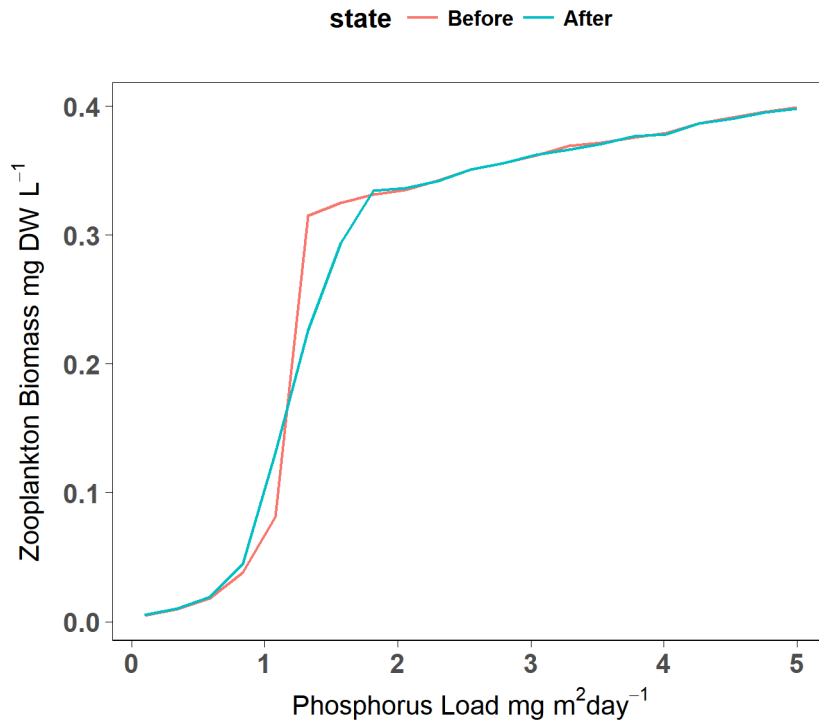


Fig. 4.4 Stressor-Response relationship between zooplankton biomass and phosphorus load in two states in Loch Leven modelled in PCLake. The before state is represented using data from 200-2005 and the after state is represented using 2008-2013 data. Critical nutrient loads (CNL) are calculated as the point directly after its sudden rise. CNL are: Before - 1.325 mg m⁻² day⁻¹, the after state does not have a CNL as it rises in 3 steps before reaching the same level as the before state. These steps are at 1.08 mg m⁻² day⁻¹, 1.325 mg m⁻² day⁻¹ and 1.57 mg m⁻² day⁻¹.

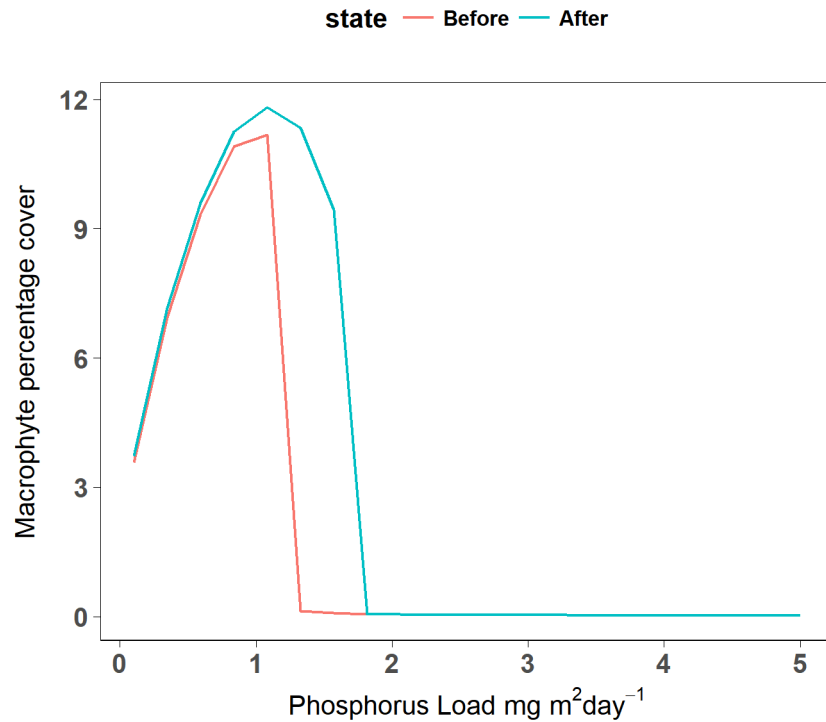


Fig. 4.5 Stressor-Response relationship between macrophyte percentage cover and phosphorus load in two states in Loch Leven modelled in PCLake. The before state is represented using data from 200-2005 and the after state is represented using 2008-2013 data. Critical nutrient loads (CNL) are calculated as the point directly after its sudden rise. CNL are: Before - 1.325 mg m⁻² day⁻¹, After - 1.815 mg m⁻² day⁻¹.

4.4 Discussion

Significant change was seen in nine of the 15 variables analysed during the before/after analysis in Loch Leven indicating significant ecological reorganisation occurring in 2007, and suggesting the presence of alternative stable states in Loch Leven. These significant variables represent major components of the Loch Leven ecosystem across multiple trophic levels, showing that widespread ecological change occurred. Eight of the nine variables were tested for non-linear behaviour, with six showing significant results of non-linear change across different trophic levels of the system. Process modelling confirmed that hysteresis in responses to nutrient loading should be expected in Loch Leven.

4.4.1 Ecological change across trophic levels

All the evidence presented here shows that non-linear change occurred in Loch Leven around 2006-2007 when TP concentrations decreased sharply (Carvalho et al., 2012; Spears et al., 2012) with changes throughout the system. It is as yet unclear what caused this shift or whether the changes occurred as part of a trophic cascade throughout the system or as a result of external forcing.

There are some events which are likely to have played a part such as a large increase in macrophyte MGD between 2004 (2.9 m) and 2006 (4.5 m) which was sustained into 2008 (4.3m) (Dudley et al., 2012; May and Carvalho, 2010). The greater MGD values seen in 2006 may offer an explanation for the decrease in TP levels following 2007, although coverage was not stated in May and Carvalho (2010). Greater macrophyte coverage would result in lower TP concentrations and increased sediment stability, reducing internal loading. A wide range of studies have shown high levels of macrophyte coverage to be a key component of the feedback mechanisms needed to maintain a clear water state, in shallow lakes (Blindow et al., 1993; Hilt and Gross, 2008; Ibelings et al., 2007; Scheffer et al., 1993). Although this would provide some explanation for the decrease in nutrient concentrations, the change in zooplankton community composition to cladoceran dominance and the increase in *Daphnia* body size, the cause of the increase in MGD between 2004 and 2006 is unknown, but potentially the result of long ecological recovery times associated with catchment management in the 1990s and 2000s (Dudley et al., 2012). Increasing evidence for the effect of local weather conditions on the competitive interactions between macrophytes and phytoplankton that aid in the establishment of the spring clear water phase may be an important factor in this shift (Phillips et al., 2016). Combinations of conditions favouring zooplankton leading to greater levels of clarity in early spring to changes in precipitation leading to reductions in lake depth further helping the establishment of macrophyte beds from overwintering propagules could have helped lead to the increased MGD seen in 2006 which in turn could have led to the increased presence of propagules and high coverage in 2007 due to the positive impact of increased coverage of vegetation in the previous year (Van den Berg et al., 1999).

The reduction of fish (brown trout) stocking from 100,000 per year to 5,000 per year after 2004, the cessation of rainbow trout stocking (30,000 fish per year) in 2004 and the cessation of fish stocking entirely in 2006 (May and Spears, 2012a; Winfield et al., 2012) may have led

to decreased predation pressure on zooplankton (Jeppesen et al., 1996; Meijer et al., 1994; van Donk et al., 1990). This is likely the cause of the reappearance of *Bosmina* as well as the increase reported here in *Daphnia* body size and the reduction in helmet presence. The shift to cladoceran dominance of the zooplankton community has been seen as a response to reduced planktivorous fish predation in other lakes which leads to increased grazing on phytoplankton (Jeppesen et al., 1996).

4.4.2 Impacts of climate on ecological change leading to a regime shift

The impacts of climate change may also be present in Loch Leven. Carvalho et al. (2007) suggested that weather events such as warm springs, which have been associated with increased *Daphnia* densities (Ferguson et al., 2007), and particularly wet, cool summers may have played a part in this response, although reduction in rainfall during the early spring clear water phase could have reduced lake depth sufficiently to lead to increased light levels for emerging macrophytes (Bucak et al., 2012) as well as reduce flushing rates during spring when zooplankton are abundant. Furthermore, high rainfall in the summer can increase the flushing rate from the loch preventing the build-up of high phytoplankton densities and subsequent recycling of nutrients (Carvalho et al., 2012). Cooler summer temperatures could also have reduced P loading from the sediment as this is highly temperature dependent (Spears et al., 2007). Another possible reason may lie in phytoplankton community composition, which was dominated by diatoms during these years (Carvalho et al., 2007). The dominant species *Aulacoseira* forms long chains of cells and has been shown to be the preferred food of rotifers (May and Kirika, 2001) as well as a major dietary component of filter feeding bivalves and benthic invertebrates (Carvalho et al., 2007). This could allow the P and N contained within the larger phytoplankton crop consumed to be retained within other biological communities in the loch rather than being recycled into the sediment or further phytoplankton growth. This shows that a wide range of possible internal and external processes could have impacted on this shift in Loch Leven, and it seems likely that multiple factors contributed to a loss of resilience leading to abrupt non-linear change; one of few reported in such detail in the literature.

4.4.3 Components of hysteresis and resilience in Loch Leven

Given the large size, moderate depth and heterogeneous morphology of Loch Leven, theory suggests that it should have low resilience to pressures and may not present hysteresis, at all

(Janse et al., 2008). The aim in this chapter was to better understand the form and extent of a particular in-lake event whilst trying to determine the presence of resilience mechanisms. The presence of significant change across multiple trophic levels, including nutrients, chlorophyll and zooplankton, combined with the fact that many of these exhibit some form of non-linear change, shows that sudden unpredictable change can and has occurred in Loch Leven and can fundamentally change the functioning of the ecosystem. This is further supported by the, admittedly sparse, data on macrophytes which shows increasing MGD preceding this event. Although without knowledge of percentage cover, it is difficult to judge how extensively macrophytes spread throughout the Loch prior to 2007. Given its size, the sustained high MGD seen between 2006 and 2008 (Dudley et al., 2012; May and Carvalho, 2010) would suggest that macrophytes could cover substantial areas of functional significance. These surveys also highlight the changes seen in macrophyte community composition, including the return of historical species, thought to be locally extinct in the contemporary record (Dudley et al., 2012) which suggest an improvement in growing conditions. Gradual degradation in macrophyte community composition and richness has been shown to lead to linear shifts when viewed over decades to a phytoplankton dominated state but could also be seen as non-linear if only phytoplankton dynamics are considered (Sayer et al., 2010a).

Modelling the before/after state transitions allowed the generation of stressor/response relationships which confirmed that low levels of hysteresis were evident between the two states. This suggests that, given the other evidence presented here, Loch Leven underwent a regime shift between two alternative states. What is less clear, however, is the stability of either state. The difference in P load between the two CNLs in the different years suggests that the new state has low resilience, and that feedback mechanisms are operating to generate hysteresis. Chlorophyll and macrophytes have the same CNL for both states whereas for zooplankton there was no obvious CNL at all for the after state. The relatively gradual rise in zooplankton biomass in the after state whilst chlorophyll remained low suggests that zooplankton grazing is the main factor preventing the switch from a clear to a turbid state. As zooplankton rises it would be consuming greater amounts of chlorophyll (which can be seen to rise slightly at the same points along the stressor axis), preventing large concentrations from shading out macrophytes.

4.4.4 Conclusions

Whilst the evidence presented here shows ecological change across multiple trophic levels with signs of hysteresis it also highlights the vulnerability of lakes similar to Loch Leven to future environmental change. The importance of zooplankton grazing was demonstrated by the modelling of stressor-response relationships in PCLake as well as the results in the before/after analysis, showing its importance to the resilience of Loch Leven. If changes in climatic variables such as temperature and precipitation occur as predicted, maintaining the 'status quo' will likely require some form of preventative management intervention, even under the most conservative projections. This could take the form of fish removal or the addition of piscivorous fish, both of which could benefit the zooplankton community, highlighted as a major component of ecosystem resilience in Loch Leven. Confirming the presence of hysteresis enables the understanding of some of the primary mechanisms involved in maintaining a desirable state, and so has the potential to target resilience enhancing management actions.

Chapter 5 - Resilience of Loch Leven to Future Environmental Change

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The candidate, as lead author, performed all statistical and modelling analysis, writing and production of graphics. PCLake was developed by W. M. Mooij and J. H. Janse and taught to the candidate by J. J. Kuiper and J. A. Elliott. Co-authors contributed to the editing of the manuscript.



5.1 Introduction

Freshwater systems are one of the most impacted ecosystem types on earth with widespread eutrophication shown to be the major cause (Smith and Schindler, 2009). Despite measures to improve and restore lakes, recent research in the U.S. has shown that in the majority of lakes sampled, in-lake total phosphorus (TP) concentration has remained broadly unchanged since 1990 (Oliver et al., 2017). Moving into the future, climate change is predicted to be one of the biggest threats to the state of freshwater ecosystems with both direct and indirect impacts predicted to occur across ecosystem structure and function (Jeppesen et al., 2010; Woodward et al., 2010). These effects are predicted to impact across scales with species level changes in distribution (Parmesan and Yohe, 2003), body size (Gardner et al., 2011), growth patterns (Yvon-Durocher et al., 2011) and phenology (Thackeray et al., 2010) coupled with physical changes including hydroclimatic forcing and hydrological alterations (Middelkoop et al., 2001).

In freshwater systems projected pressures such as rising temperatures and changes in precipitation patterns are likely to be the primary drivers of these responses as well as other physical and chemical changes. Other impacts of increased temperatures can include changes in fish species distribution and body size (Jeppesen et al., 2012; Meerhoff et al., 2007), zooplankton abundance, body size and grazing capacity (Cuenca Cambronero et al., 2018; Gillooly and Dodson, 2012; Gyllström et al., 2005; Mooij et al., 2007) and increases in cyanobacterial proportion of phytoplankton communities (Chen et al., 2003; Jeppesen et al., 2009). Variations in seasonal precipitation patterns can also have a range of impacts. Decreases in summer precipitation could lead to decreased flushing rates which has been shown to lead to increases in phytoplankton biomass (Søballe and Kimmel, 1987). Predicted increases in precipitation during winter are expected to lead to increases in external P from catchment run-off (Jeppesen et al., 2009). Recent evidence supports the hypothesis that these pressures will interact to shape ecological responses across populations of lakes, for example, low flushing rates and high nutrients represent a positive and synergistic interaction on cyanobacteria dominance in European lakes (Richardson et al., 2018). However, little is known about the effects of such interactions across trophic levels leading to changes in resilience properties in lakes.

The impact of these pressures can vary depending on lake type, for instance, increasing temperatures can affect stratification patterns in deep lakes (Wagner and Adrian, 2009)

whereas in shallow lakes increased temperatures at the sediment can stimulate increased P release (Jensen and Andersen, 1992). Other lake characteristics can also respond to these pressures in different ways. For instance, cyanobacterial abundance has been shown to respond to lake characteristics such as mixing regimes, alkalinity and the presence/concentration of humic substances (Richardson et al., 2018; Taranu et al., 2012) making the understanding of lake-type specific reactions essential. Response types at the ecosystem scale can vary across lake types with deeper lakes typically responding in a relatively linear pattern (Janssen et al., 2014; van Nes and Scheffer, 2005) although recent research has shown non-linear responses in zooplankton communities in some deeper lakes (Bruel et al., 2018). Shallow lakes have been shown to exhibit non-linear responses related to the breakdown of stabilising ecological processes where community structure and biomass are high, relative to deeper lakes (Mooij et al., 2007).

The ability of lakes to recover following pressures and remain in their current state is termed as their resilience (Holling, 1973). Non-linear changes between desirable (i.e. clear water, macrophyte dominated) and undesirable (i.e. turbid water, phytoplankton dominated) states are governed by feedback mechanisms such as the absorption of nutrients by macrophytes in a clear state or the shading of sediment by phytoplankton in a turbid state (Scheffer et al., 2001, 1993). Despite a great deal of debate about the meaning of resilience in ecosystems and our understanding of how different feedback mechanisms should interact, measuring how resilient an ecosystem is to specific levels of change is a relatively new area of research. Statistical early warning indicators have been identified as a possible approach for predicting ecosystem transitions and thus measuring a system's resilience (Dakos et al., 2012a), but have been shown to be unreliable using empirical data, both in other studies (Burthe et al., 2016; Gsell et al., 2016) and earlier in this thesis (see chapter 3). Despite the general low success rates seen in most of the analyses in chapter 3, the usage of EWIs as a group offers some hope with a ~70% success rate. However, these methods don't give a great deal of ecological information when used, which is where methods such as process modelling become particularly valuable. The ecosystem model PCLake was designed to model shallow lakes and as such can simulate non-linear shifts and incorporate the major processes that govern resilience within this lake type (e.g. Janse, 1997; Janse *et al.*, 2008) (for more details on PCLake see section 2.3).

The aim of this chapter is to better understand the effects of predicted temperature increases and changes in seasonal precipitation (overall decreases in the summer and increases in the winter) on the resilience of a large, shallow, historically eutrophic lake (Loch Leven) using real climate projections for the region (UKCP09, 2009). Using the ecosystem model PCLake we will assess the resilience of this lake to predicted levels of environmental change, under a range of nutrient loadings. The chapter has been designed to test the effect of direct predictions of climate change at different probability levels, the individual stressors (temperature and precipitation) and a combination of the worst case predictions for temperature and decreases in summer precipitation to allow an assessment of how they interact. The expectation is that the effects of the climatic variables will change with P loading. At low P loading, effects will focus on the impact on resilience as measured by the critical nutrient loading (CNL). At medium to high P loads the focus will be on effects on the response variables such as chlorophyll levels, zooplankton biomass and macrophyte percentage cover.

5.2 Methods

PCLake is an ecosystem process model based on nutrient and carbon flows between different modules in a simplified food web that transfers between the upper sediment and a fully mixed water column (Janse, 1997). Built to simulate shallow lakes, it has the ability to mirror regime shifts between macrophyte and phytoplankton dominated states (See section 2.3 for more details on PCLake model outline and setup). In this chapter we use a type of analysis called a bifurcation analysis, which allows an individual parameter to be varied incrementally between a minimum and a maximum value. At each of these values the model is run for a defined period (in this case 20 years to allow the system to reach equilibrium and to mirror medium term climate change), then an average is taken for a chosen variable (here we used chlorophyll, zooplankton and macrophytes), for a defined period in the final year (in this case late spring/summer) to assess the state of the system.

The aim of this chapter is to assess the resilience of Loch Leven and similar large shallow lakes to projected future environmental change. To do this we use the above described bifurcation analysis with P load as the incremental variable as it has been a frequent target of past management actions (May and Spears, 2012b). P load was varied between $0.1 \text{ mg m}^2 \text{ day}^{-1}$ and $5 \text{ mg m}^2 \text{ day}^{-1}$ at 21 intervals, giving a range of loading dependent outcomes. This will be varied against low, medium and high emissions projections for both precipitation and

temperature at the 10%, 50% and 90% probability levels for predictions to the 2050s (UKCP09, 2009) for Eastern Scotland as this is the closest time period to that used in the model runs (see Table. 5.1). As well as this, a selection of independent temperature and precipitation values will be used to assess their impact as separate pressures including a control run using averages for inflow/outflow and temperature for the calibration year (2005) to provide a comparison for magnitude and direction of change and a combination of the most extreme values of temperature and precipitation decrease.

Water temperature can be directly manipulated within the model and can be altered in the model for an individual run. The predictions used for air temperature were translated directly to water temperature as shallow lakes have been shown to respond quickly to air temperature changes and given the long term nature of the projections these changes are more likely to average out with minimal differences. As can be seen from the results below minor differences in temperature typically have a very minor impact on response variables. Precipitation changes will be altered by changing model lake inflow/outflow amounts to simulate the potential changes in flushing rate that could be expected under these scenarios through a calculation of percentage change. Precipitation changes are modelled as a mixture of predicted changes in summer and winter precipitation according to UK climate change projections for eastern Scotland (UKCP09, 2009)(see Table 5.1). The changes made for an individual run mean that multiple model runs will need to be conducted to account for all variations (see Fig. 5.1). To help interpret the results, each tier is assigned an identifying letter or number. In the case of single pressure, control and worst-case scenario runs these have individual codes (see Table 5.1).

Table 5.1 Overview of data used for climate change inputs to model runs (from UKCP09, 2009). Values with codes in brackets represent temperature/precipitation only runs. The worst-case scenario run values are market with *. Letter and numbers in brackets in emissions column and under probability headings represent scenario codes.

Variable	Emissions	10% probability (1)	50% probability (2)	90% probability (3)
Annual temperature (°C)	Low (D)	0.8(TG1)	1.9	3.15
Annual temperature (°C)	Medium (E)	0.9	2(TG2)	3.4
Annual temperature (°C)	High (F)	1	2.25	3.8(TG3)*
Winter precipitation change (%)	Low (A)	-2(PS1)*	6	15
Winter precipitation change (%)	Medium (B)	1	10(PS2)	20
Winter precipitation change (%)	High (C)	1	10	20(PS3)
Summer precipitation change (%)	Low (A)	-26(PS1)	-11	6
Summer precipitation change (%)	Medium (B)	-27	-13(PS2)	1
Summer precipitation change (%)	High (C)	-28*	-13	2(PS3)

The repetition of this process for chlorophyll concentration, zooplankton biomass and macrophyte percentage cover was used to examine processes governing resilience in this system. For each of these response variables a control run will be performed using settings applied in model calibration for 2005 to gauge how this predicted future change compares.

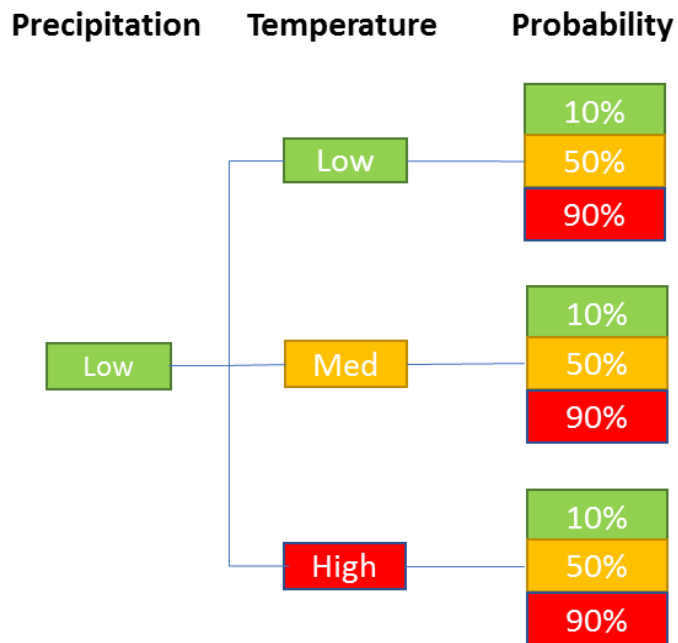


Fig. 5.1 Example experimental layout of a single tier. An example run could include a value from low emissions precipitation and medium emissions temperature for each of the probability levels.

5.3 Results

A total of 35 individual runs were performed for each response variable (chlorophyll concentration, macrophyte percentage cover and zooplankton biomass). To aid in understanding the complex interactions between stressors the probability groups are referred to as follows in the text:

10% - low temperature, less precipitation

50% - medium temperature, mixed precipitation

90% - high temperature, more precipitation

For the single-stressor scenarios the names will only include the appropriate stressor (e.g. 10% temperature-only scenario – low temperature-only).

5.3.1 Chlorophyll responses

5.3.1.1 Low P loads

Chlorophyll had two groupings at low P loads which were separated by the probability level of the predictions for temperature and precipitation with the high temperature, more precipitation probability level having a lower CNL of $0.835 \text{ mg P m}^2 \text{ day}^{-1}$ with a higher CNL of $1.08 \text{ mg P m}^2 \text{ day}^{-1}$ seen for the low temperature, less precipitation and medium temperature, mixed precipitation probability levels (see Fig. 5.2). The only exception to this was for the precipitation-only scenarios for both mixed precipitation and more precipitation probability levels which both had the same lower CNL but reached lower values than all of the other scenarios with the same CNL.

5.3.1.2 Low to medium P loads

At low to medium P loads the chlorophyll of the medium temperature, mixed precipitation probability group was slightly higher ($\sim 79.36 \mu\text{g L}^{-1}$ to $\sim 73.65 \mu\text{g L}^{-1}$ at $2.55 \text{ mg P m}^2 \text{ day}^{-1}$) than the other two probability groupings. It then shows a consistent minor dip which causes the chlorophyll levels to drop below the low temperature, less precipitation probability group at higher P loads.

5.3.1.3 Medium to high P loads

At higher P loads the probability groups run in order from low temperature, less precipitation with the highest chlorophyll levels through to high temperature, more precipitation although the differences are small ($\sim 107.1 \mu\text{g L}^{-1}$, $\sim 93.5 \mu\text{g L}^{-1}$ and $\sim 89.7 \mu\text{g L}^{-1}$ respectively at $5 \text{ mg P m}^2 \text{ day}^{-1}$). The exception is between the low temperature, less precipitation and other groups for the medium and high emissions precipitation-only scenarios. Within these groups the temperature was generally ordered, with high emissions scenarios having higher chlorophyll through to the low emissions scenarios having the lowest. The only exception to this was the medium temperature, mixed precipitation probability group which has the highest chlorophyll levels of the three variations. The single pressure scenarios for precipitation show the medium ($81.34 \mu\text{g L}^{-1}$) and high ($68.39 \mu\text{g L}^{-1}$) emissions scenarios having the lowest overall chlorophyll levels at medium-high P loads despite the lower CNL. The control scenario had the next lowest chlorophyll level ($87.72 \mu\text{g L}^{-1}$) with the low ($93.29 \mu\text{g L}^{-1}$) and medium

(101.13 $\mu\text{g L}^{-1}$) emissions temperature-only scenarios and low (105.78 $\mu\text{g L}^{-1}$) emissions precipitation-only scenario slightly higher. The high emission temperature-only scenario has the second highest chlorophyll levels (121.57 $\mu\text{g L}^{-1}$) overall with the worst-case scenario having substantially higher chlorophyll levels (140.46 $\mu\text{g L}^{-1}$) than all other scenarios.

5.3.2 Macrophyte responses

Macrophyte percentage cover has two distinct groups which both have different CNL. The lower CNL was the same as for chlorophyll (0.835 $\text{mg P m}^2 \text{ day}^{-1}$) and was only seen in the high temperature, more precipitation group (see Fig. 5.3). This same group also has a lower peak percentage cover with very minor differences between the scenarios. One notable difference between the results for macrophytes and for chlorophyll was that the mixed precipitation and more precipitation, precipitation-only scenarios did not have the same lower CNL. They had a lower peak percentage cover of 12.4% compared to other scenarios with the same CNL. The group with the higher CNL again matched that seen for the comparable chlorophyll group (1.08 $\text{mg P m}^2 \text{ day}^{-1}$) and had a higher peak percentage cover of 15.8%. Following their respective CNL all scenarios remain at low percentage cover at all remaining P loads.

5.3.3 Zooplankton responses

5.3.3.1 Low P loads

Zooplankton biomass like chlorophyll has more variability at medium to high P loads but has the same pattern of two different groupings at low P loads (see Fig. 4). The CNL remain the same as both chlorophyll and macrophytes (low - 0.835 $\text{mg P m}^2 \text{ day}^{-1}$) (high - 1.08 $\text{mg P m}^2 \text{ day}^{-1}$), but like chlorophyll the mixed precipitation and more precipitation, precipitation-only scenarios have the same a lower CNL along with all the high temperature, more precipitation probability groups.

5.3.3.2 Medium to high P loads

At medium to high P loads the differences are generally similar to those seen in the chlorophyll results with the low temperature, less precipitation probability group having the highest biomass, followed by the medium temperature, mixed precipitation and high temperature, more precipitation groups. Overall the less precipitation, precipitation-only

scenario results in the highest biomass of all (0.33 mgDW L⁻¹). The control scenario (0.28 mgDW L⁻¹) sits just below the low temperature, less precipitation group (0.31 mgDW L⁻¹) with the low temperature, temperature-only scenario (0.26 mgDW L⁻¹), worst case scenario (0.26 mgDW L⁻¹) and medium temperature, temperature-only scenario (0.24 mgDW L⁻¹) in order below at the highest P loads. The more precipitation precipitation-only scenario (0.21 mgDW L⁻¹) was just below the medium temperature, mixed precipitation (0.22 mgDW L⁻¹) multi-stressor group with the high temperature, temperature-only group even lower (0.18 mgDW L⁻¹). Within these groups, the higher temperature scenarios result in lower zooplankton biomass across almost all P loads. As well as this, the greater decreases in precipitation result in higher biomass.

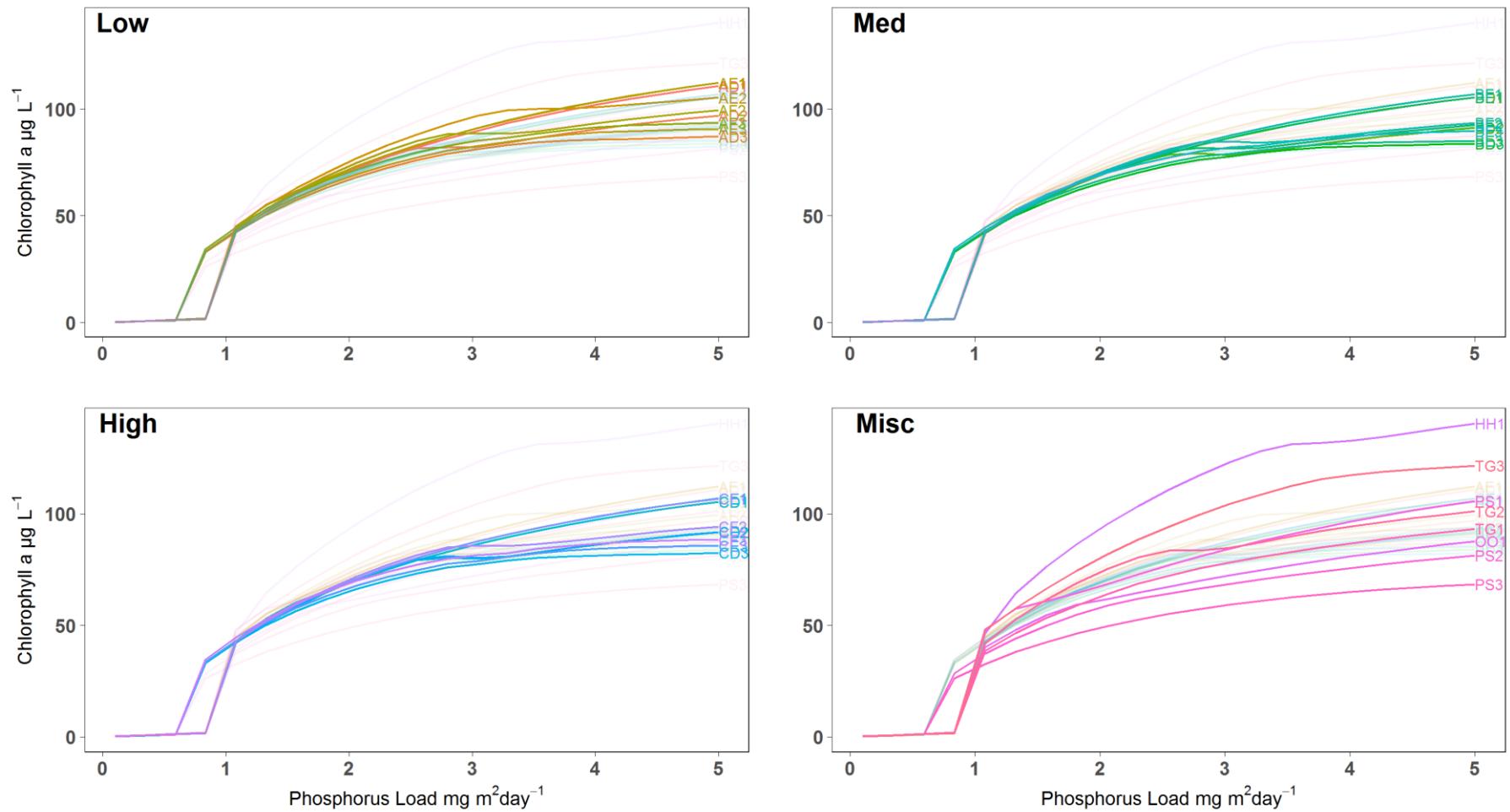


Fig. 5.2 Responses of chlorophyll a to varying levels of P loading under a range of temperature and precipitation scenarios. Low, high and medium emissions scenario groupings are for precipitation with Misc showing control, single pressure and worst-case scenarios.

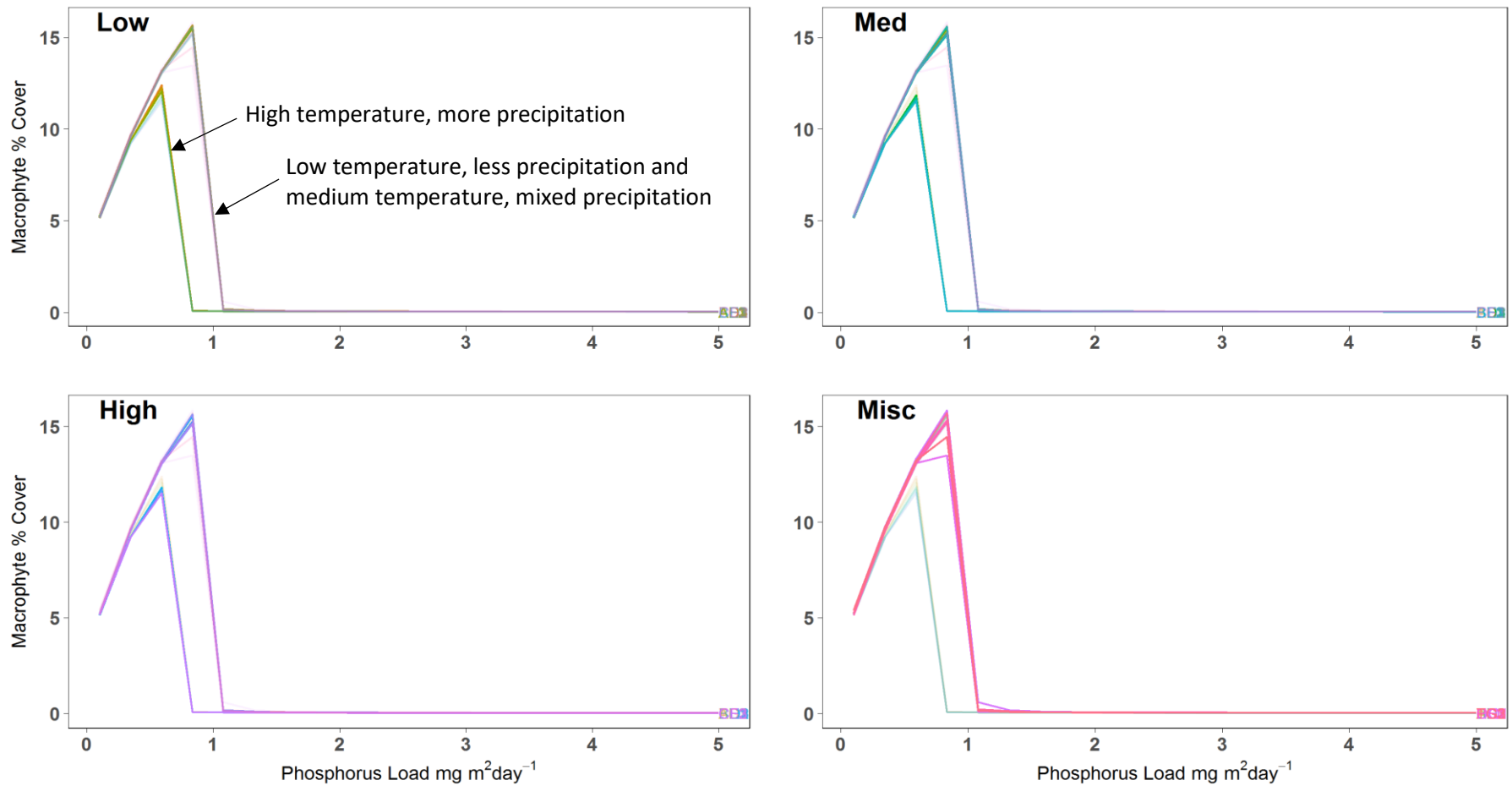


Fig. 5.3 Responses of macrophyte % cover to varying levels of P loading under a range of temperature and precipitation scenarios. Low, high and medium emissions scenario groupings are for precipitation with Misc showing control, single pressure and worst-case scenarios. Arrows describe groupings due to label grouping.

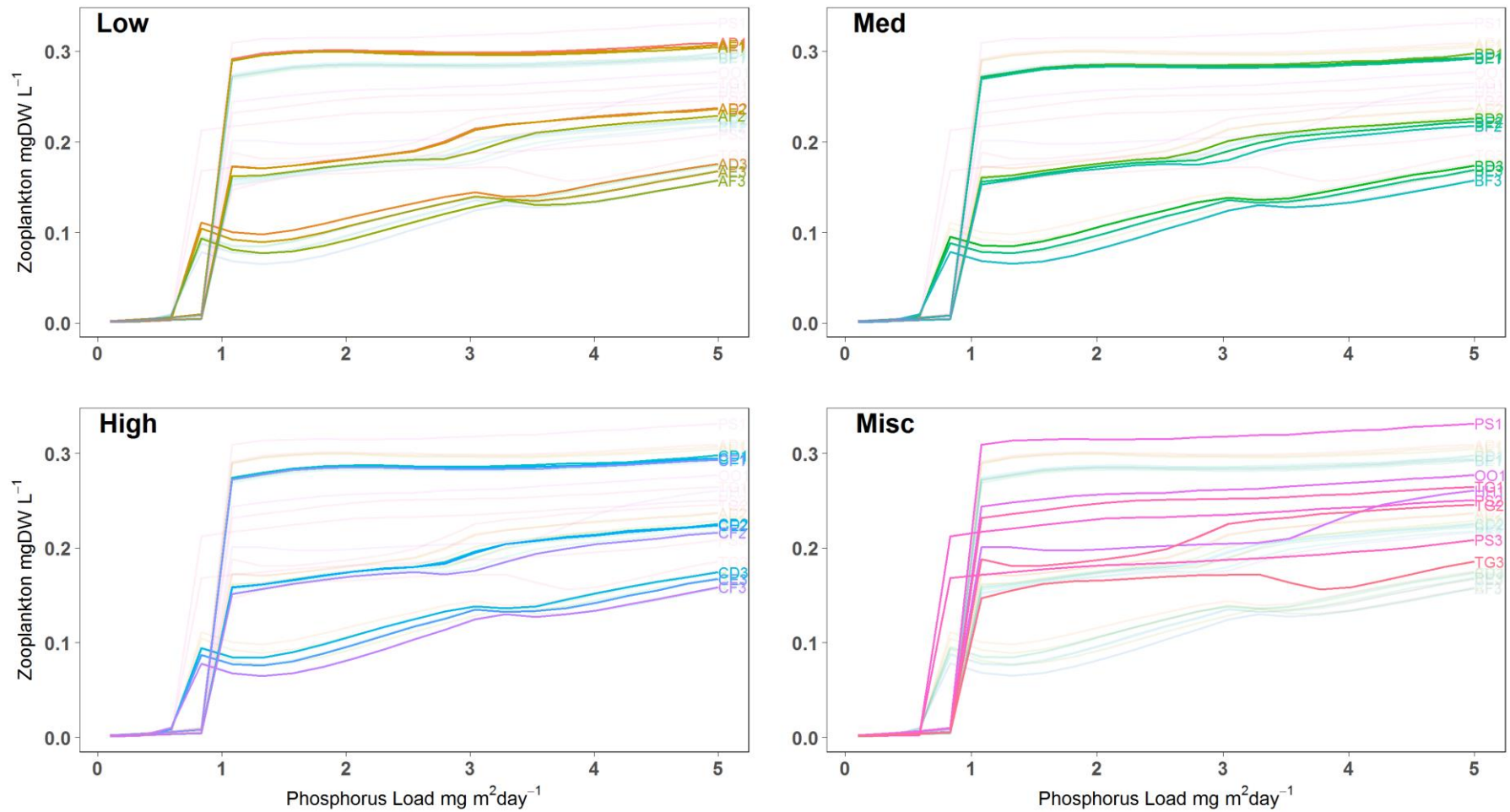


Fig. 5.4 Responses of zooplankton biomass to varying levels of P loading under a range of temperature and precipitation scenarios. Low, high and medium emissions scenario groupings are for precipitation with Misc showing control, single pressure and worst-case scenarios.

5.4 Discussion

For all response variables the different probability ranges resulted in the largest differences between scenario results and was generally grouped by these numbers. The low temperature, less precipitation probability range, which consisted of small temperature increases at all emissions levels but large decreases in summer precipitation and minimal change in winter precipitation, resulted in the highest chlorophyll levels at medium to high P loads but a higher CNL for chlorophyll and zooplankton to peak and for macrophytes to collapse. The control run in the chlorophyll set had similar chlorophyll levels at medium to high P loadings to scenarios from the high temperature, more precipitation probability ranges with only the more precipitation, precipitation-only scenario having substantially lower chlorophyll levels at higher P loads. This pattern was also evident within the macrophyte results, whilst the zooplankton results showed a different pattern with the control run only having less biomass than the low temperature, less precipitation probability group and the less precipitation, precipitation-only scenario. Together these results suggest that greater decreases in summer precipitation have the greatest impact on chlorophyll levels at medium to high P loadings, whereas higher temperatures in general have a greater impact on zooplankton biomass at all but the lower P loads. At low P loads the CNL is consistently linked to the combination of higher temperatures and increased winter precipitation seen in the high temperature, more precipitation probability group.

5.4.1 Responses to increased temperature and nutrient loading

The impact of increased temperature on lake function has been extensively studied in recent decades under a range of eutrophic conditions and has been shown to have a range of impacts. In this study the response of the high temperature, temperature-only scenario which has the second highest chlorophyll levels at medium to high P loads demonstrated the importance of warming for lake ecology, in Loch Leven.

The PCLake model indicated that the effects of temperature can resonate across multiple trophic levels in Loch Leven. Warmer waters tend to have higher algal biomass and floating plants, whilst rooted plants predominate in temperate waters (Moss et al., 2011). Perhaps the most obvious causes of higher chlorophyll levels seen in warmer waters is the substantial increases in algal growth rates with increasing temperatures, particularly for cyanobacteria (UWRAA, 1995). When combined with eutrophication this creates the perfect conditions for

chlorophyll concentrations to increase. Other factors play a substantial role in the regulation of chlorophyll levels such as zooplankton biomass and body size. Here, zooplankton biomass was lowest under the highest temperatures, which can be seen by comparing the high temperature, temperature-only scenario at medium to high P loads to the low temperature and medium temperature, temperature only scenarios. In Loch Leven the highest zooplankton densities are seen during May/June when water temperatures are still relatively low with densities generally decreasing into the summer months (Gunn et al., 2011). The impact of temperature on zooplankton includes a number of direct and indirect influences such as increased predation by fish due to conditions favouring smaller body size, increased feeding intensity and increased spawning opportunities (Persson, 1986). This form of predation typically impacts the larger bodied species of zooplankton reducing the average body size which is known to reduce the overall filtering rate (Peters and Downing, 1984). As well as these forms of top down influences, bottom up impacts, such as changes in phytoplankton community composition also occur (increasing the proportion of cyanobacteria under warmer conditions (Chen et al., 2003; Elliott et al., 2006; Paerl and Huisman, 2008) which are a poor source of food for many zooplankton (de Bernardi and Giussani, 1990)).

The relationship between macrophytes and temperature at low P loads is unclear. The lower CNL specifically linked to the high temperature, more precipitation multi-pressure scenarios suggests that the interaction between these pressures has the largest influence on resilience. The temperature-only scenarios all had a higher CNL and resulted in similar peak percentage cover to each other when compared the control.

Responses of macrophytes within lakes are determined by species specific tolerances, although in general small increases in temperature are likely to lead to increases in growth rates and earlier emergence of many species. As temperatures continue to rise, the increases in macrophyte growth rates may become more species specific and reverse direction to become declines as temperatures increase further (Bornette and Puijalon, 2011; Santamaria and van Vierssen, 1997). Past influences of temperature in Loch Leven have mostly led to increased chlorophyll concentrations during winter and increased zooplankton densities during spring. The biological effects of temperature increases during summer in Loch Leven have not been well quantified using empirical data (Carvalho et al., 2012), and so this study highlights some of the potential effects that could be operating into the future. The impacts

of temperature are variable depending on the level of available nutrients with the largest effects expected at higher P loads when phytoplankton are most able to respond through increased primary production (UWRAA, 1995).

5.4.2 Responses to changes in precipitation and nutrient loading

The impact of decreased summer precipitation seen in the less precipitation, precipitation-only scenario led to higher concentrations of chlorophyll compared to the control run. These forms of changes include the increasing likelihood of droughts which can influence lake function in a number of ways. This increase in chlorophyll could be linked with an increase in retention time often reported during periods of low flow and drought (Gomes and Miranda, 2001; Lee et al., 2012). This relationship is linked to chlorophyll concentrations in a number of ways such as increased nutrient concentrations due to declining water volume (Mosley et al., 2012), and greater stability in hydrological regime allowing greater turnover of phytoplankton, particularly in the case of slower growing species and cyanobacteria (Elliott, 2010).

In contrast, the results of the more precipitation, precipitation-only scenario show a small increase in summer precipitation and the largest increase in winter precipitation which has the lowest levels of chlorophyll at medium to high P loads but a lower CNL. This suggests that increasing precipitation could also lower the resilience of this type of lake. The lower CNL predicted in chlorophyll is also predicted for zooplankton for the same scenarios but not in macrophytes. One factor commonly associated with increased inflows to lakes particularly during winter is increased loading of particulate matter. This likely impacts on nutrients and turbidity and so will influence the resilience as quantified using PCLake in Loch Leven (Lischke et al., 2014). Another probable reason for the lower CNL during the more precipitation scenarios is the increased inflows in the winter. These are not matched by outflows, meaning that relatively small changes in depth will occur which has been shown to be a highly sensitive parameter in the model (Janse et al., 2008). Loch Leven is particularly sensitive to these changes due to its moderate-shallow depth. The increases in zooplankton food availability seen in the chlorophyll results is likely to be an important factor responsible for the increased zooplankton biomass responding at the lower CNL, allowing macrophyte percentage cover to remain higher under these particular scenarios. In Loch Leven the same process has been linked to increases in macrophyte maximum growing depth and reductions in spring chlorophyll concentrations (Carvalho and Kirika, 2003; May and Carvalho, 2010).

5.4.3 Temperature, precipitation and nutrient loading as interacting stressors

The climate change projections used in this study (see Table 5.1) show a mix of potential changes in both temperature and precipitation with the most extreme changes in temperature associated with the milder changes in summer precipitation and the more extreme changes in winter precipitation. At lower P loads the results show that the combination of higher temperatures and increased winter precipitation seen in the high temperature, more precipitation group across all emissions scenarios lead to the lower CNL seen across chlorophyll, zooplankton and macrophytes. The combination of increased particulate matter and high temperatures leading to increased phytoplankton growth and the negative impacts on zooplankton grazing seems to be the most likely cause of this difference. The presence of the increased particulate matter as the most likely detrimental impact of increased winter flushing rates due to the increased precipitation seems likely to be a factor creating this small difference in CNL along with small changes in depth. The 'worst case' scenario which includes the same level of temperature increase but only includes the worst decreases in precipitation during the summer and a small decrease in winter precipitation had the higher CNL despite having by far the highest chlorophyll concentrations at medium to high P loads. A possibility is that through a combination of nutrient limitation and zooplankton grazing, chlorophyll cannot reach high enough densities to cause the collapse of macrophytes in this scenario at low P loads. However, as nutrients become more available and the negative impacts on zooplankton become more dominant and less phytoplankton are removed from the system, the combined impact of these pressures becomes apparent (Elliott, 2010).

The low percentage cover of macrophytes predicted by PCLake is generally too low to drive feedback mechanisms responsible for resilience in shallow lakes (Scheffer et al., 1993) meaning Loch Leven is predicted to be particularly vulnerable, for a shallow lake, to the influences of a changing climate. PCLake needs a percentage cover of 20% for many of the macrophyte driven components of feedback mechanisms to begin to function (Janse et al., 2008) which was not reached by any scenario within this study. Whilst the applicability of this threshold to Loch Leven could be questioned, the exact limit is less important than the underlying assumption that large shallow lakes may be less likely to exhibit discontinuous responses to climate change, i.e. they exhibit low resilience to the stressors and their interactions. The large size of Loch Leven makes it particularly vulnerable for a number of

reasons. Its large fetch and naturally long retention times make it prone to increased P release from suspended sediment and makes establishment of macrophyte beds more difficult (Janse et al., 2008).

5.5 Conclusion

Predictions of future climate change represent a mix of potential pressures such as the level of warming and changes in precipitation at different times of the year. Overall, the predictions modelled in this study include a large number of possibilities which could have a range of effects depending on the nutrient levels entering the lake. The impacts of these pressures when considered in isolation, whilst significant, were generally weaker than interaction effects between stressors. For example, interactions between temperature and winter precipitation were most apparent at low P loads, whilst at medium to high P loads the highest temperatures combined with the greatest decreases in summer precipitation led to the highest chlorophyll levels, showing P loading can impact on climatic effects in lakes. As temperatures rise and summer precipitation decreases, the nutrient reductions and other measures needed to counteract these effects is likely to increase. Changes in winter precipitation have the potential to make matters worse depending on the surrounding catchment. For instance, arable land with loose soil could result in increases in particulate matter reducing resilience at lower P loads such as seen here. The use of modelling such as used in this chapter has the potential to highlight these risks allowing long term management actions such as the planting of forest buffer strips around lake margins or the installation of fine-mesh nets around particularly sensitive parts of the lake shoreline. Overall this study highlights the vulnerability of Loch Leven and other shallow lakes to multiple and interacting climate and land-use stressors and provides insights into potential avenues for future mitigation options.

Chapter 6 – Overall discussion and conclusions



The first part of this chapter brings together the findings from Chapter 3-5 to address the aims of the PhD as laid out in Chapter 1. First, we aim to assess the presence of statistically defined non-linear change over the long term across multiple trophic levels and examine the interaction between these changes and statistical early warning indicators (EWI), both as methods of predicting these changes and as measures of ecosystem resilience. Secondly, we focus on a single change event within Loch Leven to examine the ecosystem-wide changes and the form of those changes allowing us to understand the processes governing responses to pressures and how they impact the resilience of this system. Thirdly, we aim to predict how large, shallow, morphologically heterogeneous lakes, such as Loch Leven, are likely to react to a range of climate and environmental change scenarios under a range of nutrient loads, with discussion around long term effects and adaptation. The possibilities for future research are then identified, followed by the conclusions to draw these themes together. The overall aim is to advance the evidence base with which to quantify ecological resilience in Loch Leven and other shallow lakes.

6.1 Interaction between non-linear change, early warning indicators and resilience

It is increasingly recognised that ecosystems and ecological populations can respond to pressures in sudden and unexpected ways. Large numbers of examples of discontinuous ecological responses have been demonstrated to occur across a variety of ecosystem types. Different approaches to defining and quantifying these and other forms of change have been demonstrated, from carefully designed experiments on single populations (e.g. Dai *et al.*, 2012; Veraart *et al.*, 2012) to large scale statistical analyses of long term data from multiple ecosystem types (e.g. Burthe *et al.*, 2016).

6.1.1 Detection of non-linear change in ecosystems and time series

In Chapter 3, we focused on identifying tipping points in time series data through statistical analysis of 26 variables from the Loch Leven Long Term Monitoring Programme across multiple trophic levels. The detection of these tipping points was focused around significant deviations from moving trends under a predetermined level of 'flexibility', an approach that was consistent with that reported by Burthe *et al.*, (2016). Two advantages of this methodology are that it can define the timing of the tipping point and screens out short-term variability. Other approaches have also been demonstrated to assess discontinuous

responses at the ecosystem scale (Gsell *et al.*, (2016)). These forms of analysis allow exploration of large scale ecological responses using time series data and are useful in that they have demonstrated the occurrence of ‘tipping points’ in a large number of lakes as well as a marine system. However, this general approach can be limited. For instance, they do not provide information on either the cause of the tipping point or the presence of self-sustaining feedback mechanisms (Litzow and Hunsicker, 2016). An example is that linear responses to nonlinear drivers can have the appearance of within-system non-linear change (Di Lorenzo and Ohman, 2013) which can be detected by these methods but not have any wider impacts in ecosystem dynamics. The Brock-Dechert-Scheinkman (BDS) test method used in chapter 4 is generally considered a conservative test for the presence of non-linear dynamics but does not provide information on when these dynamics have occurred. Most of the variables that showed significant change in the before/after analysis also showed non-linear change according to the BDS test. The tests in chapters 3 and 4 have shown that Loch Leven is prone to non-linear change as defined by two distinct measures. Like chapter 4, most cases where the BDS approach has been used have focused on the detection and verification of single, well-defined events (Carpenter *et al.*, 2011; Seekell *et al.*, 2013). The methods applied in chapter 3 do not rely on such process understanding, making interpretation of the results in the context of ecological resilience theory challenging.

6.1.2 Success rates of EWIs and problems with their use

The benefits of finding reliable and easy-to-use early warning indicators (EWIs) are potentially huge both for ecosystem understanding and management, such as being able to prevent an algal bloom prior to its occurrence (Pace *et al.*, 2016). The types of EWIs used in chapter 3 are broadly similar to those used in many of these studies previously discussed (Burthe *et al.*, 2016; Carpenter *et al.*, 2011; Gsell *et al.*, 2016) in that they are considered generic indicators, theoretically capable of predicting regime shifts and other forms of non-linear change subject to critical slowing down (CSD) or flickering with no prior knowledge of the target system (Carpenter and Brock, 2006; Dakos *et al.*, 2012a; Scheffer *et al.*, 2009). Successful uses of EWIs include predicting a ‘regime shift’ in a whole-lake experiment (Carpenter *et al.*, 2011; Seekell *et al.*, 2012) and predicting algal blooms in the same set of lakes (Wilkinson *et al.*, 2018). These successful uses have all been focused on a single variable (chlorophyll) in a single lake with high frequency data and a nearby control lake to account for false positives. In chapter 3 when EWIs were considered individually the percentage of

successfully detected tipping points was 40.5% for the best performing EWI (standard deviation) across multiple trophic levels and window sizes. Other studies have shown 50% agreement or lower between EWIs and detected tipping points (Burthe et al., 2016; Gsell et al., 2016).

There are still a number of knowledge gaps in our understanding of how EWIs work. One difficulty in using EWIs is the impact of differences in data frequencies. Theory suggests that high frequency data is necessary for effective use of EWIs (Dakos et al., 2012a; Scheffer et al., 2009). For instance, monitoring variables such as chlorophyll should theoretically have a measurement frequency shorter than the typical life cycle of most phytoplankton species in order to capture the fine-scale dynamics these types of populations can exhibit. Despite this theory, the aforementioned whole-lake experiment is the only ecosystem scale experiment with high frequency data used to test EWIs, with most other high frequency data relying on single population laboratory studies or models (Carpenter and Brock, 2006; Dai et al., 2012; Guttal et al., 2013). In another study, tests on modelled data showed a highly positive correlation with increasing data frequency and EWI detection rate. However, this same pattern was not seen in experimental data from the same study (Clements et al., 2015). The analysis presented in chapter 3 utilises long-term monitoring data which varies between fortnightly and annual in frequency. It is possible that the low data frequency reduced the success rate of the EWIs tested. However, the lack of agreement between experimental and modelled high frequency data in the study performed by Clements et al., (2015) suggests that although higher frequency data may improve detection, other factors can still affect their predictive capabilities. Widespread testing utilising high frequency monitoring buoys and remote sensing in real-world systems, as well as further experiments under different conditions are needed to help better understand the role of data frequency in detection of EWIs.

6.1.3 Rolling window size and the occurrence of false positives

How different forms of variability are dealt with can also be significantly impacted by statistical analytical decisions. In chapter 3 we varied the rolling window size across all tested EWIs and datasets to assess their ability to predict detected tipping points and minimise false positives. Although there were differences in these measures between different window sizes there was no clear pattern in relation to how well smaller versus larger window sizes performed. The generic impact of changes of window size is predictable in that smaller

window sizes include fewer sample values when calculating the mean and so can pick up short-term changes in the target variable. For larger window sizes, more sample values are included when calculating the rolling mean which tends to have a smoothing effect, making them less sensitive to minor deviations (Lenton et al., 2012; Spears et al., 2017). In chapter 3, the difference in detection between window sizes was minimal (16.4%) however the difference between testing across a single window size and all window sizes was substantial, indicating that testing across multiple window sizes and finding the highest agreement in the number of true positives and least false positives could improve detection. Despite this knowledge, much less is known about how variability in target variables of natural systems interact with these changes. Current recommendations are to perform a sensitivity analysis to aid in selection of the window size prior to analysis (Dakos et al., 2012a; Lenton et al., 2012). Whilst prudent, this is effectively a blind procedure that only examines the raw data. Careful consideration of the typical dynamics exhibited by the target variable should also be taken into account along with the ability of the data frequency to capture that behaviour.

Even with the varying of window size, false positives were still more numerous than true positives in chapter 3 although the numbers for these two measures were much closer than that seen by Burthe *et al.* (2016). Regardless, the presence of false positives erodes confidence in the use of EWIs as it is difficult to control for them in non-experimental systems. A few methods have been proposed to help reduce their occurrence, such as analysis using non-stationary models to determine trends from which a baseline variability can be calculated (Livina et al., 2012). Other methods suggest the use of a likelihood approach based on the target data to test the significance of false positives (Boettiger and Hastings, 2012) and, in the case of EWIs suited to it (e.g. conditional heteroscedasticity), calculation of probability values (Seekell et al., 2012, 2011). Almost all these methods require significant preceding data to calculate these measures and none have yet been tested using real-world monitoring data. It seems likely that some systems are likely to be more suited to the use of these methods than others. For instance, high baseline variability could cause real warnings to be disregarded. Calculating baselines from past data needs to be treated with caution, particularly if little information of the target system is known. Past land use changes can severely impact lakes (Bunting et al., 2016) and, if they are unknown, the calculated baseline may end up being too high or even too low in some cases. For example, it is thought that, the pre-human state of some lakes may have been nutrient-rich due to the presence of large grazing herds (Moss, 2015). Our current understanding of how the ecology in lakes

relates to EWIs, non-linear change and regime shifts, whilst impressive in some parts, is lacking in others and it is unlikely that a 'one-size-fits-all' approach exists when predicting regime shifts or other forms of non-linear change.

6.1.4 Capturing and understanding variability

To further our understanding of how EWIs and organisms interact we need to understand the way organisms and variables act in response to pressures. This is likely to depend on the type and direction of the pressure (e.g. top down, bottom up). For instance, if testing TP for EWI signals rather than chlorophyll, it would be expected to act differently if the pressure occurred from a change in land use which lead to increased water colouration or 'browning'. Increases in temperature seen with no comparable increase in air temperatures (Williamson et al., 2015) and the negative impacts on macrophytes (Reitsema *et al.*, 2018) could increase variability in TP due to internal loading (Jensen and Andersen, 1992). Chlorophyll levels could remain low for longer due to shading and chemical interactions with dissolved organic carbon (DOC) (Carpenter et al., 1998; Deiningner et al., 2017; Williamson et al., 2015) leading to changes in response patterns that could alter how EWIs react. Differences in the causes (e.g. increases in nutrient loading, fish kills) and forms (e.g. cyclic algal blooms/crashes, steady moderate increase of chlorophyll levels) of variability are also likely to depend on lake-specific characteristics such as depth, fetch, sediment type and hydraulic loading (Janse et al., 2008) which can influence the interaction of pressures with target variables. These factors can raise doubts about the potential usefulness of EWIs but also highlight avenues for research to help better understand resilience processes in lakes.

Variations in pressure duration and magnitude have been shown to impact how EWIs respond in modelled data (Ratajczak et al., 2017), but much less is known about the difference in how pressure types such as top-down or bottom-up forms impact on variables used to calculate EWIs. One method of trying to control for such unknowns is to use multiple different EWIs at the same time to try and capture different forms of responses. In chapter 3 we used 5 different EWIs both individually and as a group to determine how this impacted on their ability to predict tipping points. The difference in true positives (tipping point preceded by an early warning) detected was an increase from 40.5% (the largest percentage detected by an individual EWI) to 70.2% (percentage detected by all EWIs as a group) across all window sizes. We also found that the majority of the tipping points were detected by one EWI which suggests either that a number of different processes are causing the tipping

points, each being picked up by a different EWI, or natural variability in responses is leading to these differences and so reducing confidence in prediction. Given the number of false positives found by most EWIs, it is hard to deny that Loch Leven has high levels of natural variability, which may be due in part to specific characteristics of the lake but also some level of inherent 'flexibility' of the turbid water state seen during the data collection period.

In this thesis, the combined measures of using multiple EWIs and varying window size have been shown to increase the success rate of EWIs when trying to predict statistically defined non-linear change. Whilst there is still much we do not understand and need to test about the use of EWIs, these findings provide some hope that they can become a more reliable tool for policy and management of ecosystems at risk from regime shifts. Utilisation of new and emerging technologies for data collection have a lot of potential to further improve the predictive abilities of EWIs. High frequency data collection technologies such as automatic monitoring buoys capable of high frequency *in situ* measurements of nutrients using colourimetry and zooplankton and phytoplankton using automated imaging flow cytometry (Álvarez et al., 2011; Read et al., 2014; Stanislawczyk et al., 2018). Satellite imagery is also another source of high frequency data capable of giving data on chlorophyll levels (Bresciani et al., 2018) and have the potential to expand data to a wider catchment and landscape scale and combine it with a range of species distribution data and land cover data (Andrew et al., 2014). Hydroacoustic technology can be used to greatly increase frequency of macrophyte and fish surveys (Winfield et al., 2012, 2007), potentially unlocking their usage as indicators of ecosystem state. The use of DNA metabarcoding techniques (Bucklin et al., 2016) to get community composition measurements at high frequency has potential to open new avenues not only in the use of various forms of EWIs but also as a new way of understanding the community dynamics of resilience.

Whilst being able to maintain desirable states is of the upmost importance, many lakes still remain in poor condition with very little improvement over the last 10-20 years (Oliver et al., 2017). Through improving our understanding of how ecological interactions respond to specific pressures and combinations of pressures under a wide range of changes (e.g. linear, non-linear, threshold, hysteretic) we can begin to identify the appropriate indicators for use on appropriate variables within systems most likely to display non-linear change and regime shifts. Mapping ecological changes during a shift when being able to characterise the form of the change that occurred is an important first step towards this goal.

6.2 Ecological change and stressor-response relationships: the dominant role of zooplankton

In chapter 4 we found widespread change across multiple variables and trophic levels in Loch Leven consistent with ecosystem reorganisation. This is consistent with one of the four characteristics of regime shifts identified by Lees *et al.* (2006), along with change across trophic levels, change in different types of variables (e.g. physical, chemical, biological) and their occurrence at high amplitude but low frequency. Significant decreases in nutrients (both TP and nitrate), chlorophyll and reorganisation of the zooplankton community from copepod dominance to large-bodied cladoceran dominance have all been seen in other studies, often in response to some form of biomanipulation (Carpenter *et al.*, 2011; Ibelings *et al.*, 2007; Jeppesen *et al.*, 1997). Although there was no specific removal of fish or introduction of piscivorous fish in Loch Leven, the cessation of fish stocking between 2004 and 2006 could have acted in a similar way. Prior to this, the reduced grazing capacity of the zooplankton community due to annual introductions of 100,000-160,000 young-of-the-year fish (May and Spears, 2012b; Winfield *et al.*, 2012), which have been shown to be particularly impactful due to their almost exclusive reliance on zooplankton as food (Jeppesen *et al.*, 1997), could have delayed the recovery shift seen in 2007.

In Loch Leven it is unlikely that the change in fish stocking alone led to the increase in macrophyte MGD in 2006 and 2008 (Dudley *et al.*, 2012) and the drop in TP concentration in 2007. In Lake Veluwe, Netherlands, increased flushing using low nutrient water was enacted as part of the restoration process (Ibelings *et al.*, 2007) which would have helped remove high nutrient water already in the lake and prevent build-up of phytoplankton (Carvalho *et al.*, 2012). A similar process could have happened naturally in Loch Leven with the occurrence of some particularly wet summers in the preceding years, leading to particularly high annual average Secchi depth readings (Carvalho *et al.*, 2007). The season within which high flow events happen can be of particular importance, for instance high flow during the summer months is likely to result in less soil erosion than similar events during months with lower vegetation cover and density such as winter and spring (Steege *et al.*, 2001). This is important in the context of the results from chapter 5 where almost all of the increases in precipitation led flow occurred during the winter months. These abnormal years prior to the regime shift may be responsible for the lack of significant change seen in Secchi depth readings in chapter 4 due to their effect in raising the average Secchi depth for the before period. Despite the high Secchi depth readings not being sustained throughout the years

leading up to 2007, this could have allowed the early establishment of macrophyte beds. Macrophyte species such as *Potamogeton pectinatus* and *P. perfoliatus* which have been present in Loch Leven in most recorded macrophyte surveys (Dudley et al., 2012) are particularly suited to exploiting short-term clear water events. Their ability to compress their lifecycle into short time periods in spring/early summer using stored energy in tubers and/or seeds allows establishment of beds that have the potential to survive, providing there is at least a short period of clearer water in spring (Hilt et al., 2018; Spencer, 1986; Woolf and Madsen, 2003). The establishment of these macrophyte beds is likely to have played a part in the shift seen in 2007 due to the importance of macrophyte communities in preceding years in the establishment of dense propagule banks (Van den Berg et al., 1999). The survival of macrophytes under eutrophic conditions is also heavily impacted by the presence of periphyton in combination with shading by phytoplankton. Invertebrates that feed on periphyton are often a source of food for fish (Jones and Sayer, 2003) and so the cessation of fish stocking could have also reduced predation pressure on these grazers allowing increased consumption of periphyton, further increasing the survival of macrophytes. Widespread ecological change is an important factor when considering regime shifts and the resilience of a lake's state afterwards, but the speed and form of the changes is also an important factor.

6.2.1 Hysteresis and the presence of feedback mechanisms

Many of the changes seen in the before/after analysis in chapter 4 appeared to be non-linear (see Table 4.1). The presence of non-linear dynamics has been identified as another defining factor in the characterisation of regime shifts (Lees et al., 2006). Whilst non-linear change is an important part of defining a transition or regime shift, it can take a number of forms. Stressor-response relationships can serve as a useful tool in understanding how variables within ecosystems respond and can be related to both ecological and mathematical functions (Larned and Schallenberg, 2018). For instance, a logarithmic relationship is typified by a sudden drop which gradually levels out. This could be likened to a disease or contamination event in which vulnerable members of a population are killed quickly but the death rate decreases as the population increasingly comprises the more resistant individuals. This could cause a sudden change in the system that could resemble a regime shift but could be reversed once the population recovers.

A form of response where deterioration and recovery follow the same trajectory has been termed the 'rubber-band' model which shows the theoretical response of a system or variable with no feedback mechanisms (Lake et al., 2007). The detection of a difference in trajectory in a stressor-response relationship between deterioration and recovery is a hallmark of hysteresis (Scheffer et al., 2001) and, whilst this does not conclusively prove that a critical transition occurred (Beisner et al., 2003), it does provide strong evidence for the existence of feedback mechanisms. Direct tests for the presence of hysteresis have proven extremely difficult using observational data (Faassen et al., 2015) as it requires data from both trajectories. In chapter 4 we used process modelling to help us simulate responses between a 'degraded' (before) state and a 'recovered' (after) state to test the form of the stressor-response relationship. Whilst the analysis did provide evidence of hysteresis in Loch Leven (see Figs 4.4, 4.5 and 4.6) the 'hysteresis offset' (distance along the stressor axis between the two trajectories (Larned and Schallenberg, 2018)) was relatively small, indicating low levels of resilience in the recovered state. Chlorophyll and macrophyte responses were comparable in their hysteresis offset (they both had the same critical nutrient loads (CNL)) (see Figs 4.4 and 4.6), whereas zooplankton had no measurable hysteresis offset at all. The rise in zooplankton biomass in the after state covers the same distance across the stressor axis (P Loading) as the hysteresis offset for chlorophyll and macrophytes (see Fig 4.5). The low chlorophyll at these P loads suggests that zooplankton grazing is the main factor preventing the switch from a clear to a turbid state. As zooplankton biomass increases, the effects of grazing on chlorophyll will also increase, preventing large concentrations from shading out macrophytes. This demonstrates one of the key resilience mechanisms in Loch Leven.

Another component of Lees *et al.* (2006)'s definition of a regime shift (occurs at high amplitude but low frequency) implies that systems that experience high frequencies of change have high natural variability (Capon et al., 2015). In shallow lakes, feedback mechanisms are a key factor in determining the occurrence of a regime shift which can be related to this part of the definition. In essence, it means that a new state needs to be sustained for a minimum amount of time based on general inter-annual variability. One problem with this definition is that a system could experience what appears to be a regime shift, but an external forcing factor could potentially 'hold' it in the new state. A new state should be self-sustaining for a change to be considered a regime shift with stabilising feedback mechanisms. Other studies have also identified that at intermediate nutrient

values shallow lakes can switch between clear and turbid states (Scheffer *et al.*, 1993; Hargeby *et al.*, 2007) or even have spatial variation within the same lake between clear and turbid regimes at the same time (Ibelings *et al.*, 2007). This has been termed 'flickering' and can serve as a warning that a lake is in the unstable medium between a clear and turbid state which means it is at much higher risk of moving to a different regime. Given the relatively high TP concentrations still maintained in Loch Leven and the lack of significant change in variables such as Secchi depth, it could be regarded as currently existing within such an intermediate state. Thus, without substantial further reductions in P load it may continue to be at high risk of a return to a turbid state.

For systems like Loch Leven that appear to be at the boundaries of exhibiting hysteresis-like behaviour (Janse *et al.*, 2008), it seems that, although these feedback mechanisms can and do exist, they are typically weaker than in smaller, shallower, more uniform lakes. This may result in low levels of both resistance and resilience in Loch Leven and lakes with similar characteristics, meaning initial deviations such as algal blooms can occur more readily and the recovery of the lake afterwards takes longer. In terms of the stressor-response relationships discussed above, Loch Leven is somewhere between the hysteresis model and the rubber band model. The ecological processes governing this difference in stressor-response relationship seem to be broadly the same as generally seen in shallow lakes with interactions between zooplankton, phytoplankton, nutrients and macrophytes serving as the main factors as can be seen in chapter 4. Nevertheless, it seems likely that some unique characteristics of Loch Leven impact how these interactions function and the forms of responses expected to stressors.

6.2.2 Resilience in Loch Leven and implications for management

Loch Leven is a large shallow lake and as such has long fetch from most directions, making it particularly vulnerable to wind disturbance. Coupled with this, its large size is likely to lead to limitations in macrophyte dispersion and colonisation in relatively isolated lakes (Salgado *et al.*, 2018) such as Loch Leven, particularly when considering its unique bed morphology and depth profile (see Fig. 2.1). Model studies have identified factors such as spatial and morphological heterogeneity as important factors in determining the possibility and level of hysteresis (Scheffer and van Nes, 2007; van Nes and Scheffer, 2005). In Loch Leven a mean depth of 3.9 m and a median depth of 3.17 m show that macrophytes would need to be growing to depths of ~4 m to achieve above 50% coverage. Beyond this point increasing

macrophyte MGD would result in comparatively small gains in percentage area covered. One of the causes of the difference between the mean and median depths is the presence of two, ~25 m-deep holes in the central north and south of the lake. The depth of these holes means that periodic stratification is likely to occur which has the potential to lead to anaerobic conditions in small parts of the lake and subsequent release of P from lake sediment. The potential presence of both shallow and deep water sources of internal P loading further increases the lake's vulnerability to increased nutrient concentrations, particularly in the warmer summer months (Jensen and Andersen, 1992; Spears *et al.*, 2007). This highlights the importance of zooplankton herbivory in maintaining a clear water state in lakes like Loch Leven and as one of the factors that makes it so vulnerable to a regime shift. Low redundancy (low number of unique species contributing to the same biological processes (Wohl *et al.*, 2004)) in filtering grazers of the zooplankton community is relatively common in northern lakes, such as in sub-arctic Sweden (Angeler *et al.*, 2013), which, like Loch Leven, are generally considered vulnerable to environmental stressors. Past studies have shown that in the early 1970s pesticide discharged into Loch Leven from a woollen mill resulted in the complete removal of *Daphnia* from the ecosystem. This discharge was stopped in approximately 1971 and *Daphnia* returned very shortly after, resulting in a substantial drop in chlorophyll a:TP ratio (May and Spears, 2012b), demonstrating the significant impact of zooplankton on chlorophyll levels in Loch Leven.

The dominance of zooplankton grazing in determining resilience in Loch Leven has vulnerabilities in the fact that the most prolific grazers consist of a single species (*Daphnia hyalina*), making them particularly prone to disease or a pollution event such as that seen in the past (May and Spears, 2012b). Another vulnerability is the maintenance of an unnaturally low diversity fish community. The presence of sluice gates on the outflow prevents fish migration and resulted in the loss of species known to be present in the past, such as salmon (*Salmo salar*), flounder (*Platichthys flesus*) and Arctic char (*Salvelinus alpinus*) (Winfield *et al.*, 2012). This likely results in less predation pressure on zooplankton than may exist if more species existed in the loch. Any failure in this barrier, either accidental or through installation of a bypass, has the potential to significantly alter the competitive dynamics of the Loch Leven fish community and, through that, the zooplankton community. Relatively minor losses of grazing capacity in the zooplankton community could result in increases in chlorophyll and decreases in macrophyte MGD. Under conditions of higher stress through high temperatures or droughts, this has the potential to lead to significant reductions in

macrophyte coverage and a possible reversion to a turbid state. Therefore, it is important to consider predicted changes in climatic variables when preparing management strategies for the future. Adapting and using new technologies such as hydroacoustics for macrophyte MGD surveys and flow cytometry for and DNA metabarcoding for zooplankton has great potential in improving our understanding and the monitoring and management of Loch Leven particularly headed into an uncertain environmental future.

6.3 Predicting resilience to climate change in large shallow lakes

After gaining a better understanding of the types of dynamics seen in Loch Leven during recovery, understanding how it could react to climate change at different nutrient loadings becomes critical. A large amount of research has examined the impact of changing temperatures on aspects of lake function, particularly in conjunction with eutrophication (e.g. Carvalho and Kirika, 2003; Elliott, Jones and Thackeray, 2006; Jeppesen *et al.*, 2007, 2009; Mooij *et al.*, 2007; Moss *et al.*, 2011). Some other studies have also considered the effects of changing precipitation, as functions of increased nutrient runoff during the winter (e.g. George, Hurley and Hewitt, 2007), increased flushing rates (Carvalho *et al.*, 2012) and increased retention time under low flow and drought conditions (e.g. Gomes and Miranda, 2001; Mosley *et al.*, 2012). This range of pressures has significant potential to interact in both expected and unexpected ways. In chapter 5, the modelling of responses in chlorophyll, macrophytes and zooplankton to changes in temperature and precipitation patterns in PCLake showed some surprising results. The interactions resulting in lower critical nutrient loads (CNL) between increased precipitation and temperature seen at low P loads proved surprising across all response variables. In PCLake, 20% has been defined as the threshold coverage of macrophytes for feedback mechanisms to kick in (Janse *et al.*, 2008) which has also been defined as a threshold in real lakes (Søndergaard *et al.*, 2016). Given that coverage never reached this threshold in this study, it suggests high system vulnerability. The lower CNL (first point at which the target variable is at a higher/lower level depending on the direction of response) in Loch Leven for both chlorophyll and zooplankton was mostly linked to scenarios modelling increases in winter precipitation and the highest temperatures, with precipitation playing the largest role due to the presence of a lower CNL in the two highest precipitation-only scenarios. In the macrophyte responses, the lower CNL was limited to the high temperature, more precipitation scenario group which included the highest increases in

both temperature and winter precipitation and even a small increase in summer precipitation.

6.3.1 Climate change, nutrients and resilience in Loch Leven

There are two probable reasons for the dynamics described above. The first is the presence of increased particulate matter loading with increased inflow. P loading was uncoupled (increases in P loading did not necessarily occur with increases in inflow) from flow rates in this analysis as it was the main stressor variable and so the main mechanism is most likely the increased shading effect resulting from increased particulate matter concentrations in the water column. In another study using PCLake on its default settings, particulate matter was found to reduce resilience, leading to a substantially lower CNL in both clear and turbid states (Lischke et al., 2014). The second probable reason is highly related to the first in that it links to lower light penetration into the water column. The increased inflows seen in future climate change scenarios, particularly in the winter, are not matched by outflows, meaning that relatively small increases in lake depth are created, which has been shown to be a highly sensitive parameter in the model (Janse et al., 2008). It is unclear whether both or just one of these factors is responsible but they both pose a risk moving into the future. The moderate-shallow depth of Loch Leven makes it particularly sensitive to these changes especially when combined with increased turbidity from other sources such as particulate matter. Part of the reason for choosing to model the scenarios in this way was due to the artificially controlled outflow on Loch Leven which is typically managed to increase the water levels from autumn through to spring to help maintain a more even flow downstream during the typically drier summer (Sargent et al., 1995; May and Spears, 2012). Although installations such as this are relatively rare, it could emulate how lakes prone to changes in depth could behave under future climate change. The similar chlorophyll and zooplankton responses to climate change scenarios gives a strong indication of the cause of the different CNL in the macrophyte responses as the two precipitation-only scenarios in which the difference lies, result in a slightly lower peak macrophyte percentage cover than others with the same CNL. The lower chlorophyll levels seen during this same scenario point to the zooplankton grazing as the key factor keeping chlorophyll levels low enough to limit shading until higher P loads allow phytoplankton growth rates to exceed loss through zooplankton grazing.

Despite the lower CNL seen in results from the high temperature, more precipitation climate change scenario group, the same factors are also the most likely reason for the lower

chlorophyll levels seen at higher P loads. The decrease in light penetration due to particulate matter can impact on phytoplankton as well as macrophytes (Jones, 1992) and, combined with increased flushing rates, this could reduce the chlorophyll levels at higher P loads (George et al., 2007) whilst still having the negative effect on CNL seen at low P loads. Overall the model shows a larger impact of light limitation on macrophytes, which has also been reported in laboratory experiments where phytoplankton were found to have a light utilisation efficiency seven times that of macrophytes at low light levels (Sand-Jensen and Madsen, 1991). This further highlights the importance of how changes in precipitation patterns need to be considered in the context of the surrounding landscape. These effects can manifest through run-off from looser arable soils in some cases and dilution of point sources in others. The factors that led to the highest chlorophyll levels involved scenarios with the greatest reductions in summer precipitation combined with the highest temperatures.

Increased temperature impacts multiple aspects of lake ecology and so creates a complex set of changing interactions. Growth rates increase in algae (Robarts and Zohary, 1987b; UWRAA, 1995) and macrophytes, although they are highly dependent on species, phenology and uptake of nutrients (Dhir, 2015; Thackeray et al., 2010). Furthermore, reductions occur in zooplankton growth rates, body size and filtering rate at higher temperatures (Moore et al., 1996). These impacts can be clearly seen in chapter 5 (see Fig. 5.4) where the high temperature only scenario led to lower zooplankton biomass along with the high temperature, more precipitation scenarios. Reductions in fish body size, earlier reproduction and general decreases in piscivorous fish (Jeppesen et al., 2010; Moss et al., 2004) are some of the major impacts that could also result from increasing temperatures. As well as impacts on the biological components of lakes, physical and chemical changes can also occur due to increasing temperatures. Increases in P release from sediments in shallow lakes (Jensen and Andersen, 1992; Spears *et al.*, 2007) and lengthening of stratification periods in deeper lakes (and deeper parts of shallow lakes) (Winder and Schindler, 2004) will also impact on lake processes to increase both nutrient and chlorophyll concentrations. Coupled with reductions in summer precipitation leading to increased water retention time and stability, this can create conditions that greatly increase chlorophyll levels at higher P loads without necessarily impacting on resilience at lower P loads.

This can be clearly seen in chapter 5 where high temperature only scenarios did not impact on the CNL but had increased chlorophyll levels at higher P loads. Part of this non-linearity in response can be attributed to reductions in water levels in some lakes allowing greater light penetration into the water column, and even onto the sediment in shallower lakes, which can lead to reductions in internal loading from sediments (Spears et al., 2008). Another study using PCLake found similar results based on the default settings of the model, where temperature and reduced hydraulic loading did not impact resilience of the clear water state but led to higher chlorophyll levels and increased the resilience of the turbid water state when considered as individual pressures (Mooij et al., 2009). The same seems to be true for Loch Leven when the interaction of these stressors was modelled in PCLake.

How closely reality would mirror the results from the PCLake modelling of climate change scenarios is currently unknown as models are by necessity a simplification of real-world processes. PCLake is one of the more complex models of lake ecosystems with its ability to include most of the major physical and chemical processes along with most trophic levels, albeit as broad scale functional groups (Janse, 2005, 1997). Despite this, process modelling provides a useful tool with which to not only highlight the impact of climate change on response variables, such as chlorophyll a, but also allows the assessment of CNL. Thus, a quantified guideline can be provided for how stressor-response relationships are expected to behave under a range of potential conditions defined by their interaction with P loading.

6.3.2 Evolution and the impact of parasites on lake resilience

One important aspect of ecological functioning often not included in either process modelling or when trying to understand resilience, particularly when considering responses over time, is that of evolutionary selection and responses. How populations respond to environmental change over time is generally based on comparatively short-term experiments and field data. Our predictions of how they will respond are contingent on these responses remaining broadly the same over time when, depending on system and population specific selection pressures, these could change (Dam, 2013). Although research into the effects of multiple pressures is expanding, much is still unknown about short term responses, let alone evolutionary responses over time. Considering the effects of environmental change in a more holistic way is essential when considering evolution as recent studies have found that temperature is a poor predictor of past evolutionary change in certain species of marine plankton (Brombacher et al., 2018). When planning against future environmental change,

especially when considering ecosystem and population variability as a potential predictor of sudden change, considering evolutionary selection and responses in frameworks and models becomes even more important (Mooij et al., 2019). Evolutionary changes are also likely to impact species interactions with unexpected pressures such as pollution. Reduced genetic diversity due to adaptation to climatic factors or pollution events could impact a population's ability to cope with further unexpected factors such as diseases and parasites (Altizer et al., 2003; Lopes *et al.*, 2009). This is particularly relevant under a warming climate where warmer winters become more common, which removes a common control on pathogen and parasite spread (Harvell et al., 2002).

Diseases and parasites are a natural component of almost all ecosystems (Dobson et al., 1986) and their prevalence has become increasingly apparent in recent decades (Lafferty et al., 2006; Dobson *et al.*, 2008), including in Loch Leven (Huxham et al., 1995). What is less clear is how climate change will alter common disease/parasite/host interactions and also the spread and emergence of new forms in aquatic systems. In basic terms, most of the interactions between a host and a parasite, particularly in water, are temperature dependent (Marcos-López et al., 2010). Increases in temperature have the potential to favour both the host and the parasite and so the outcome can be difficult to predict without specific research. These factors have not been explicitly tested in this thesis, and yet studies are beginning to highlight a range of impacts across ecosystem types. The diseases of both farmed and wild salmonids, such as salmon and trout, are predicted to worsen with increasing ambient temperatures, leading to higher mortality rates (Peeler et al., 2008; Sterud et al., 2007). How this will impact on the overall state of a lake will likely depend on the community composition of ecosystem compartments such as zooplankton and fish. For instance, cyprinid fish species are predicted to benefit from warmer temperatures and be less susceptible to disease and so will gain competitive advantages in lakes where these fish types coexist (Marcos-López et al., 2010). In Lake Maarsseveen, the Netherlands, warming temperatures have led to earlier onset of chytrid fungus infections of specific diatom species (*Asterionella*) limiting their ability to form blooms (Ibelings et al., 2011). Again, the wider impacts of this and similar infectious agents will most likely be dependent on specific community composition and nutrient concentrations as it allows other species to become competitively superior. Another study has highlighted how differences in lake bed morphology can increase the prevalence of fungal infections in some species of *Daphnia*. The presence of increased gravity currents in U-shaped lakes, compared to V-shaped lakes, leads to increased spread of fungal pathogens

from near-shore areas. Larger bodied individuals have been found to be more susceptible and so this can lead to significant loss of grazing capacity and thus increased chlorophyll levels (Hall et al., 2010). Overall, the impact of parasites and disease on ecosystem dynamics in lakes is likely underrated, but the impact of climate change on these interactions is highly specific. Factoring such considerations into the resilience framework is currently untried and yet it is possible that they could play a substantial role in both the variability seen in natural systems, and the point at which a system would undergo a shift when combined with a range of other factors.

6.4 Future research

Ecological resilience has become an increasingly important framework both when considering ecosystem management and when aiming to understand the complex dynamics that underlie non-linear change. Despite the theoretical foundations of the field dating back to the 1970s (e.g. Holling, 1973) much is unknown about how this theory translates to the real world. Much of this knowledge gap lies in how these sudden changes in ecosystems act through fine-scale (individual populations) and large-scale (landscape and catchment) interactions across both space (regional to biome) and time (evolution). A great deal of research is required to develop this understanding into something both usable and useful for practitioners and researchers. In this work, the use of new and emerging technologies to improve data collection would be particularly useful and important. Technology and methodologies highlighted earlier such as automatic monitoring buoys, satellite imagery, hydroacoustics and DNA metabarcoding all have great potential to greatly improve our understanding of ecosystem and community dynamics. Suggestions are outlined below for further work in the form of experiments, analyses and modelling towards this goal.

6.4.1 Development of EWIs as predictive tools and ecological indicators

The mixed results seen in the use of EWIs thus far highlights how little we know about their functioning in lake ecosystems. Addressing this requires analysis of extensive time series datasets from the field, coupled with carefully designed and controlled mesocosm experiments to replicate and test a range of pressure scenarios including climatic, pollution and disease related pressures at targeted variables. High frequency measurements during the experiments including can allow a comprehensive assessment of how EWIs respond to different response types and help us understand how different EWIs pick up on the different

pressures. In addition, an assessment of the impact of frequency of measurement could be undertaken through systematic reduction in measurement frequency to assess the impact on EWI efficacy. Further analysis of differences in variance patterns could also help us understand ecosystem behaviour seen during particular pressure scenarios and response types (e.g. hysteretic, threshold, linear). The ability to have both direct pressure data combined with the impact on the stressor-response relationship could result in better understanding of how they interact.

6.4.2 Interaction of stressors-response relationships with direction of impact

Stressor-response relationships provide a convenient and understandable theoretical framework with which we can better understand resilience processes within and across ecosystems and time. Understanding how different forms of stressors impact on particular parts of a system's trophic structure and how that relates to the stressor-response relationship can inform us on how these stressors affect the resilience of a system. To understand how different stressors effect stressor-response relationships, large scale analyses of existing datasets from past lake restoration studies could provide a vast resource with which we can begin this process. Combining such analysis with computer modelling using lake ecosystem models such as PCLake to hindcast the mixture of restoration treatments from a range of lake restoration studies will allow us to better understand the in-lake dynamics that take place during the various forms of responses. The use of bifurcation analysis will also allow the assessment of hysteresis present in the modelled changes, giving a greater understanding of the kinds of change taking place in these lakes. To further understand the mechanisms of change, carefully designed laboratory and mesocosm experiments using a genetics 'knock out' style approach (e.g. treatments involving removal/addition of particular zooplankton species) could shed some light on the importance of particular ecosystem and trophic components and species. The results could then be incorporated into models to test on a 'virtual ecosystem' level.

6.4.3 Landscape impacts on resilience: patterns of vulnerability in scale

Understanding how features of landscapes impact on the vulnerability of the systems within them is critical to understanding their resilience to changing pressures. Coupling lake ecosystem models such as PCLake with catchment scale models of hydrology, water quality and land-use would allow the exploration of lake/catchment interactions and how they

impact on overall ecosystem resilience across landscapes. Combining these models with the use of satellite data to better understand links between landscape features within catchments (e.g. using imagery to understand characteristics of vegetation and how this may affect erosion and soil stability) could open new avenues for research both experimentally and within the modelling construct. Using climate change projections whilst working with the agricultural sector to better understand how changes in the environment could alter agricultural land use and practices (e.g. warmer temperatures leading to change from sheep to cattle farming or changes in fertiliser application patterns) could help managers plan accordingly. From this PhD research one particular area identified for further work is the need to better understand how lake and catchment specific characteristics, such as variations in depth due to heterogeneous bed morphology, impact population and ecosystem scale interactions with pressures. Improved understanding could be achieved through the combination of established models such as PCLake with new iterations better designed to simulate greater variations in depth such as PCLake+ (Janssen et al., 2019), and linking these together using a hydrodynamics model to create an improved 3D lake model. Working to better understand how these physical characteristics alter a lake's vulnerability could help prioritise lakes in need of protection, as well as identify lakes that may prove particularly difficult to restore, within the context of future environmental change.

6.5 Conclusions and wider implications

The application of the resilience framework to both scientific understanding and management of ecosystems has thus far seen mixed success. However, its ability to conceptualise and quantify the theory and mechanisms involved in unpredictable, non-linear change with potentially irreversible consequences across multiple ecosystem types makes furthering our understanding of resilience critically important. Through the research presented in this thesis a better understanding has been gained of how well resilience indicators such as EWIs reflect statistically defined non-linear change. The substantially improved accuracy gained through usage of EWIs as a group shows significant promise to improve both the understanding and usability of EWIs. Further research to understand the capability of individual EWIs to detect variability in different forms can unlock their potential as both research and management tools to predict regime shifts in a range of ecosystem types. Through the detailed analysis of a non-linear event in a real-world ecosystem we have gained valuable insight into the ecological processes that took place and identified the

aspects of the lake's ecology primarily responsible for its resilience. Combining an ecological understanding of this shift with resilience through the generation of stressor-response relationships has not only provided understanding of the resilience of this specific system but provided evidence of a quantifiable component of resilience in the 'hysteresis offset'. Also, highlighting the larger scale features of lake typology that influence the vulnerability of Loch Leven, allows the extrapolation of these features to other lakes to help identify management targets in terms of specific lakes and the variables within them. It seems likely that these factors, such as moderate average depth, large area and a heterogeneous bed morphology, will significantly increase a lake's susceptibility to stress regardless of geographic location. The vulnerability of these lakes to stress is further highlighted by the critical role of zooplankton herbivory in maintaining good status, even at lower P loads. Assessing how these vulnerable lake systems are likely to respond to predicted forms of climate change generated some surprising results, in that factors such as increased loading of particulate matter during wetter winters as well as minor changes in depth, combined with warmer temperatures pose the biggest risk to resilience in lakes of shallow to moderate depth. The large combined effects of nutrient loading, high temperatures and decreased summer precipitation suggest that, even to maintain the 'status quo', many lakes with similarities to Loch Leven even in a single typological factor are likely to need management intervention.

Not all types of lakes are subject to the risks of regime shifts although most have potential to exhibit some form of non-linear change, particularly in response to non-linear change in drivers. Through the use of tools such as stressor-response relationships, the identification of simple typological indicators such as lake size, depth and bed heterogeneity and process models such PCLake, ecosystems most at risk can be identified so that appropriate monitoring (e.g. high frequency chlorophyll measurements) can be enacted along with identification of the management interventions most likely to succeed (e.g. biomanipulation, geoengineering). Assessing the surrounding landscape to understand the likely inputs during periods of high precipitation (e.g. particulate matter) can highlight other factors increasing the risk of regime shifts. How these findings apply to other ecosystem types, depends on the identification of appropriate variables for use with EWIs, the dominant feedback mechanisms and the variables that regulate them. Once these factors are known, the generation of stressor-response relationships can give a quantifiable measure of the systems resilience and with appropriately designed models based on these principles, the impacts of environmental

change can be better understood. With this understanding comes the potential to mitigate deleterious impacts before they lead to a regime shift to a less desirable state.

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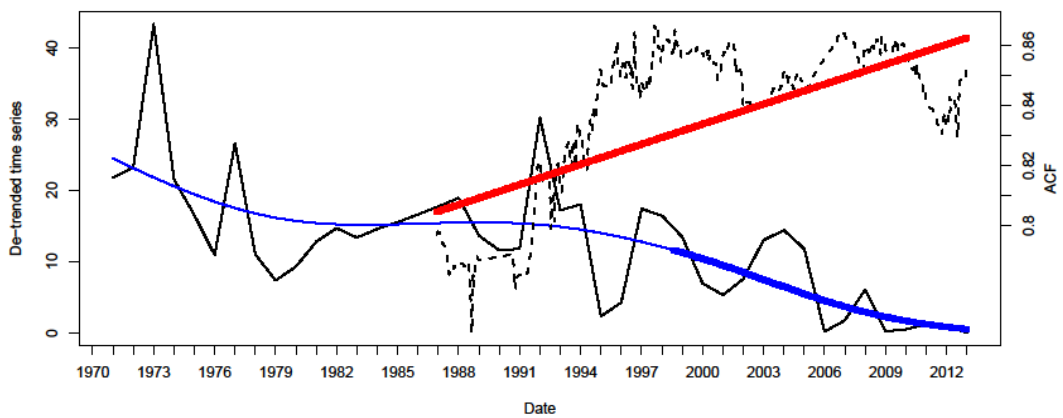
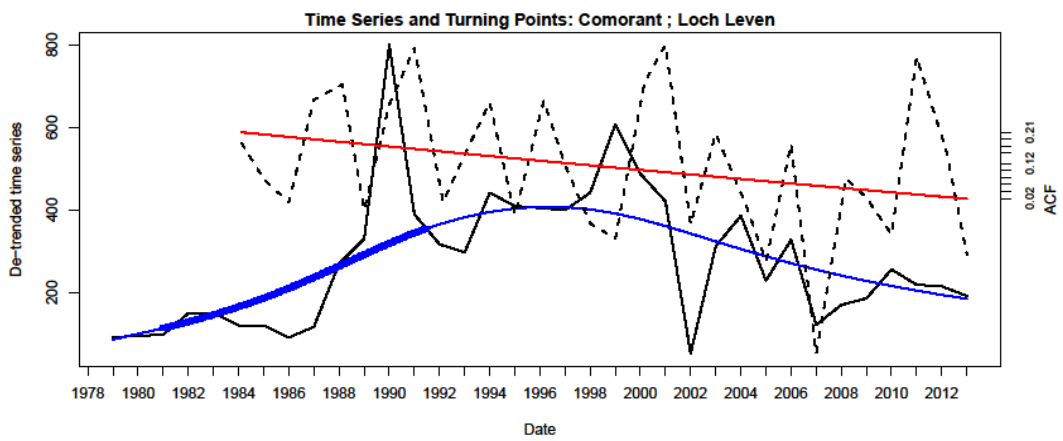
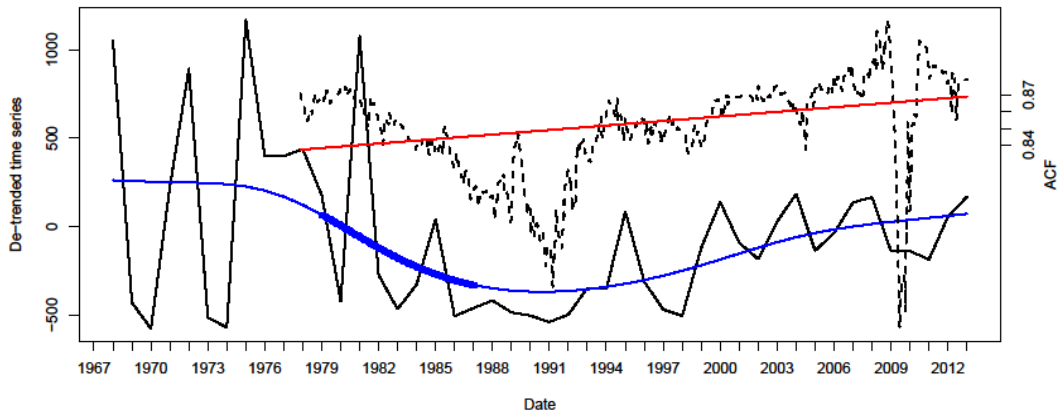
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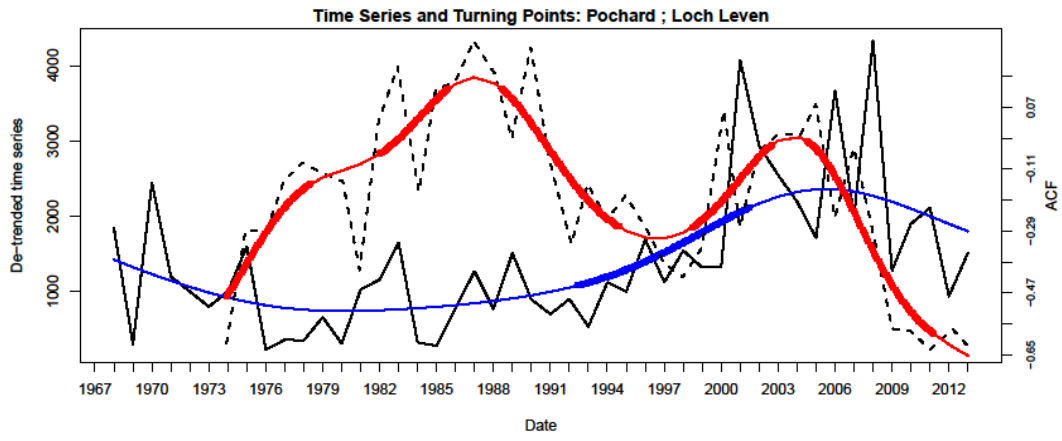
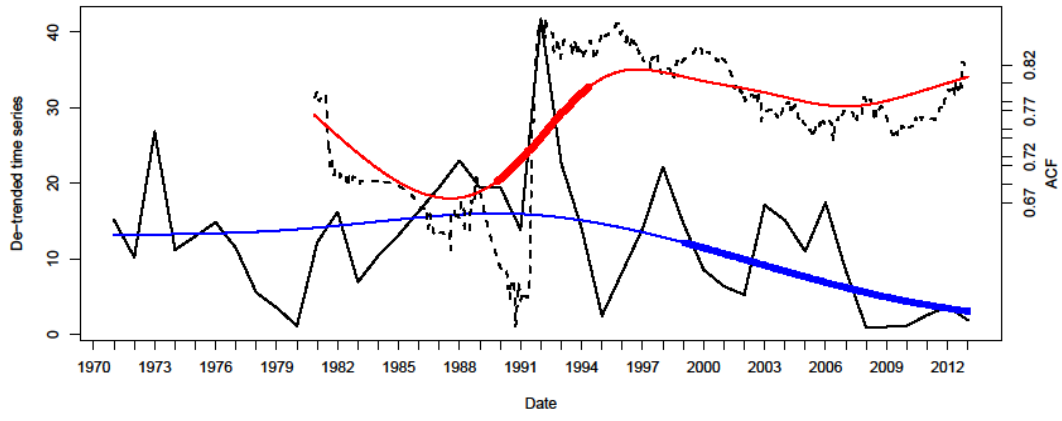
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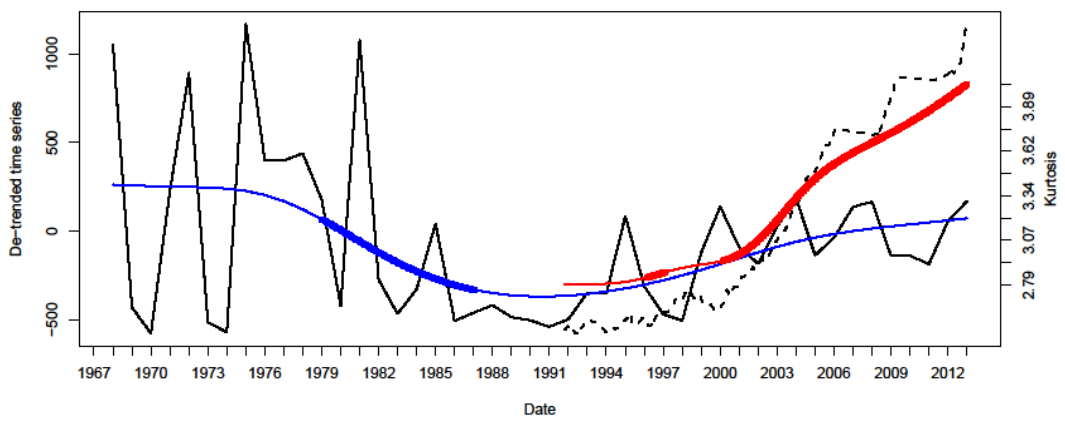
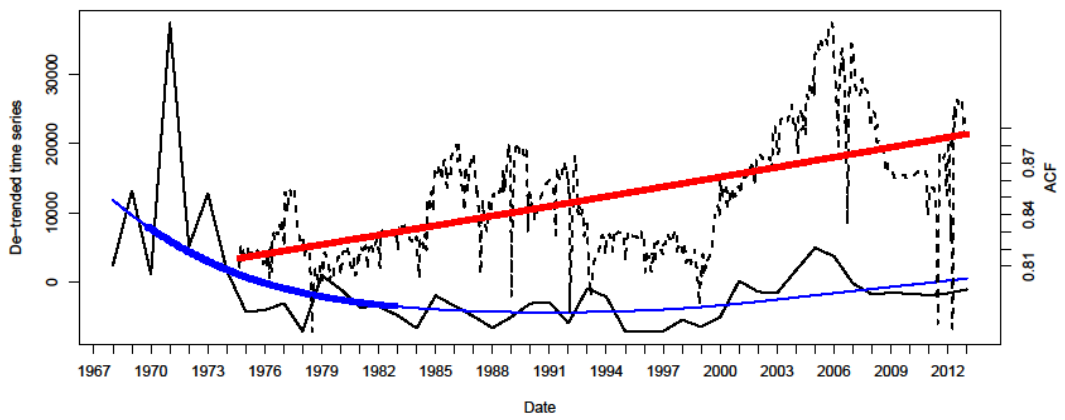
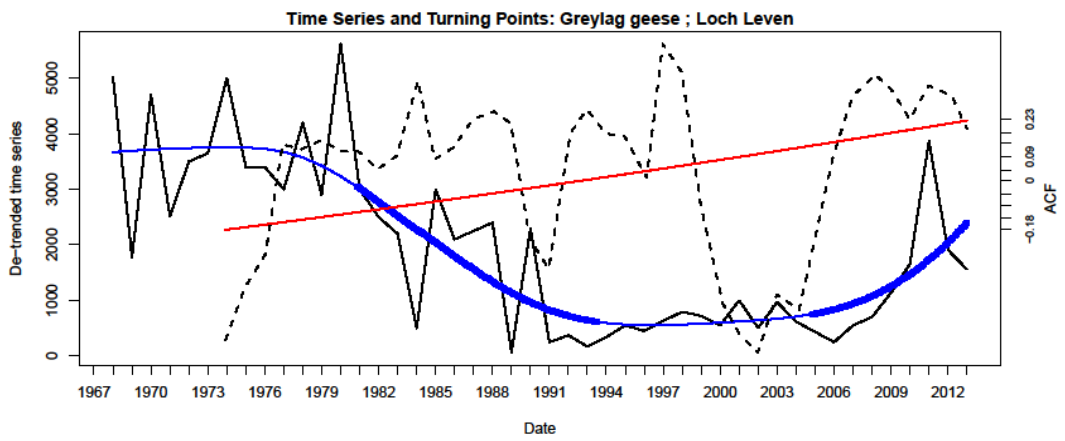
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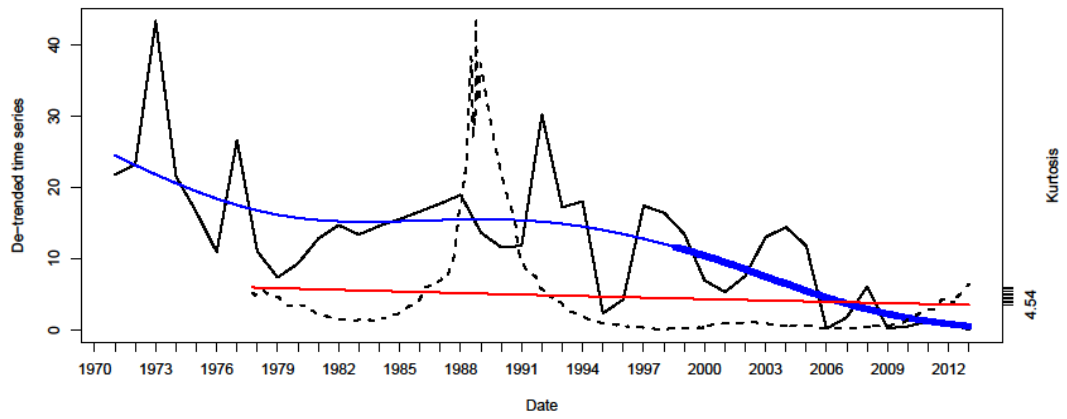
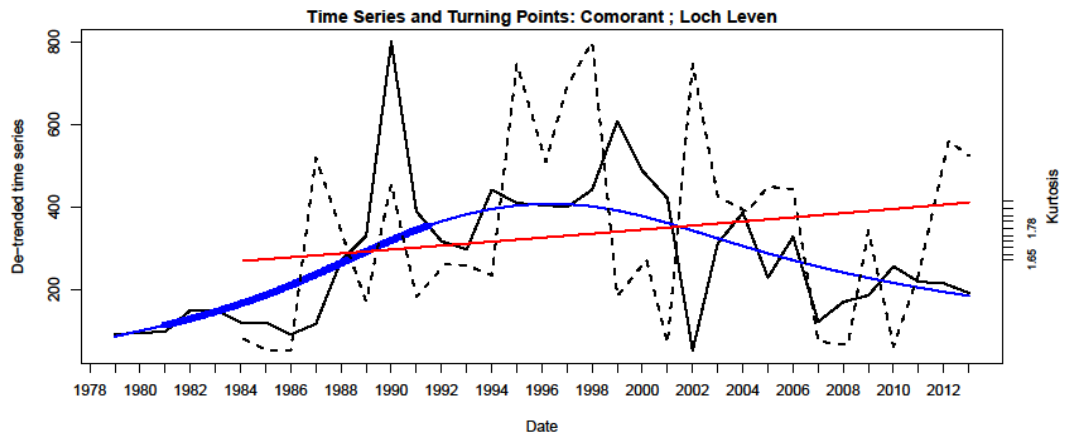
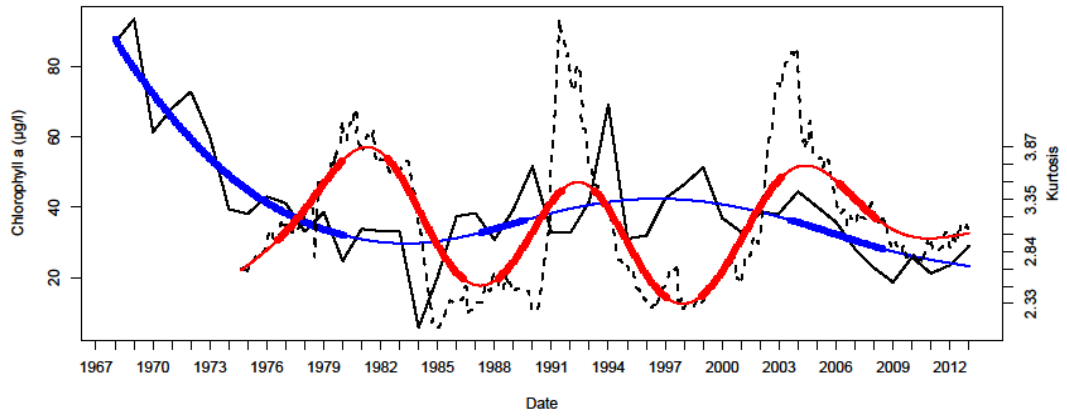
Appendix A

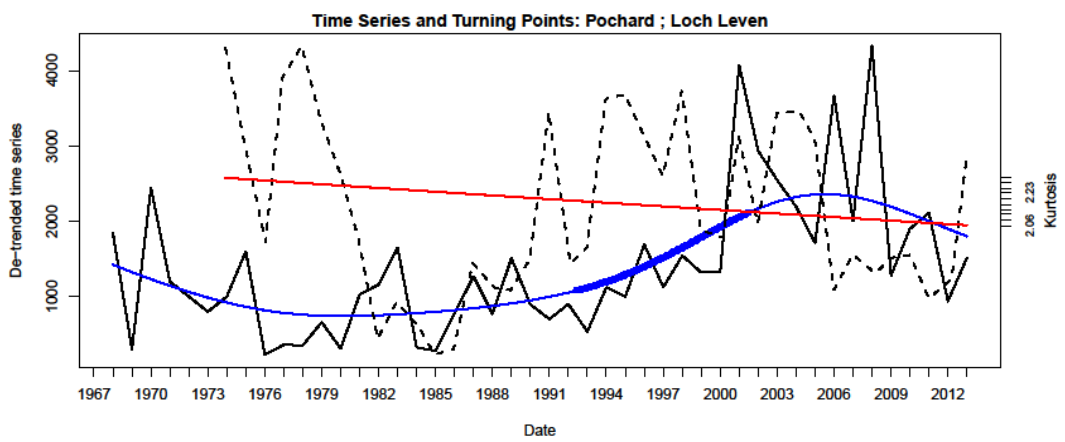
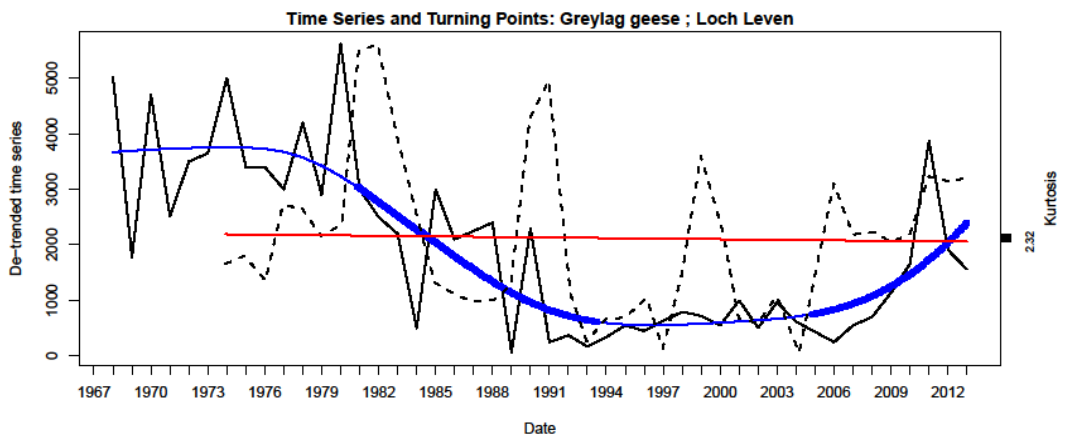
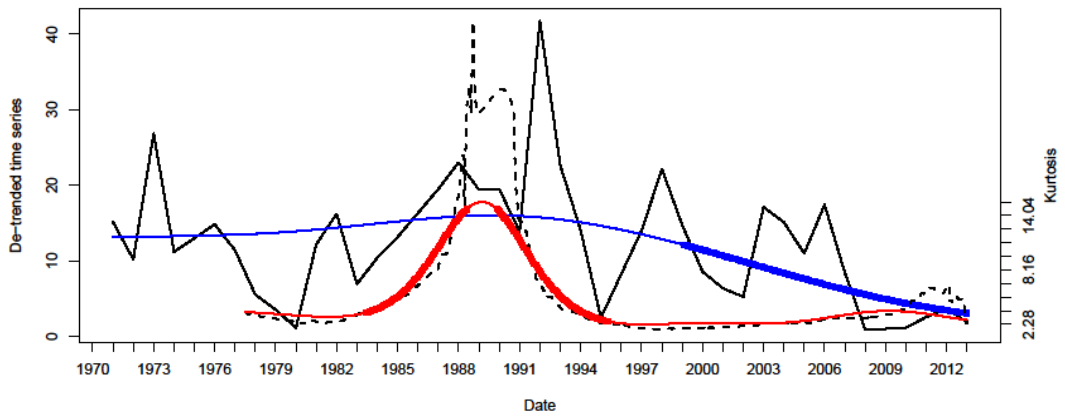
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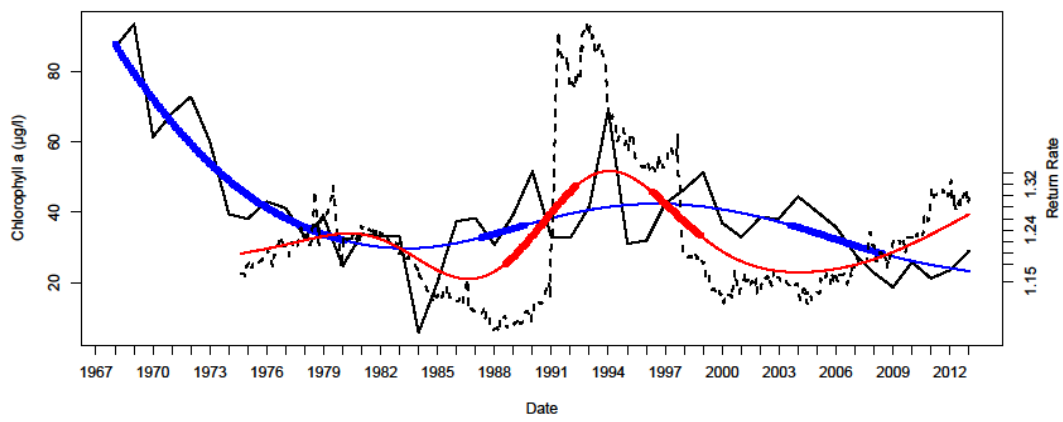
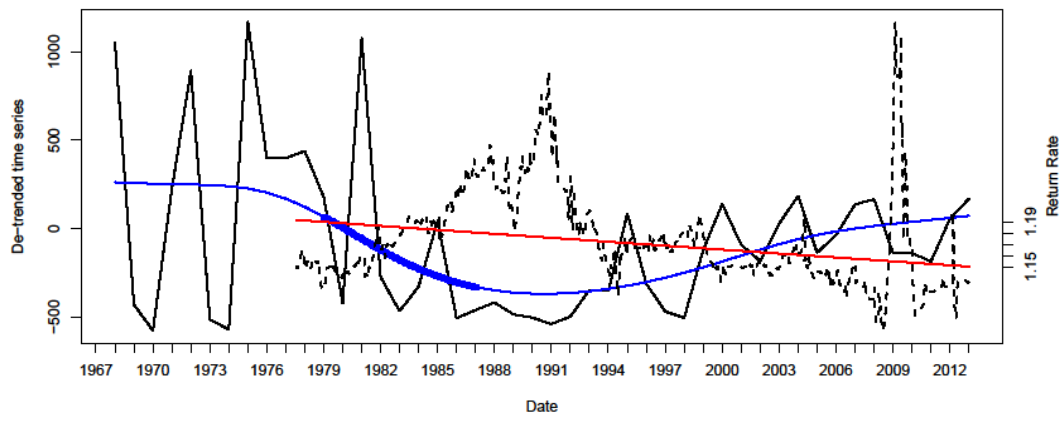
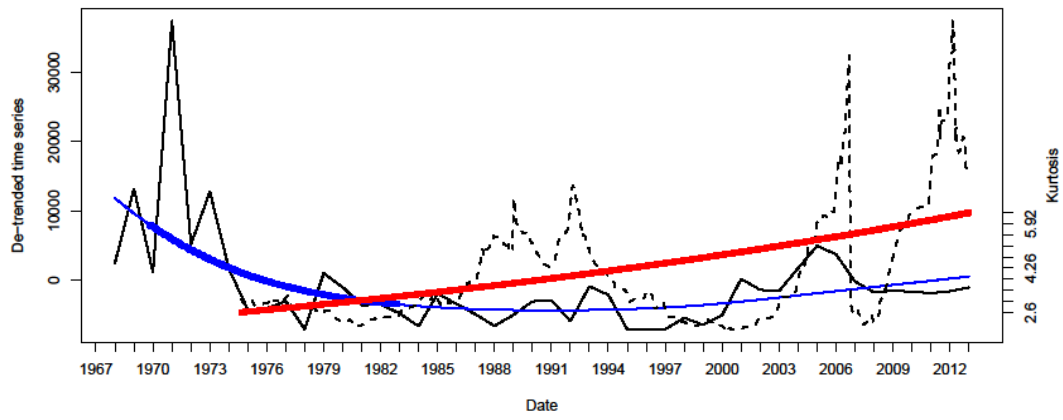


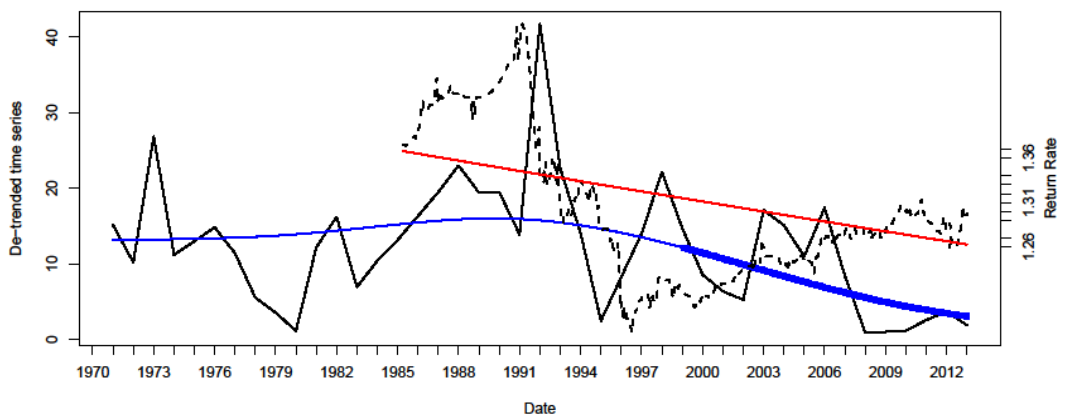
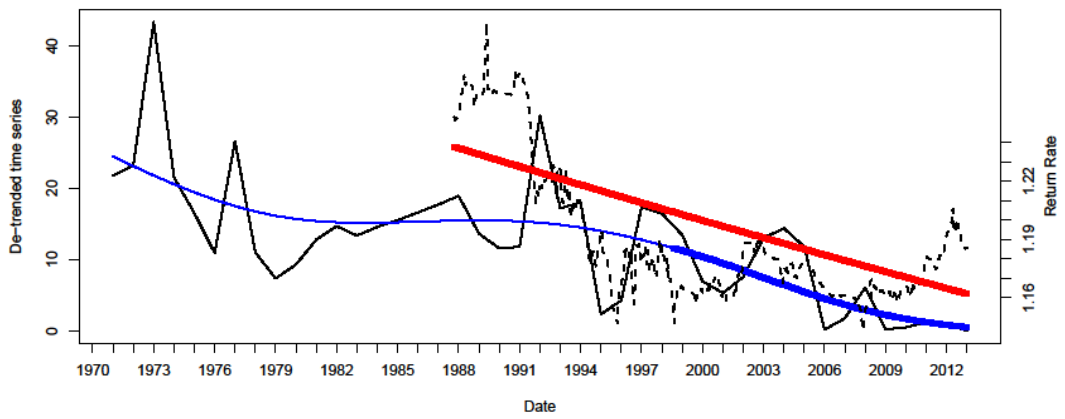
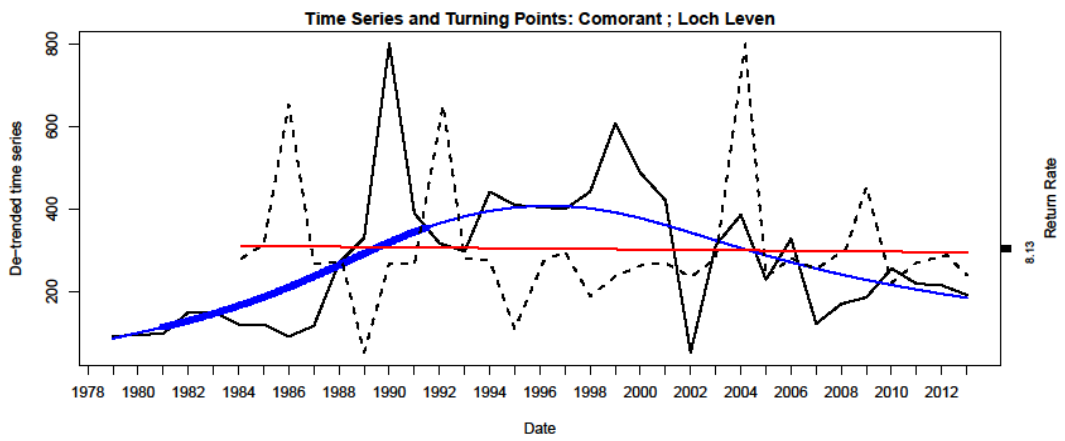


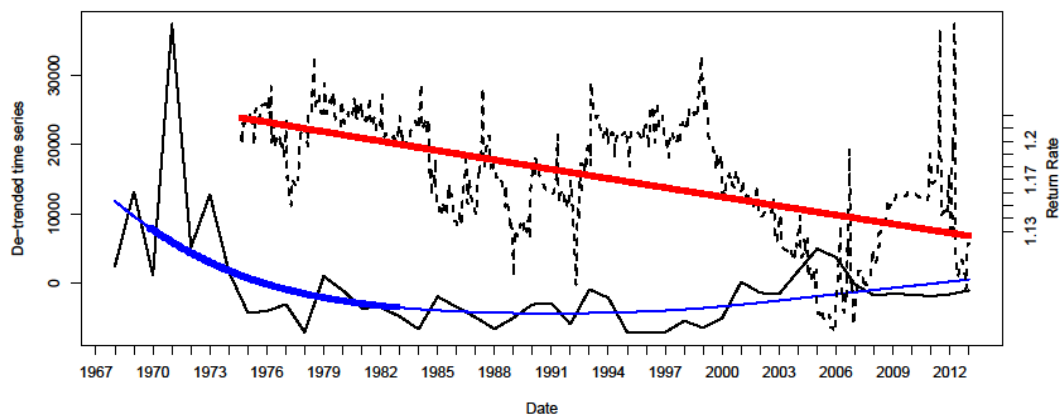
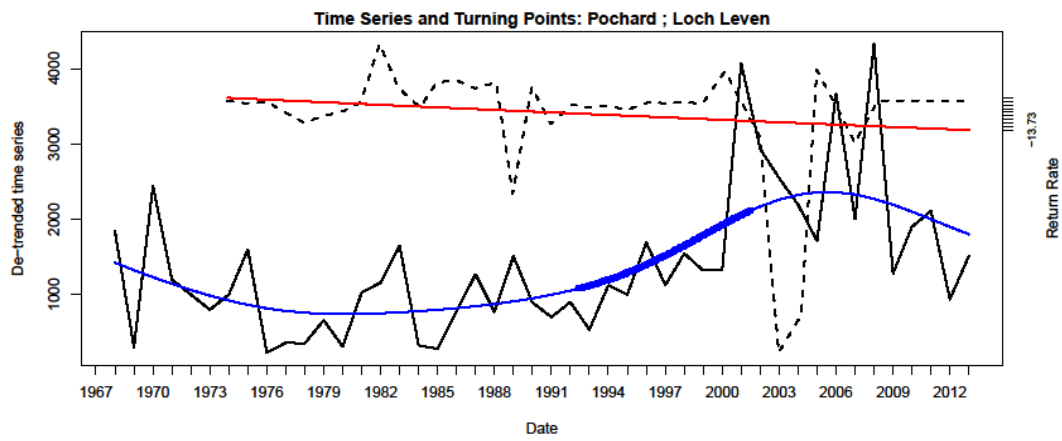
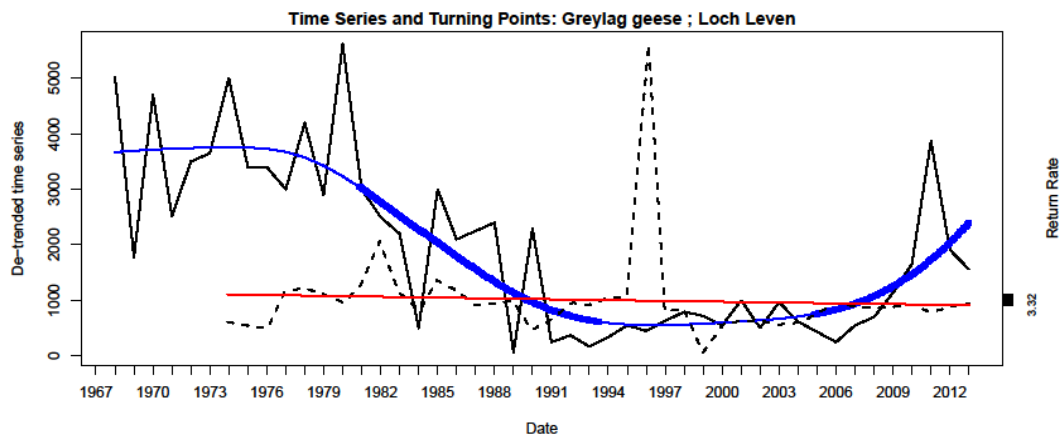


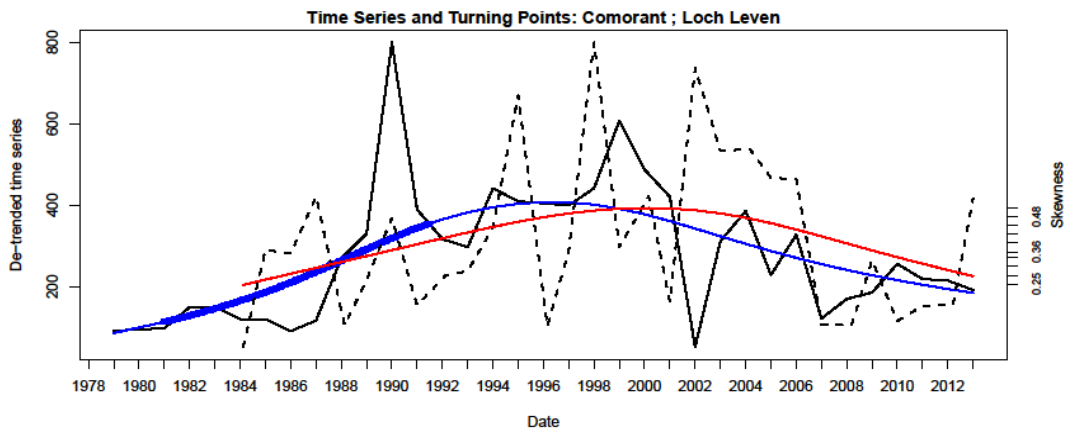
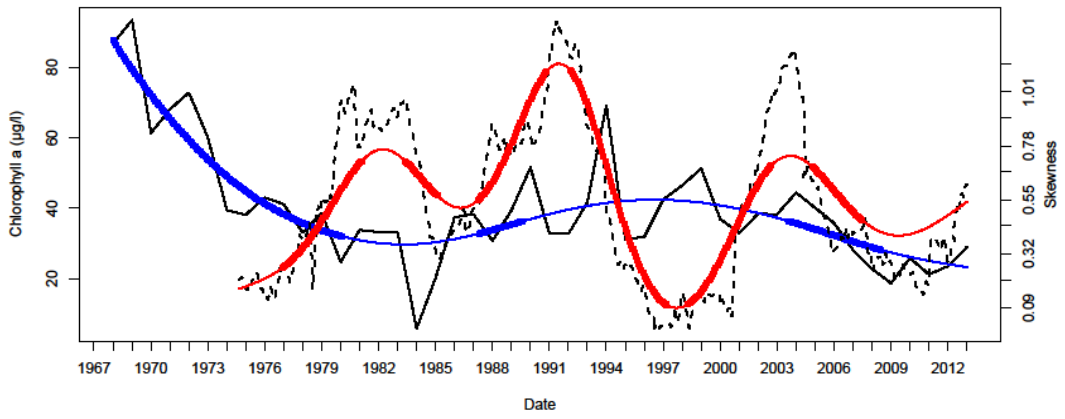
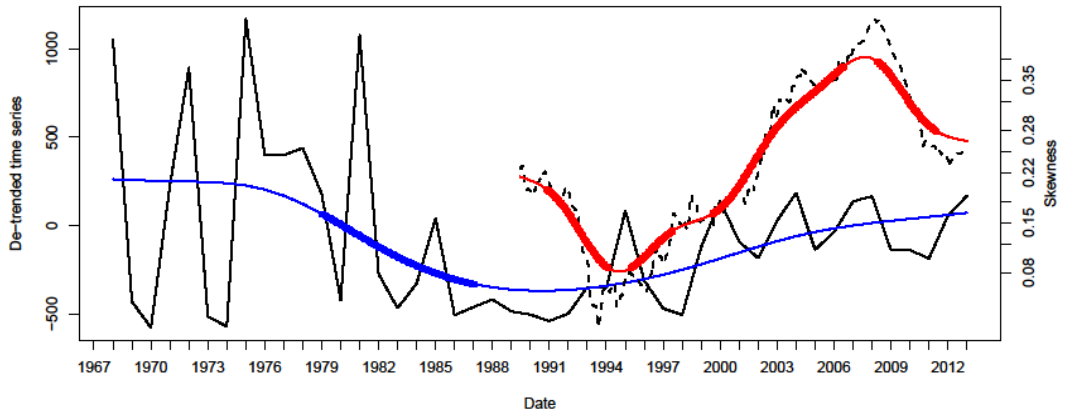


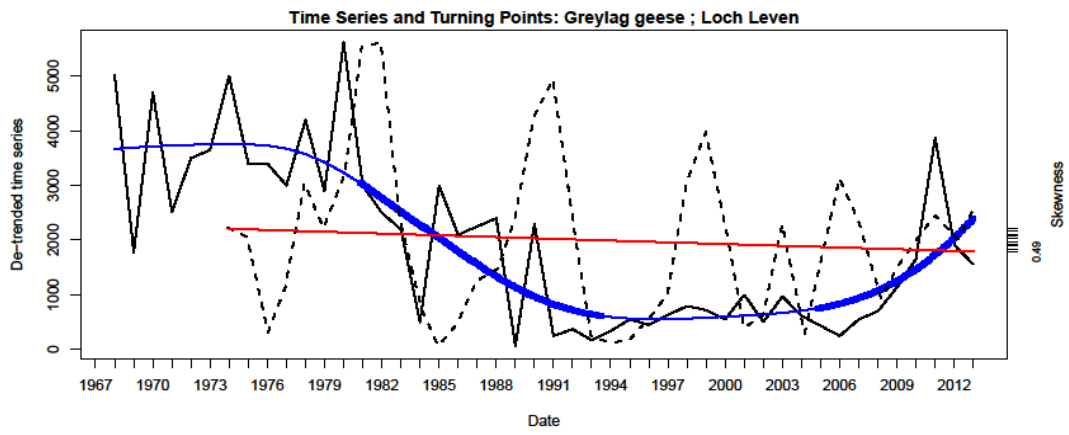
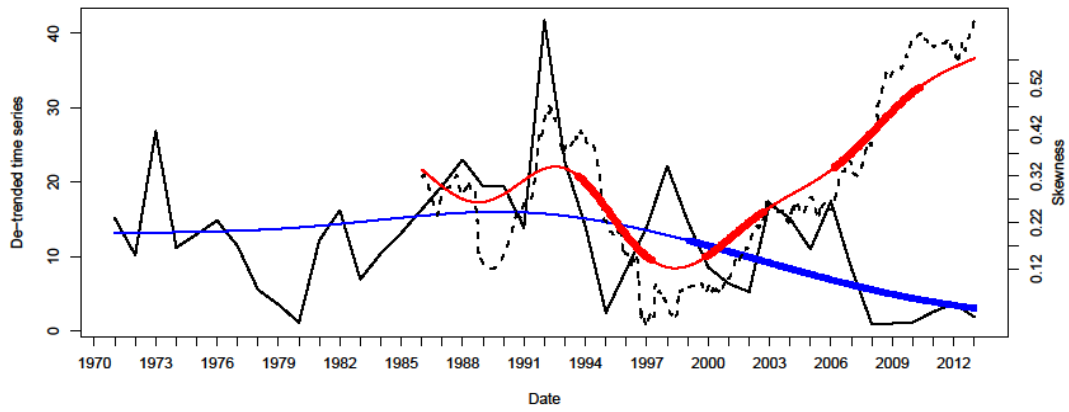
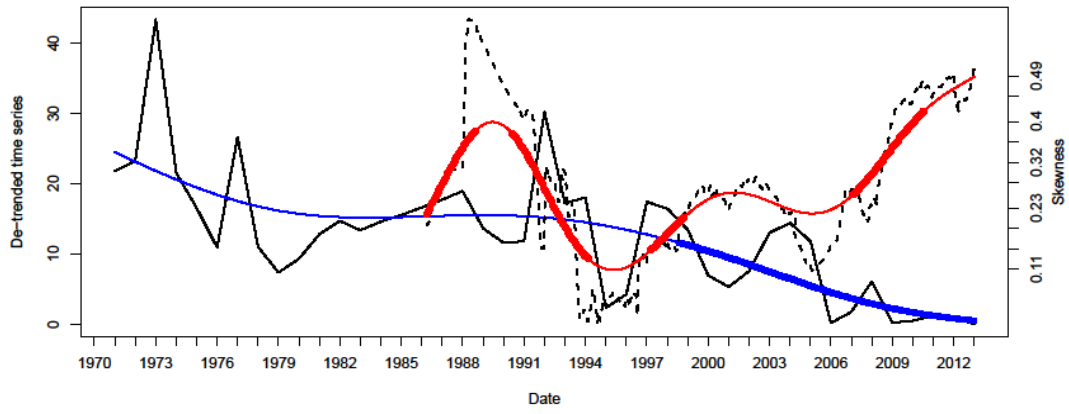




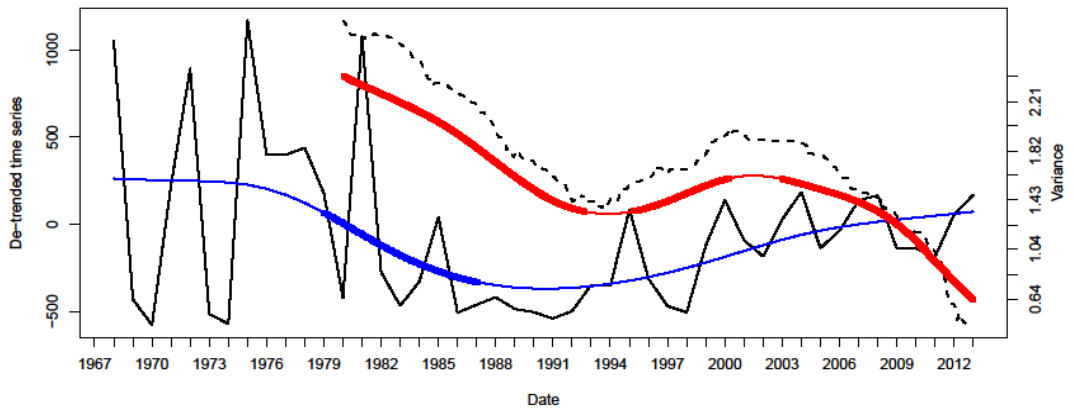
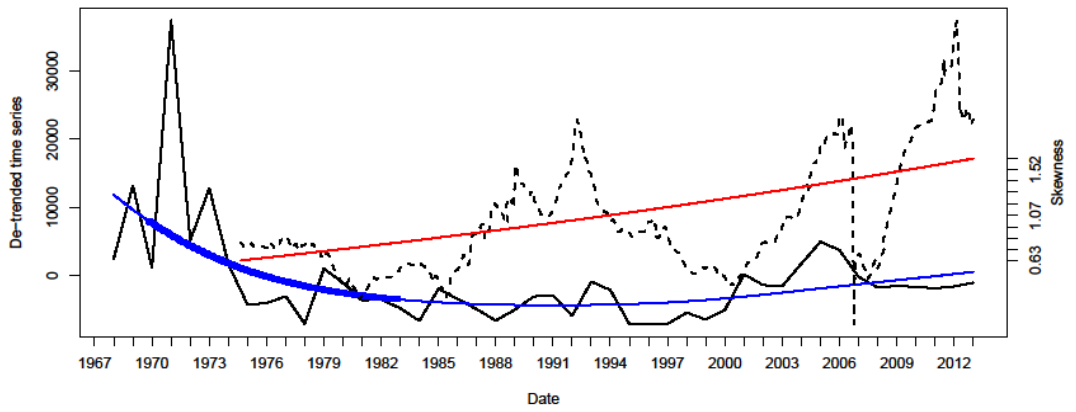
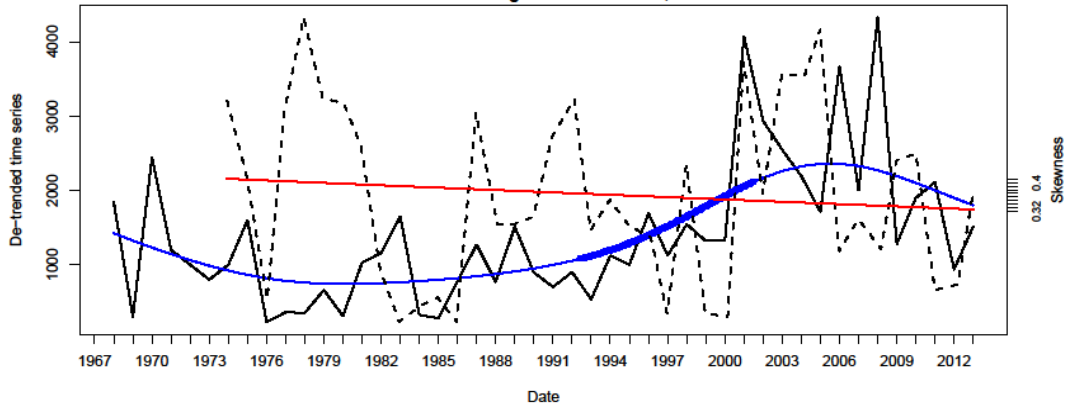


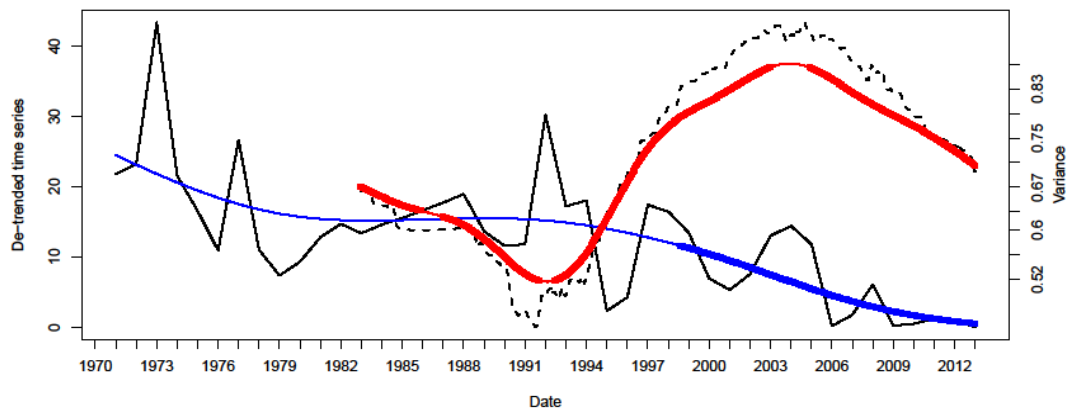
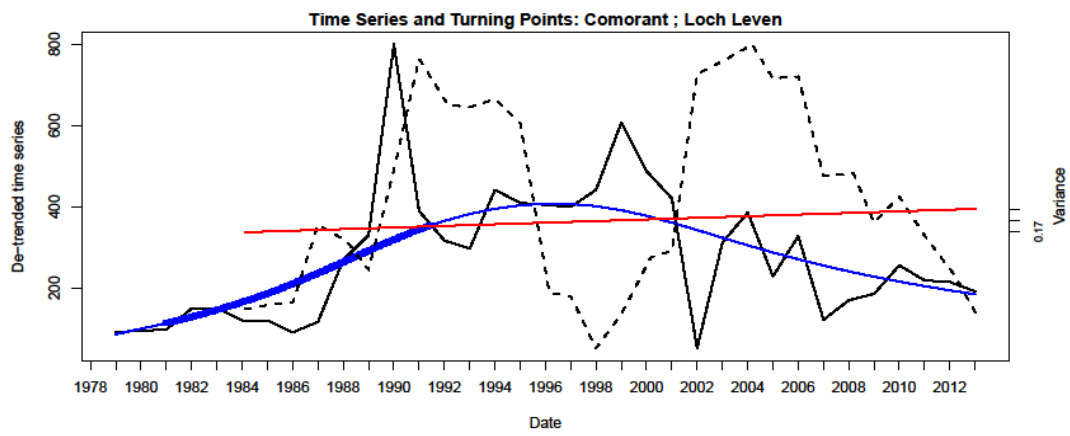
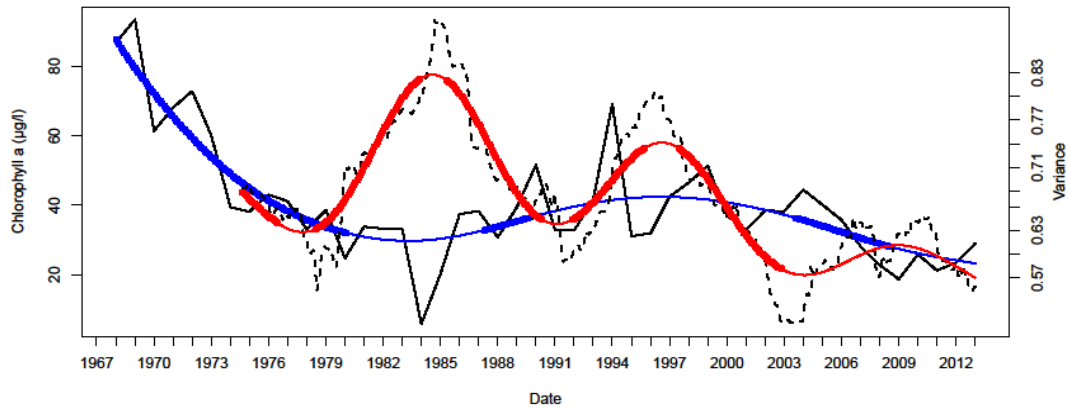


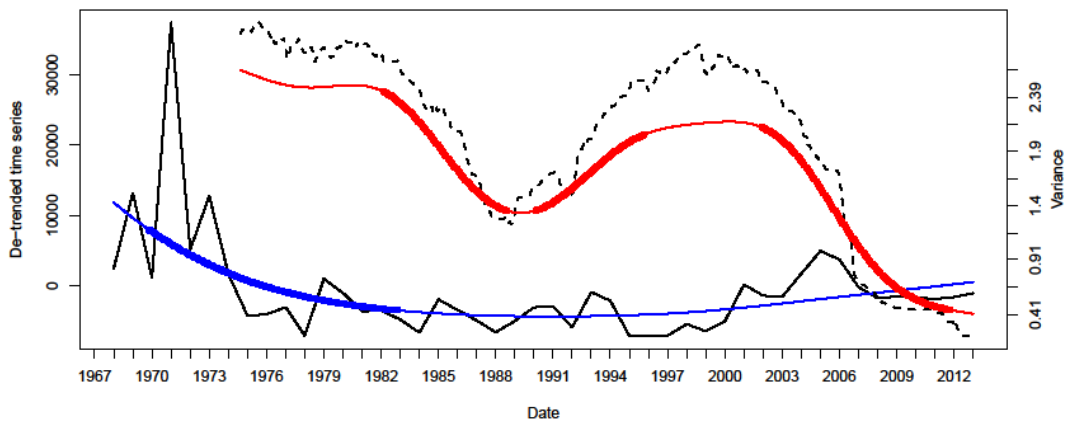
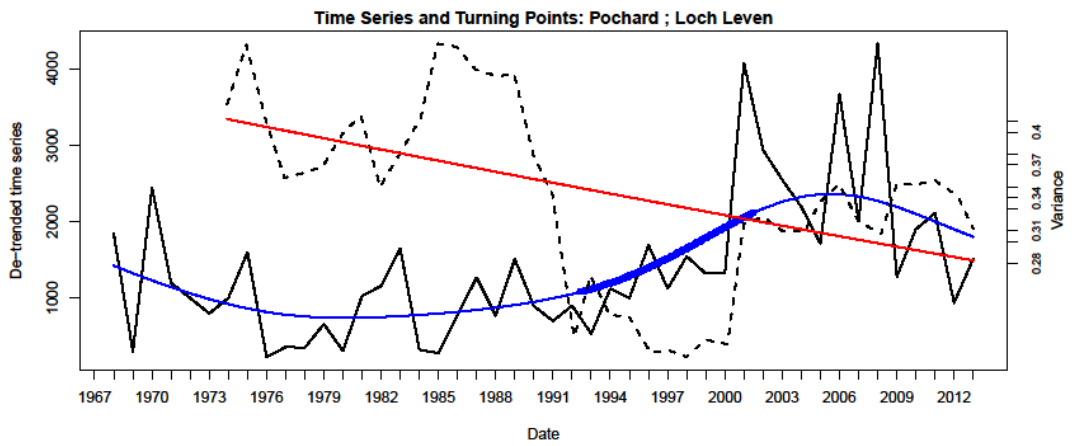
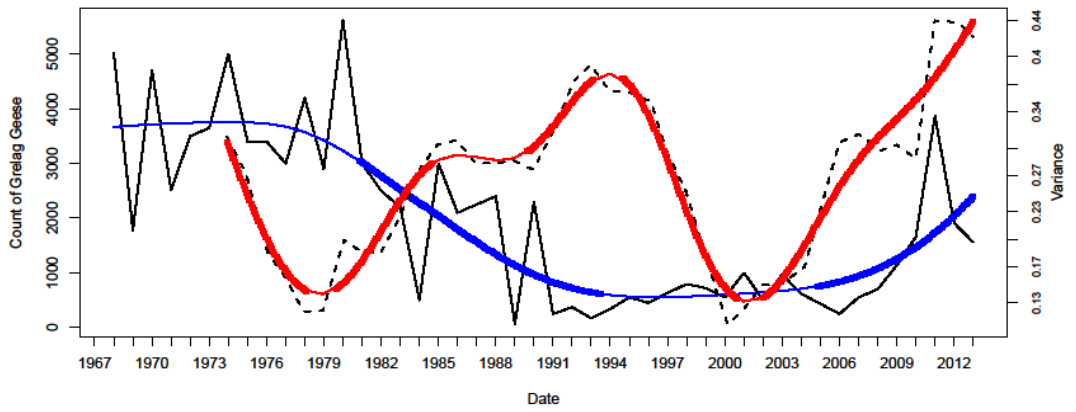
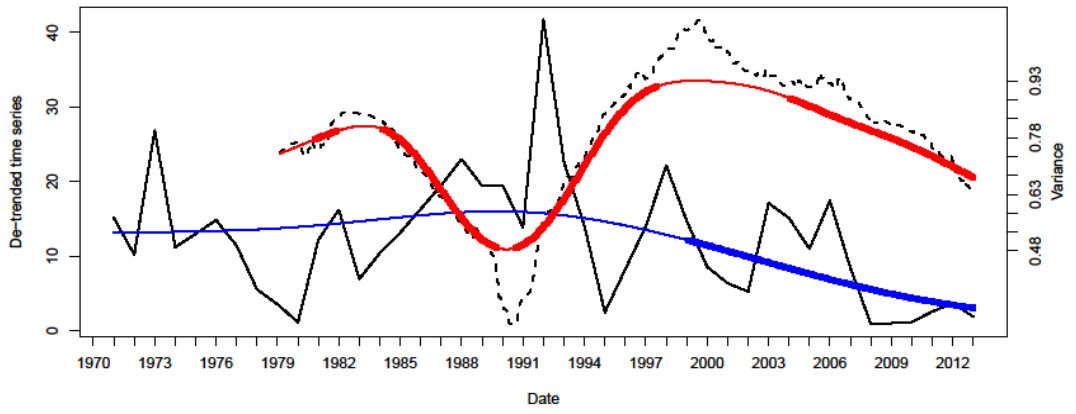


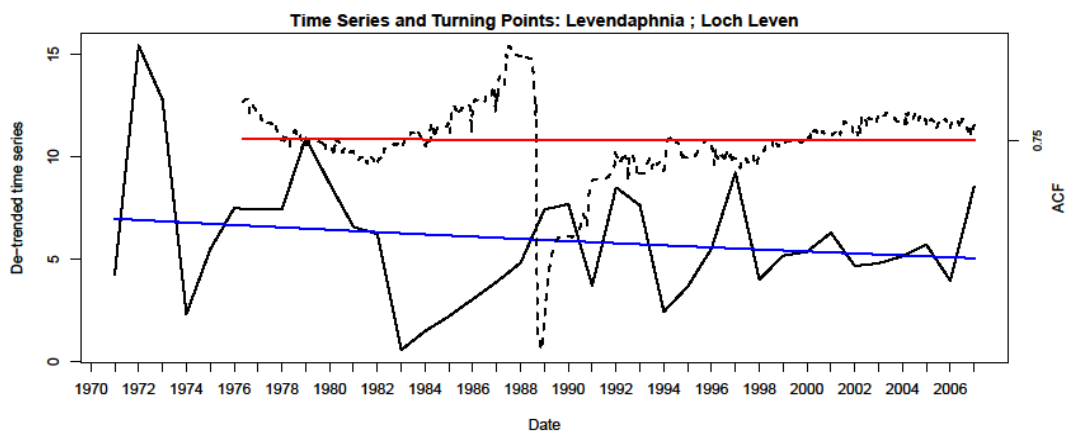
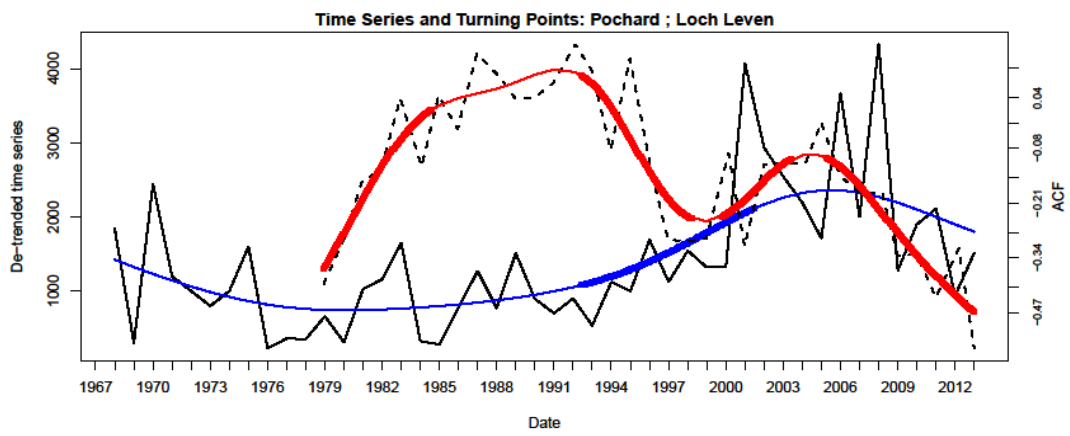
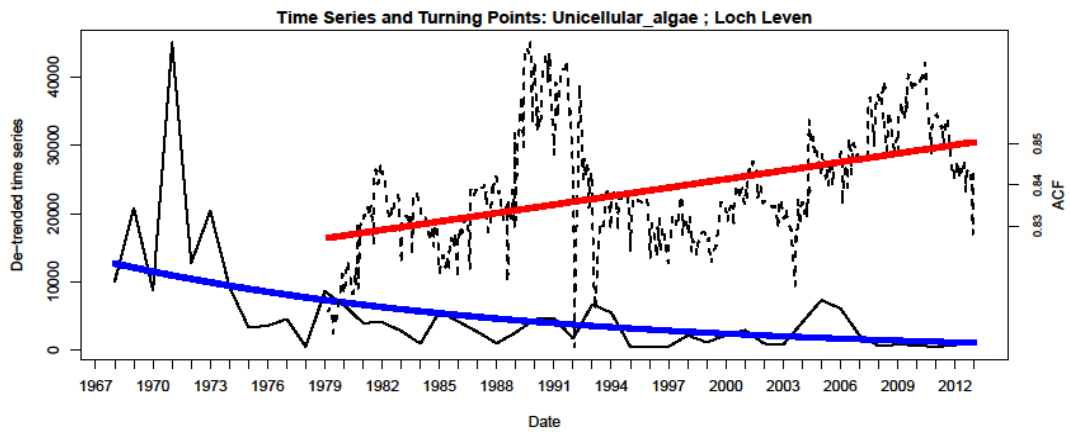


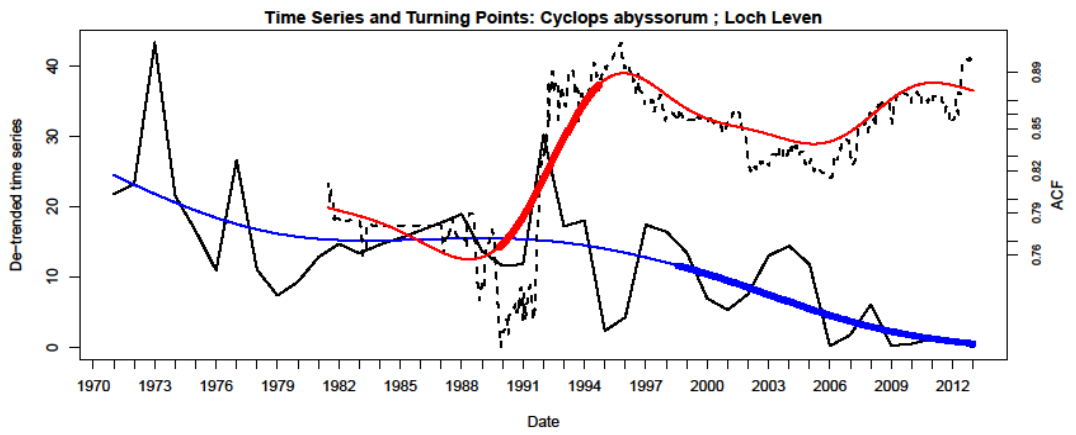
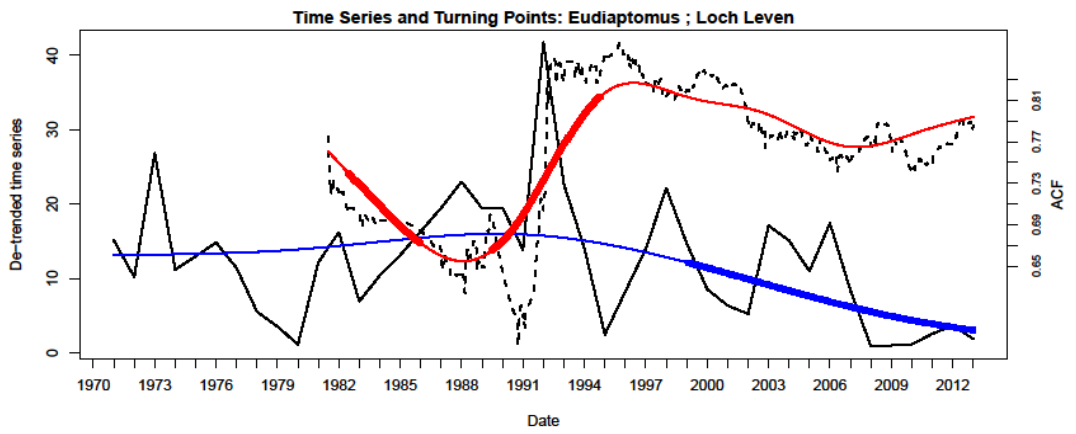
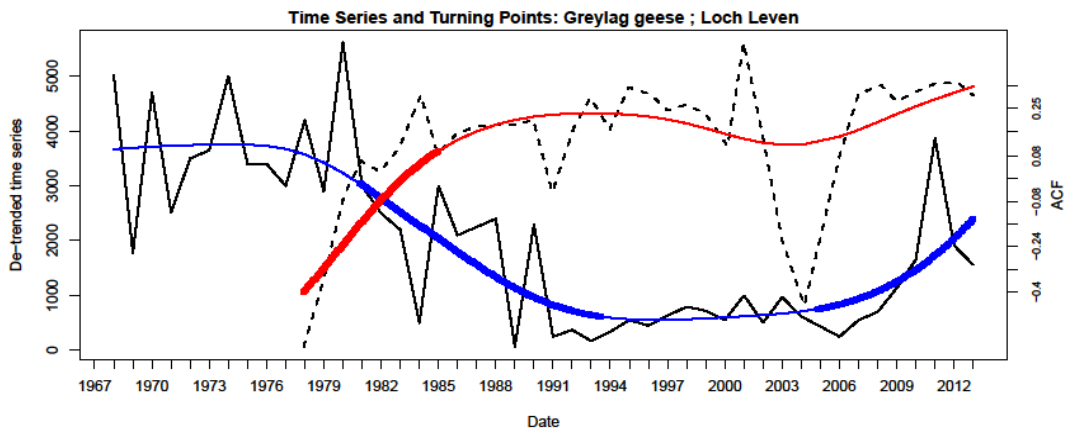
Time Series and Turning Points: Pochard ; Loch Leven

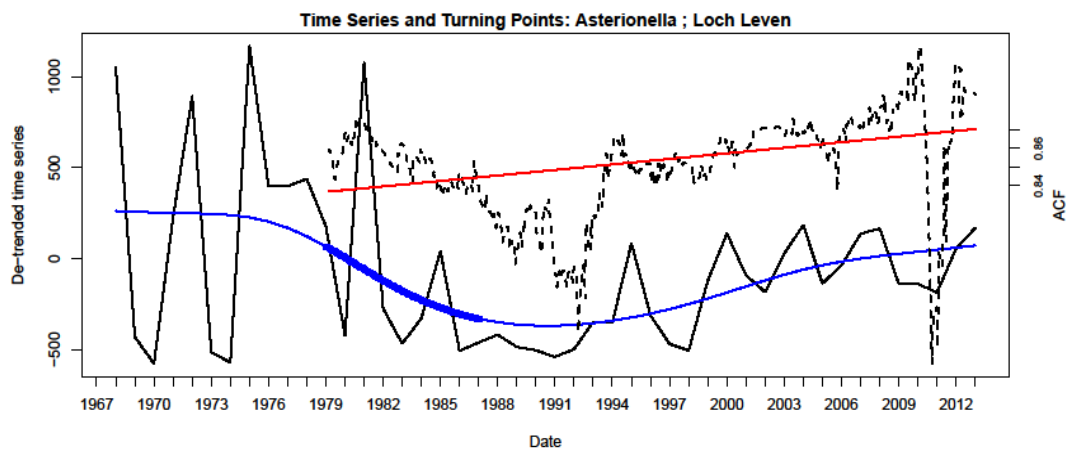
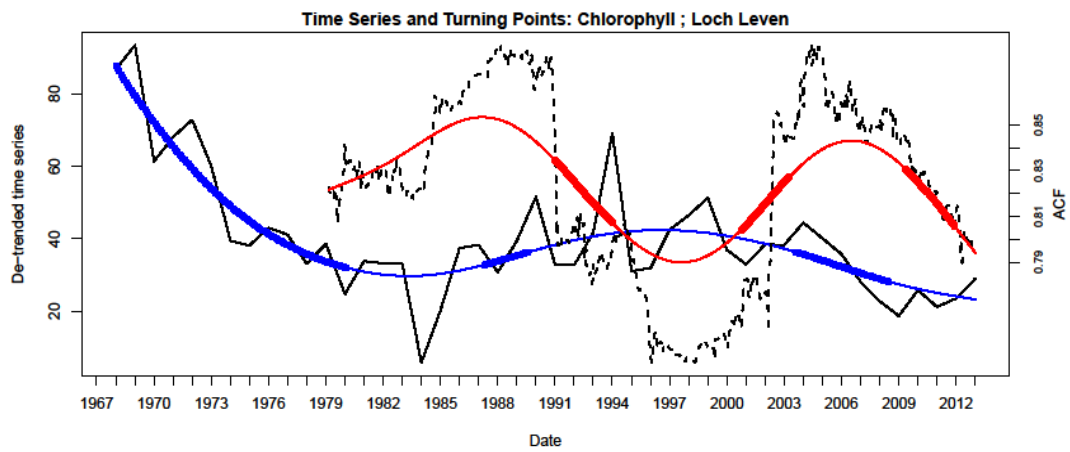
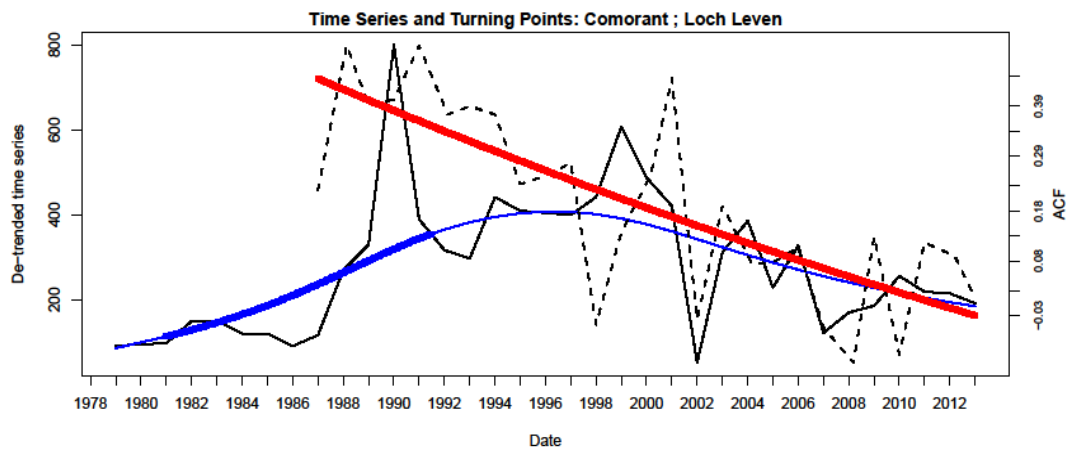


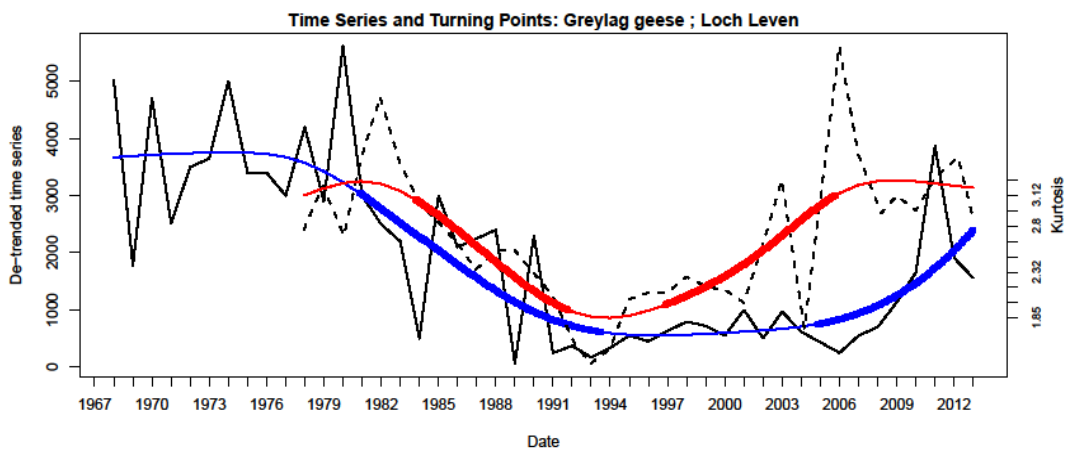
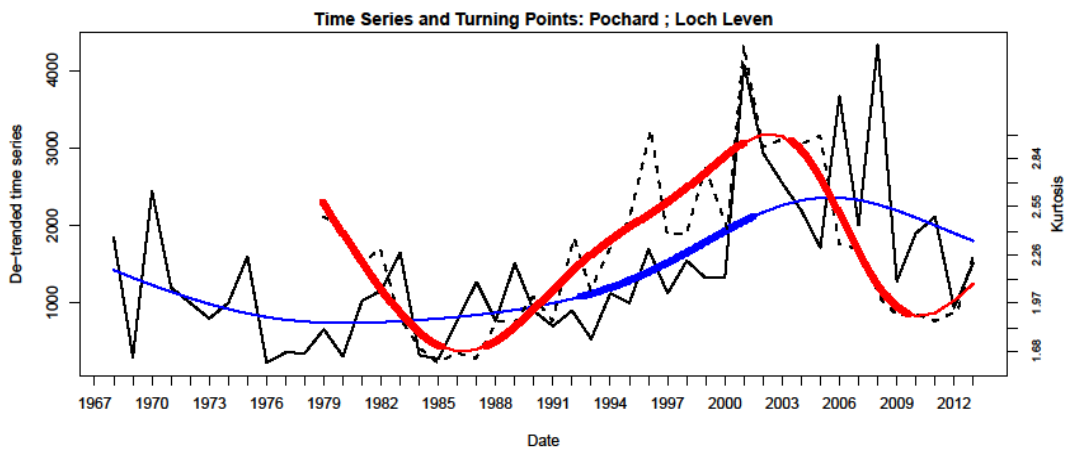
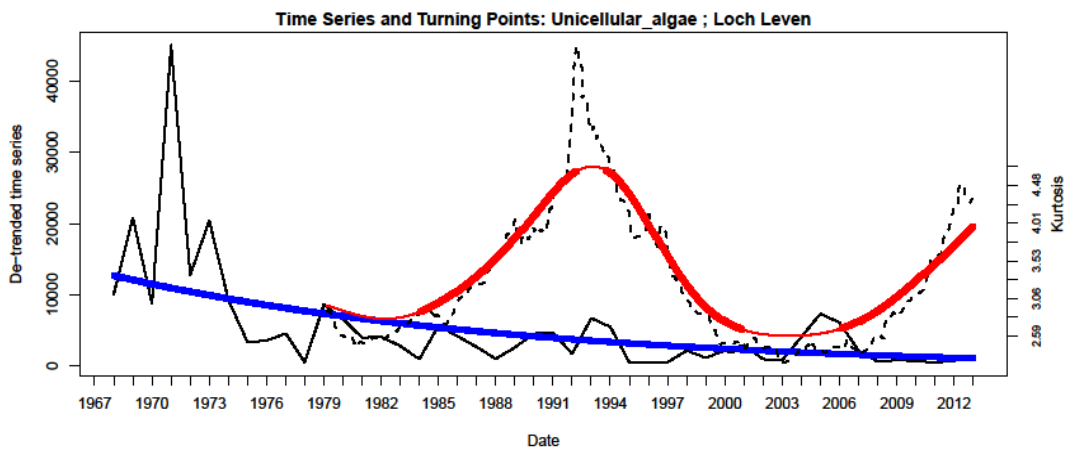


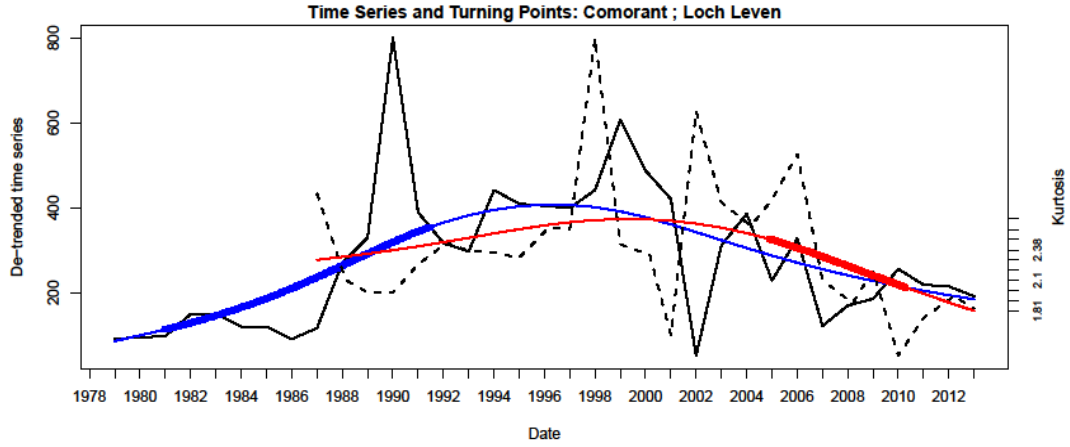
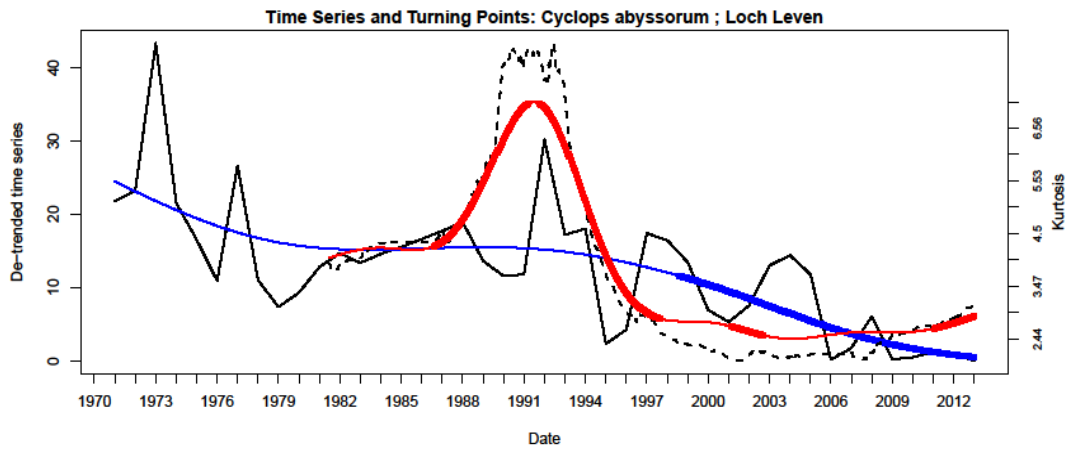
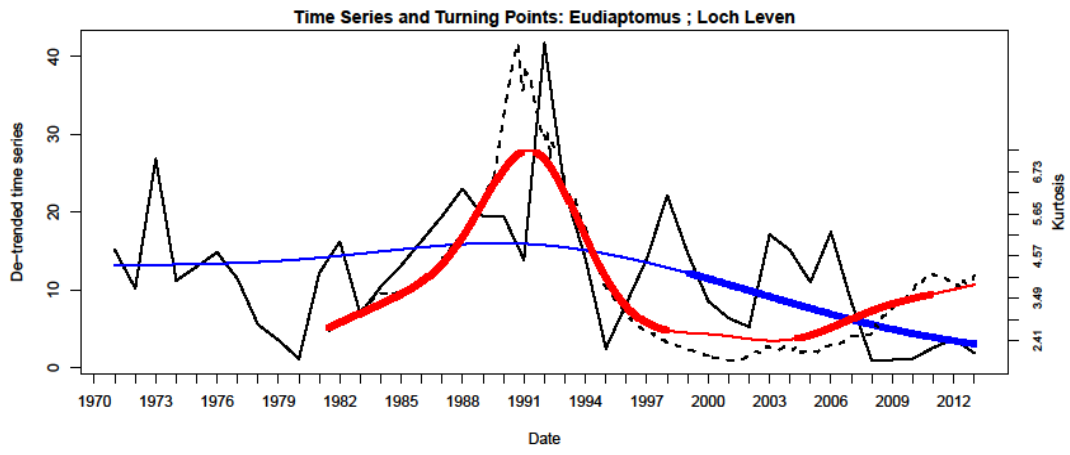


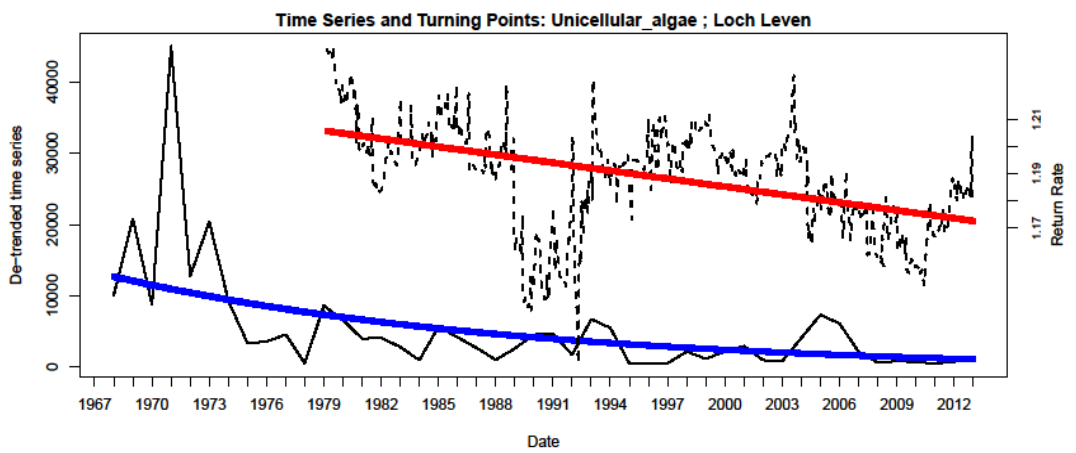
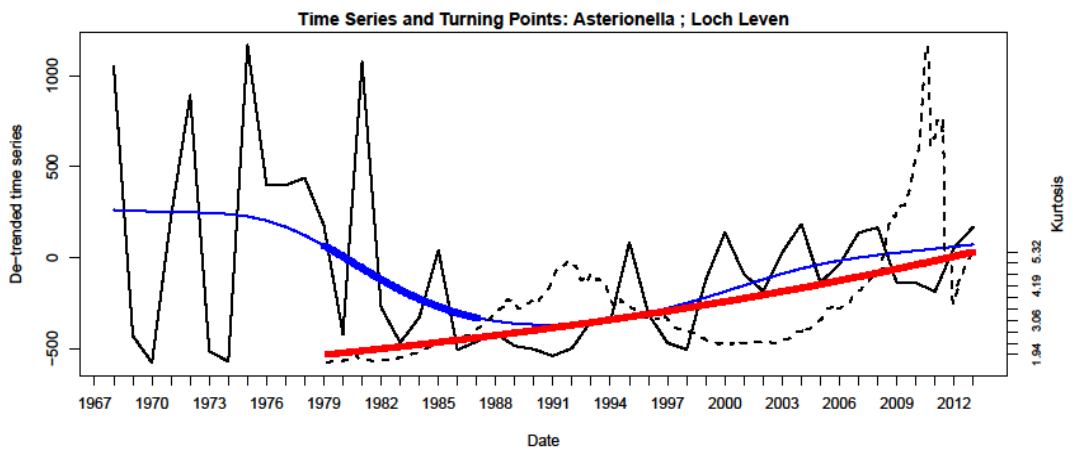
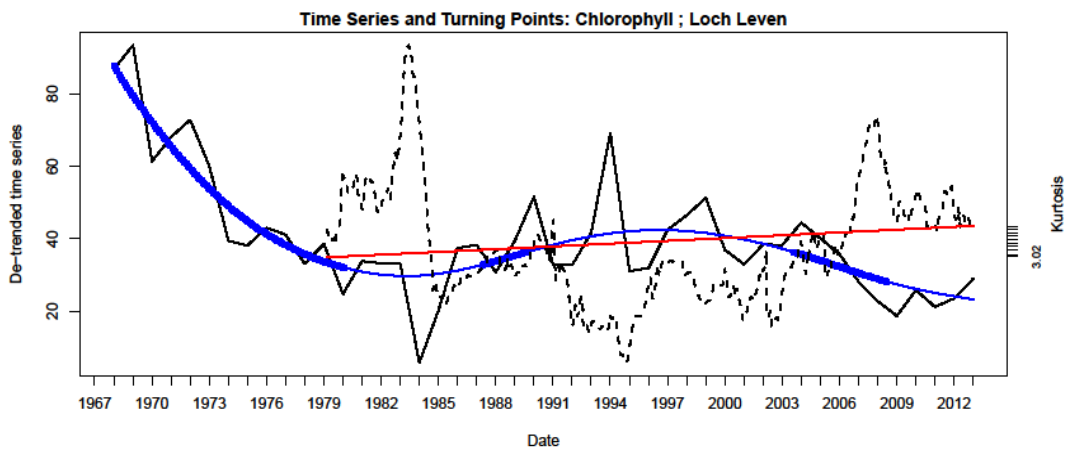


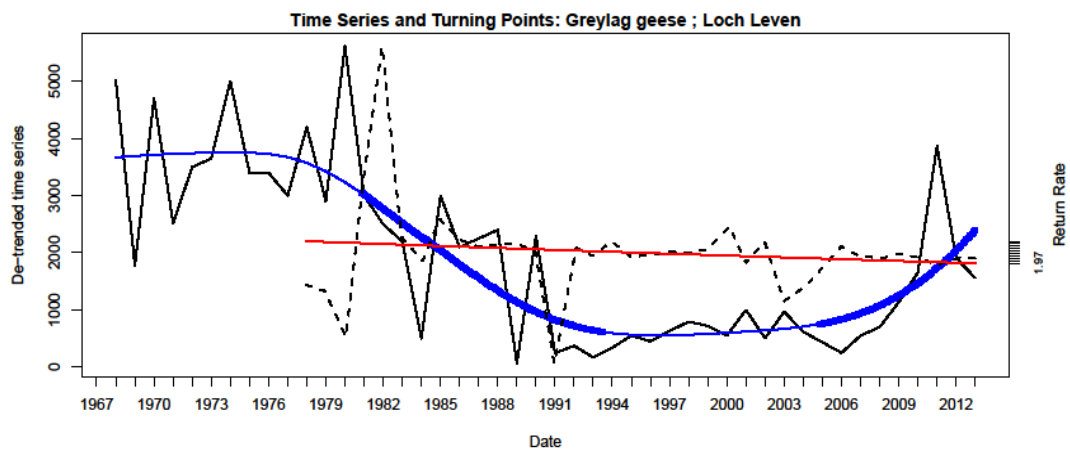
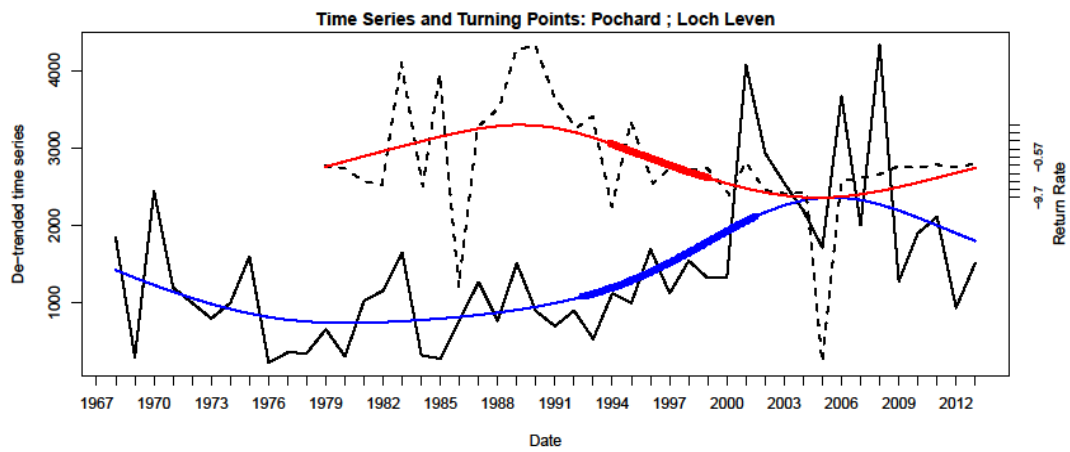
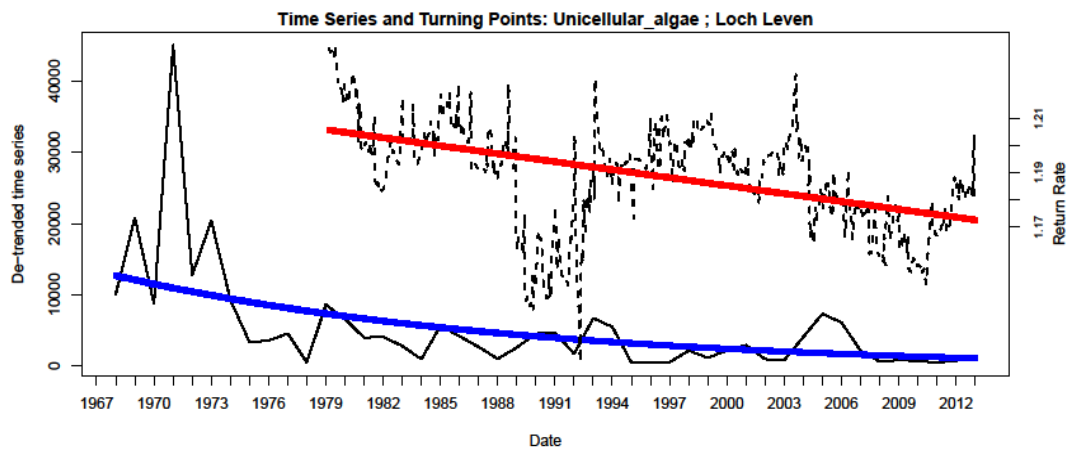


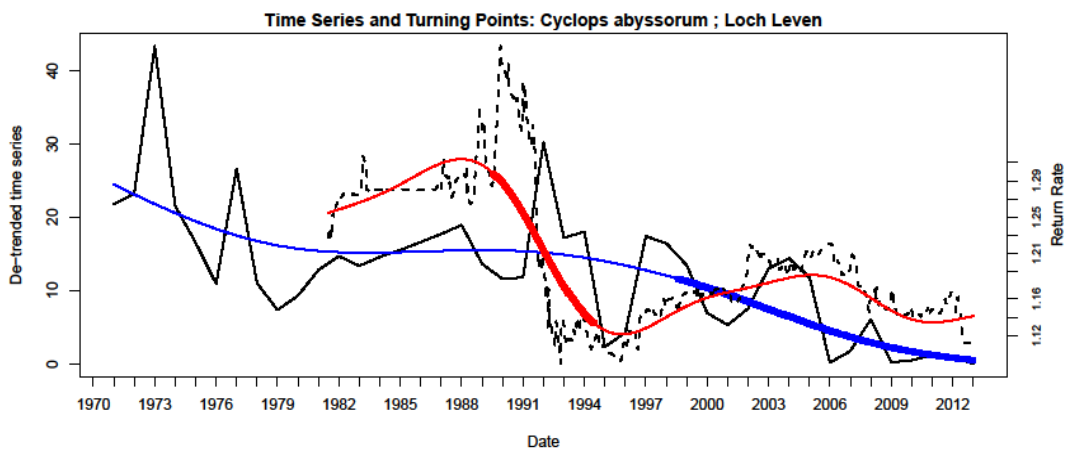
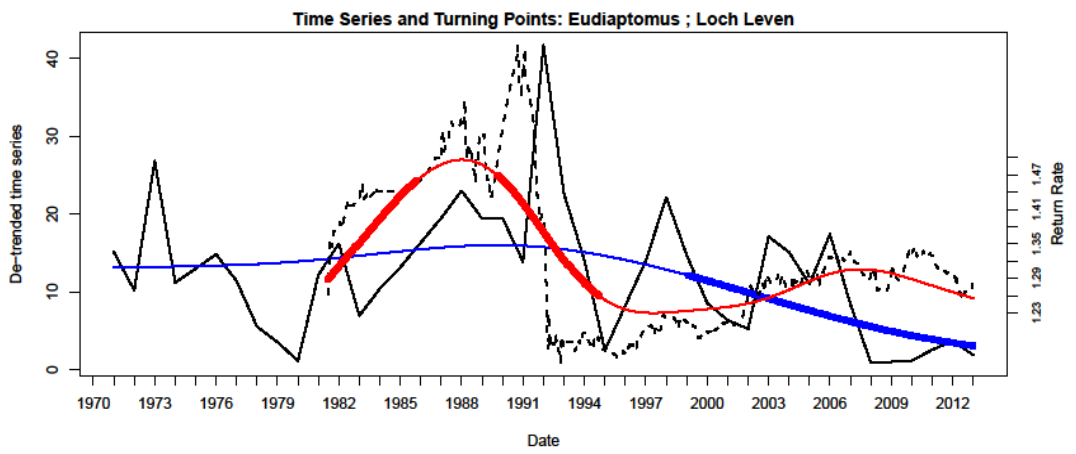
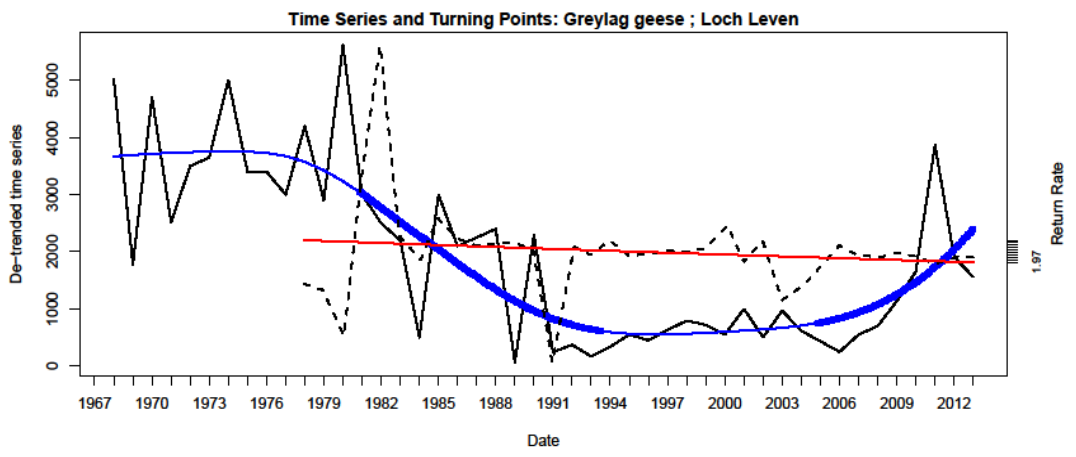


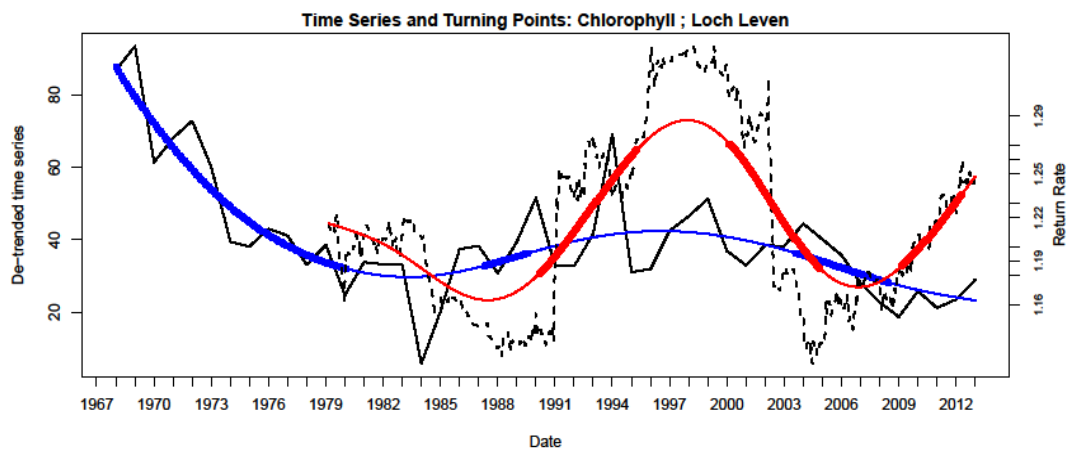
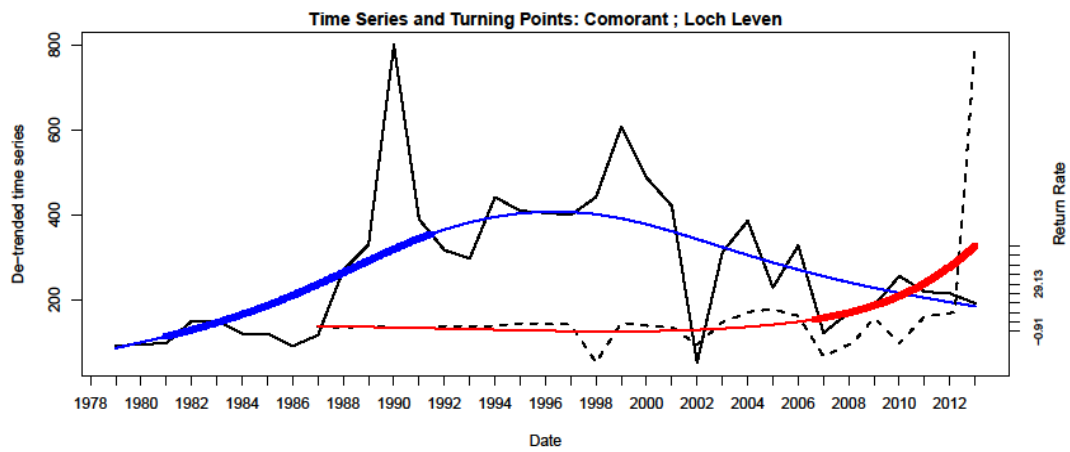
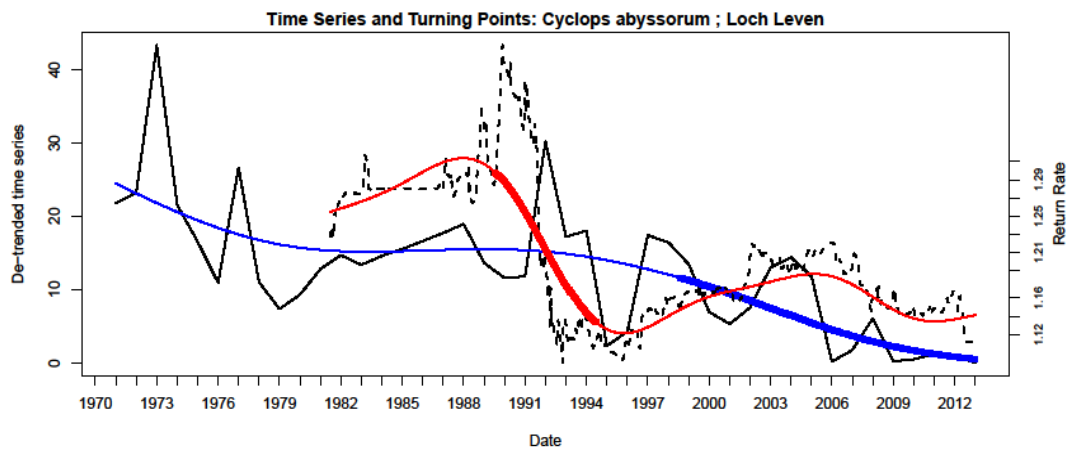


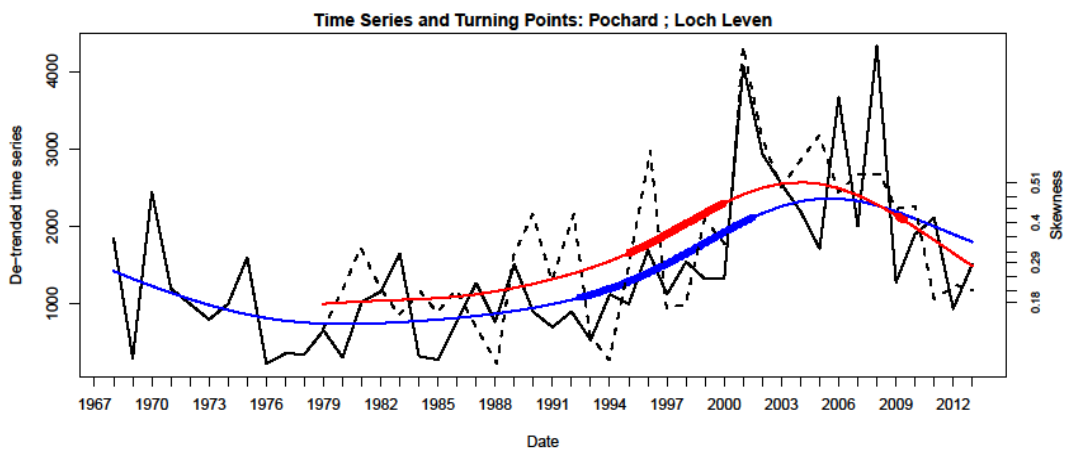
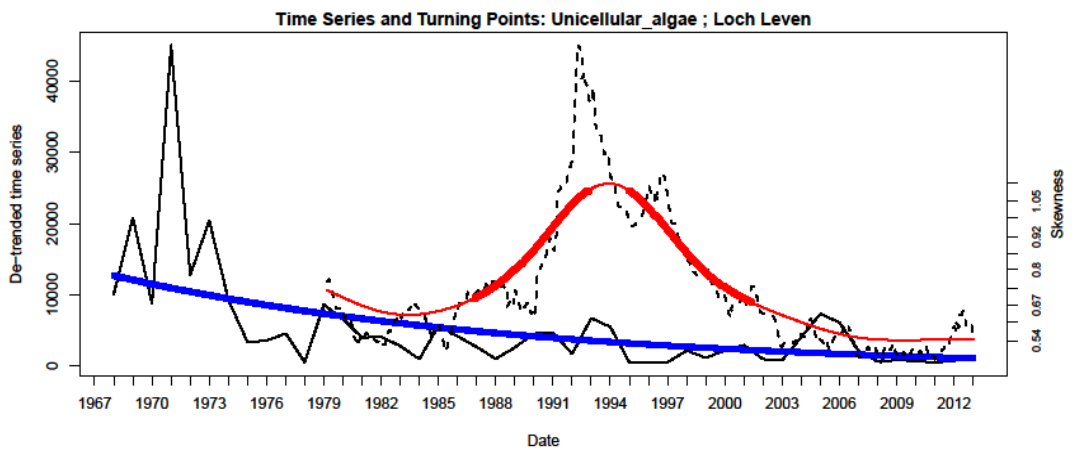
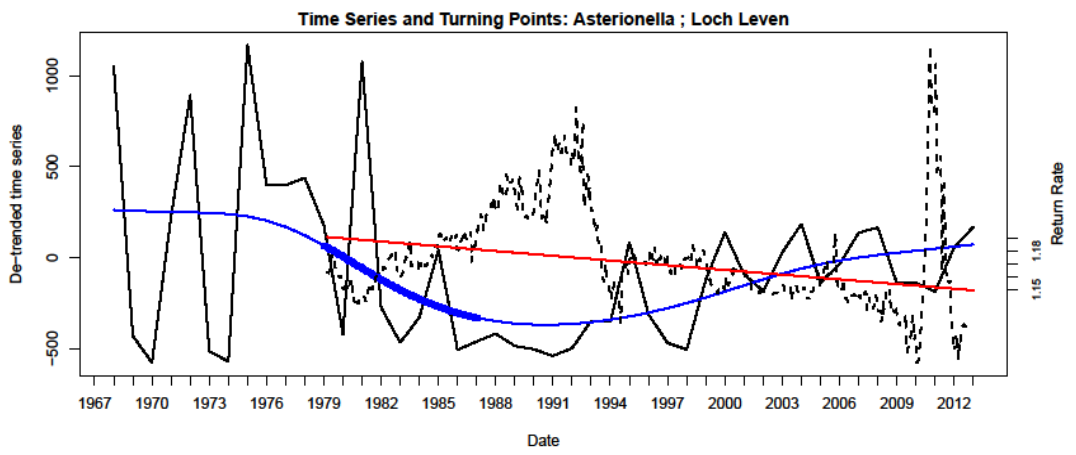


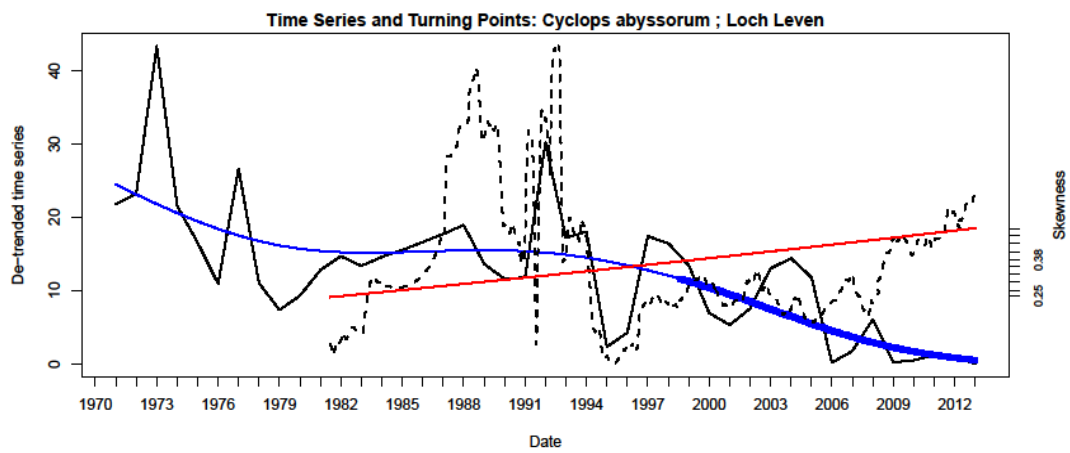
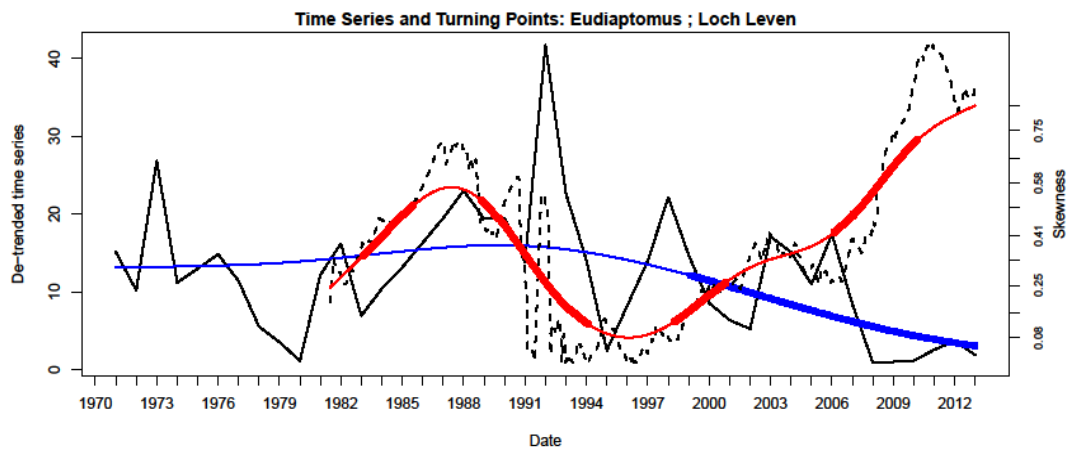
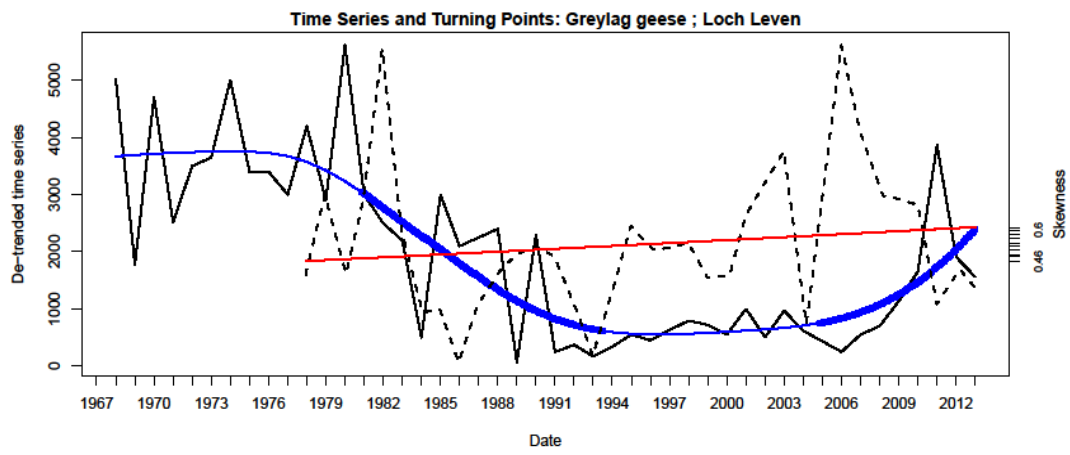


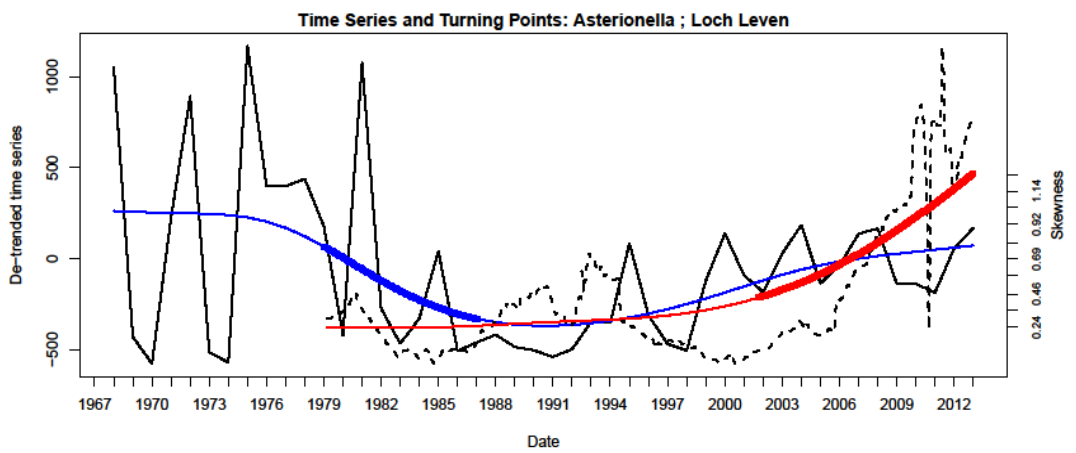
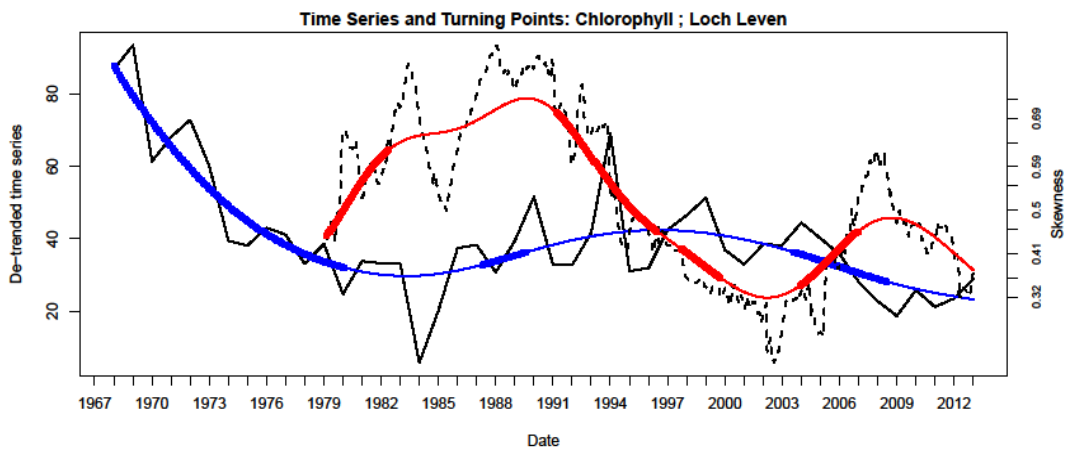
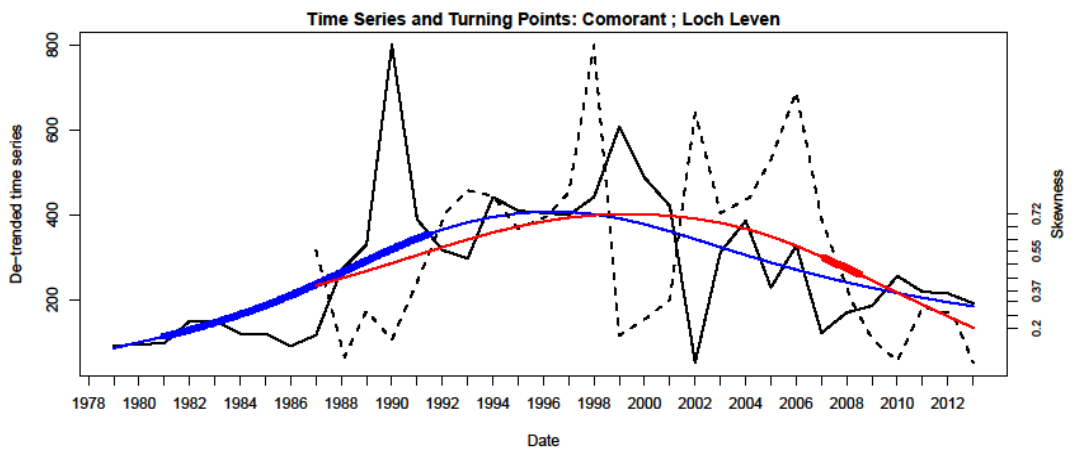


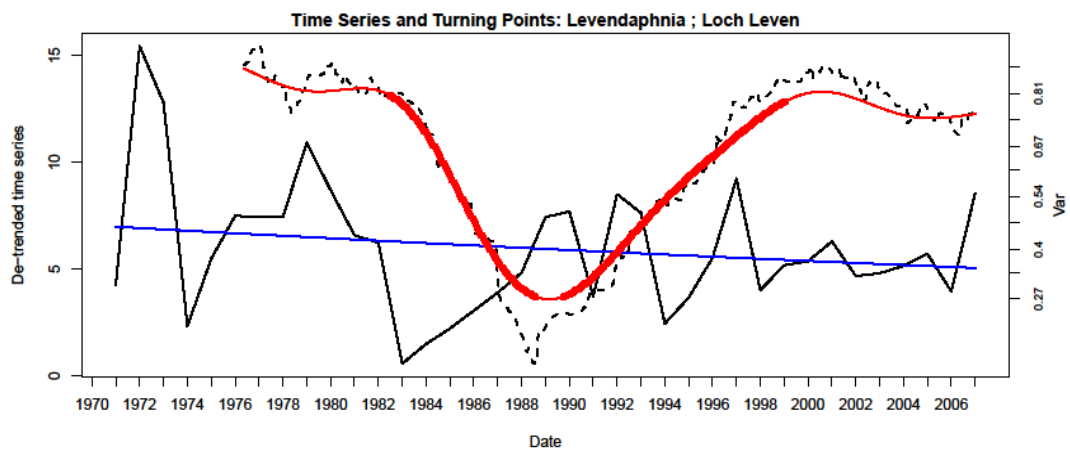
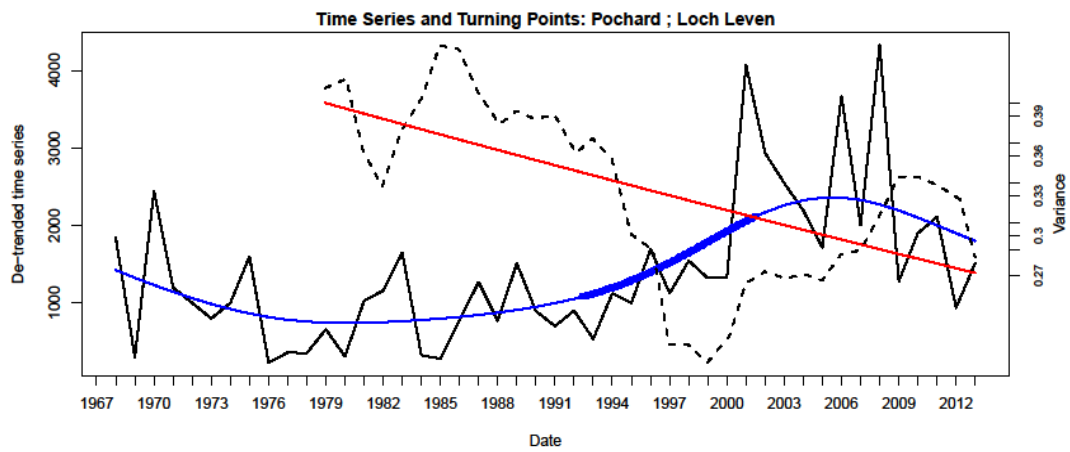
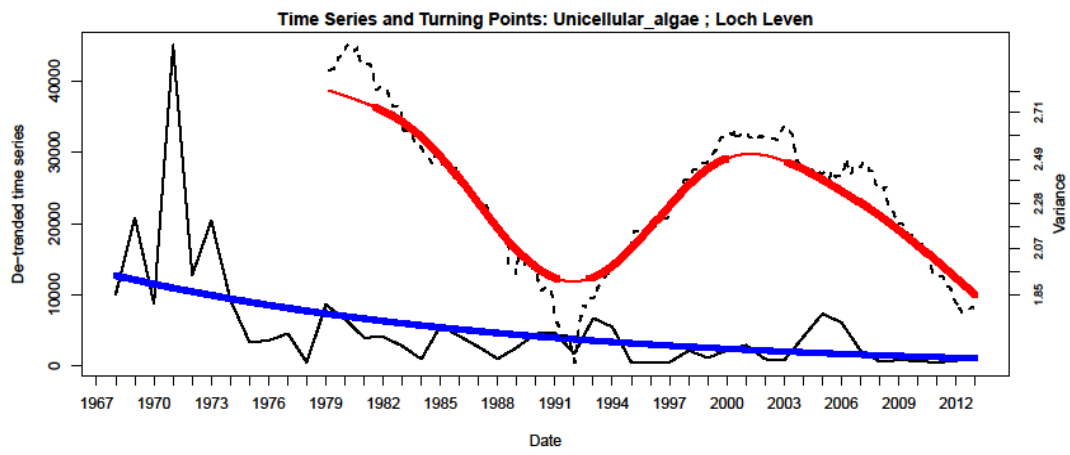


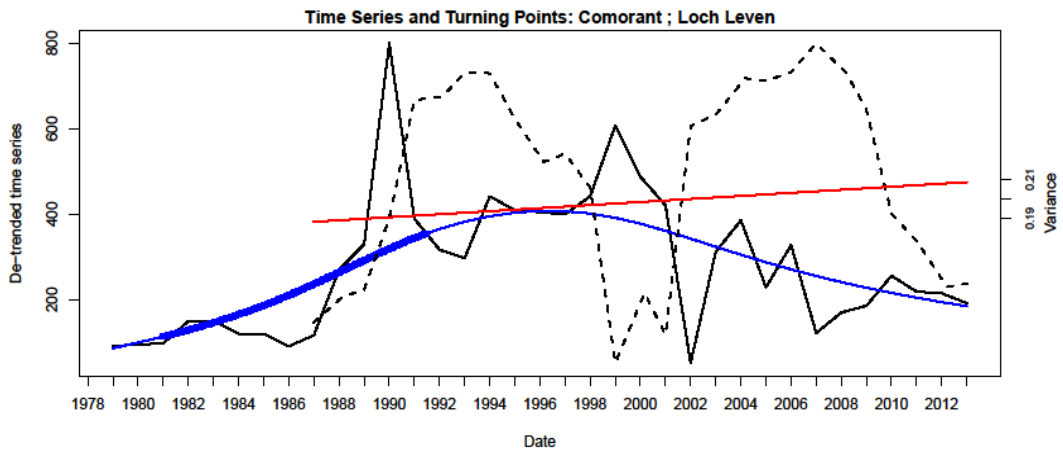
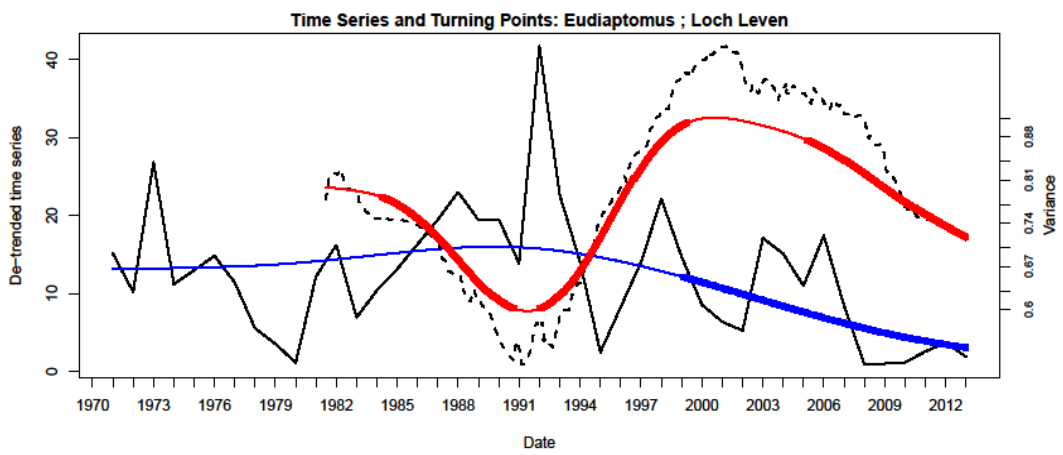
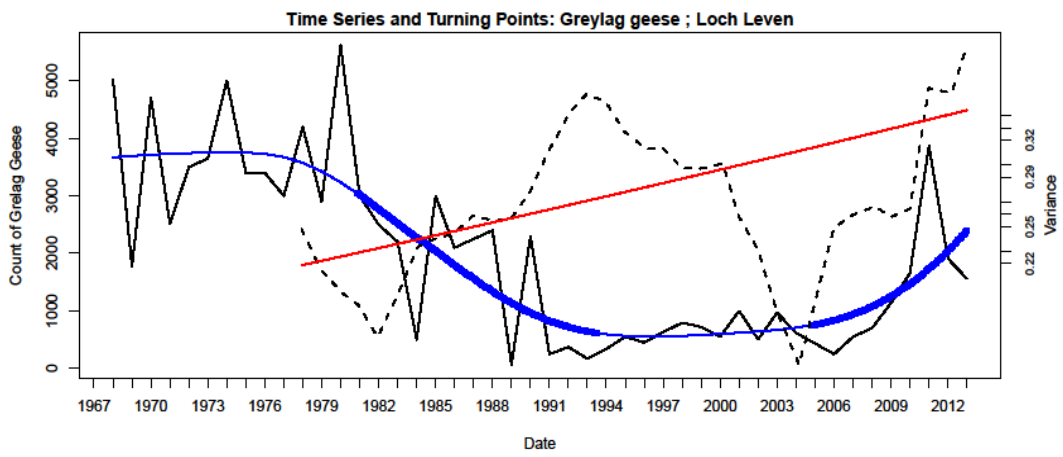


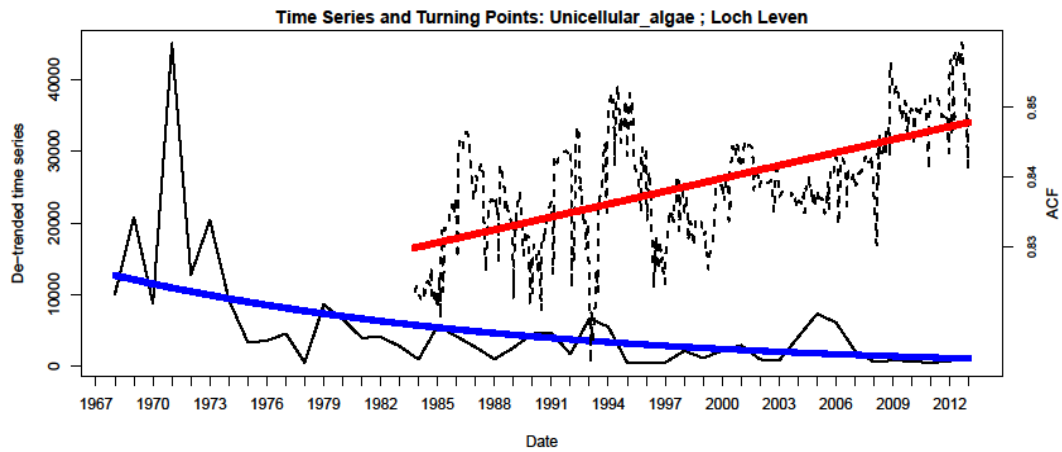
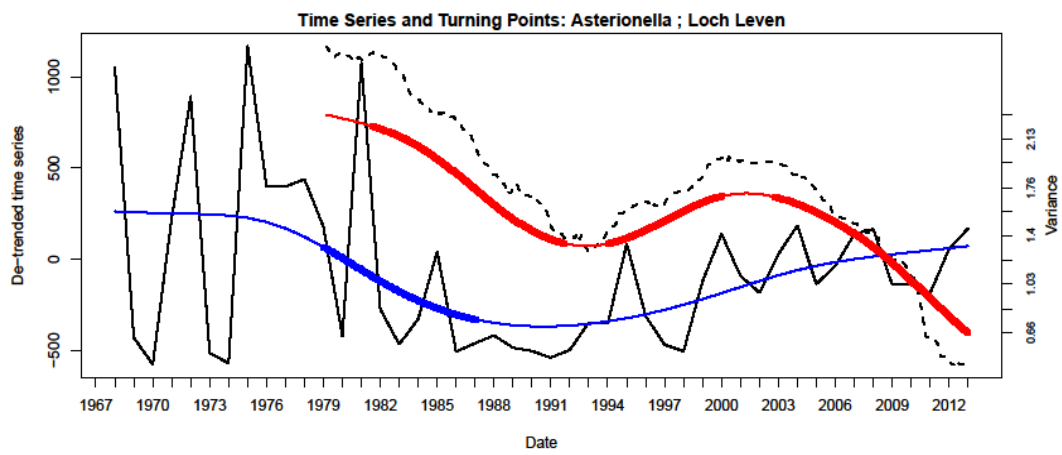
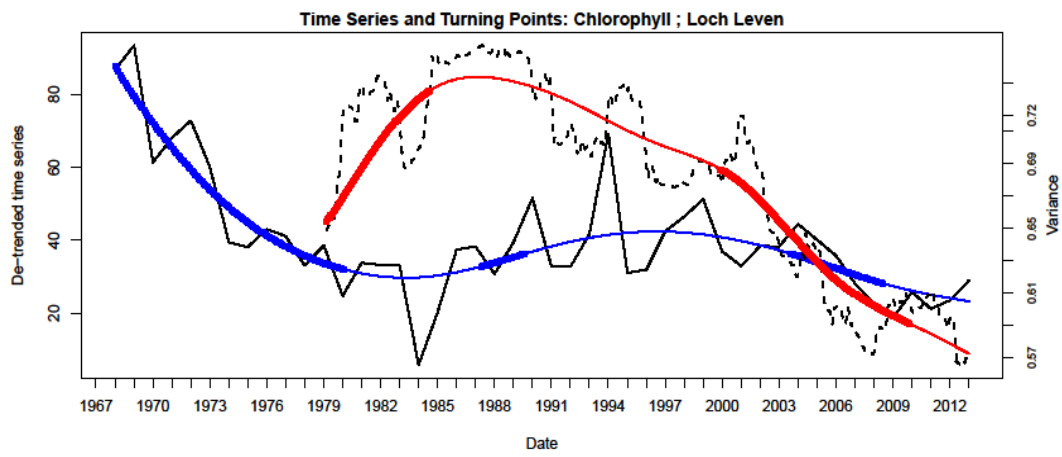


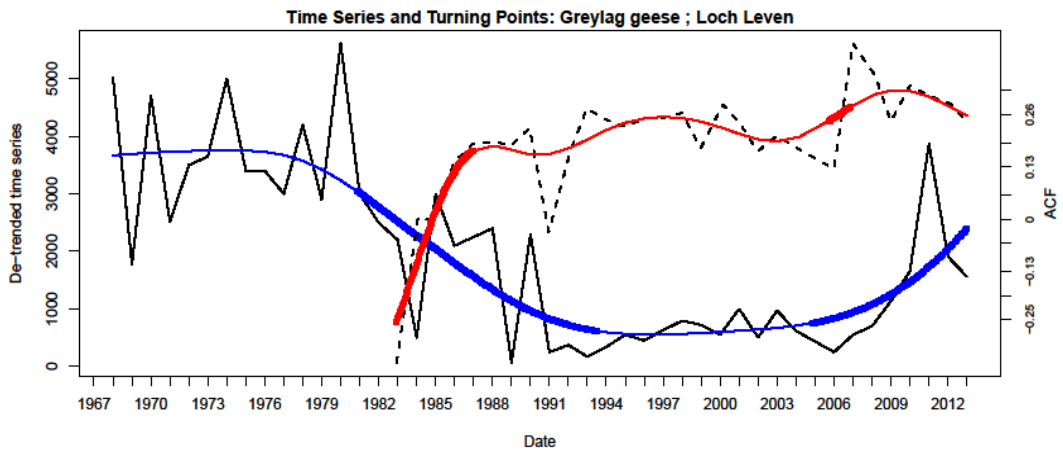
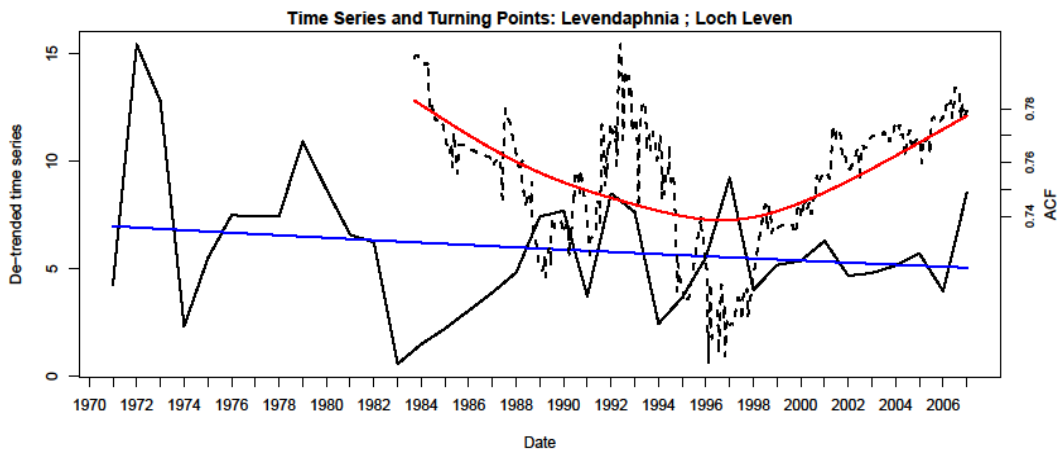
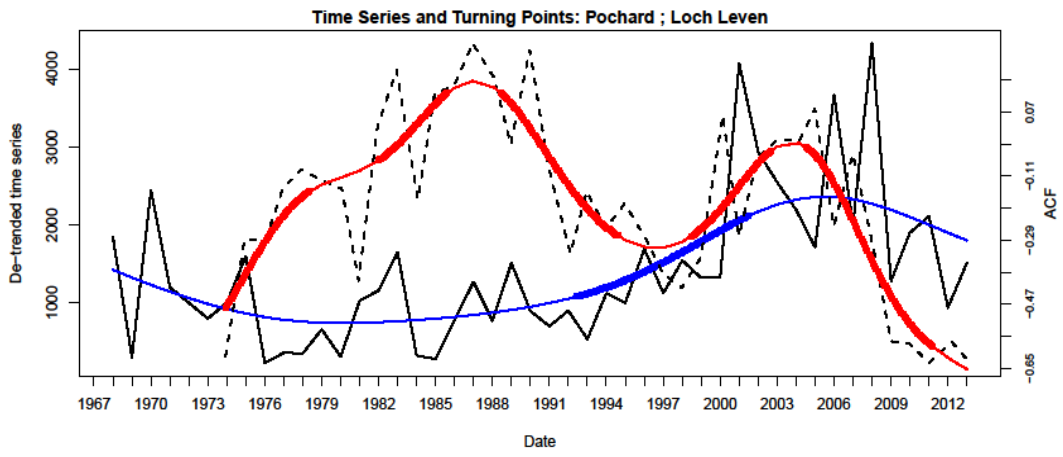


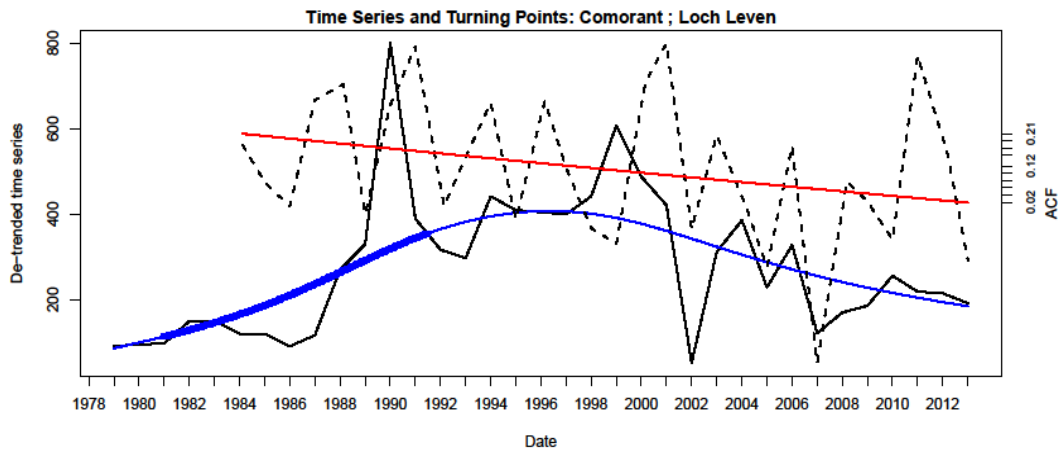
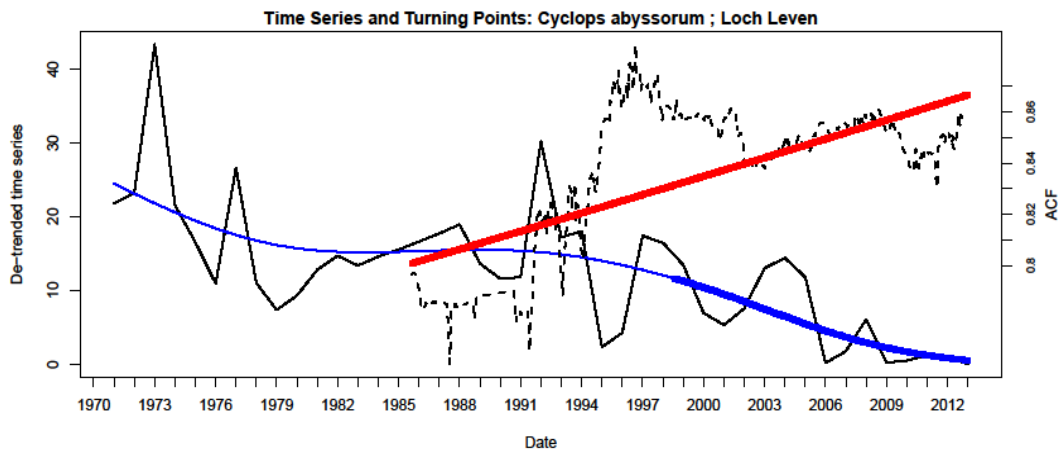
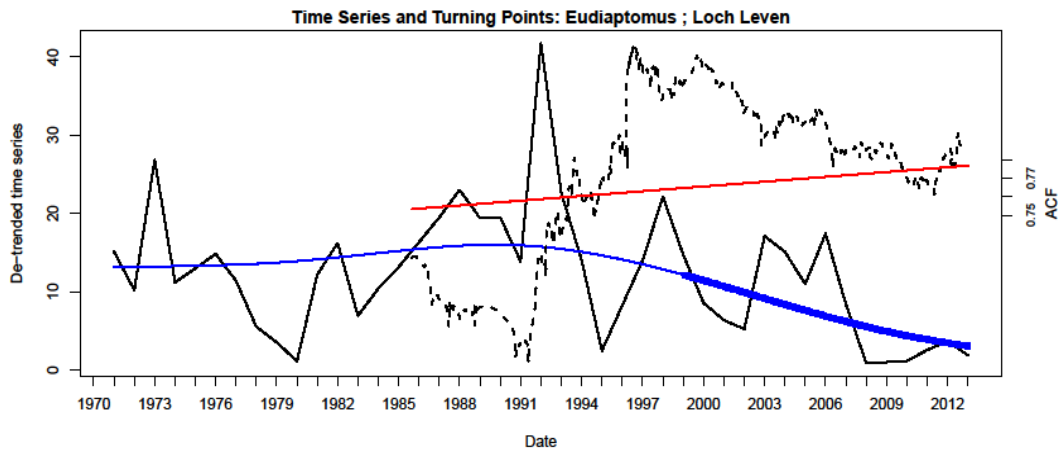


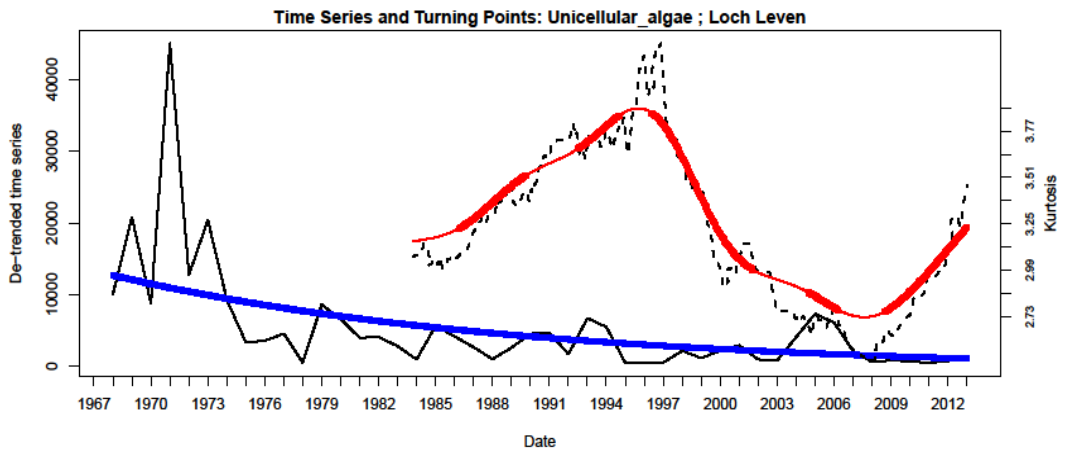
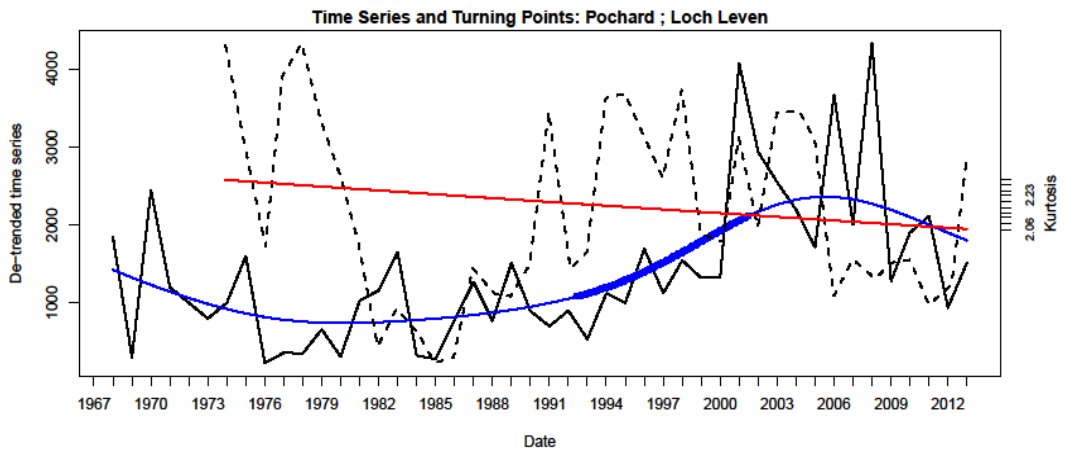


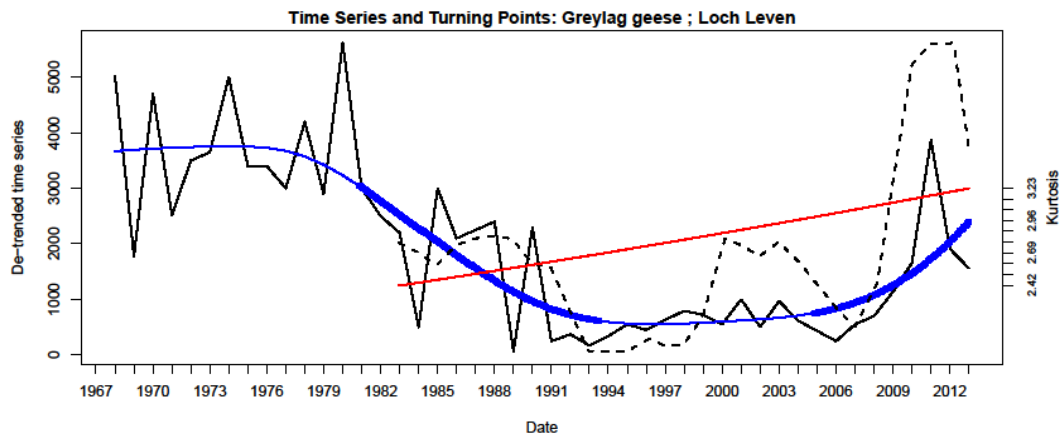
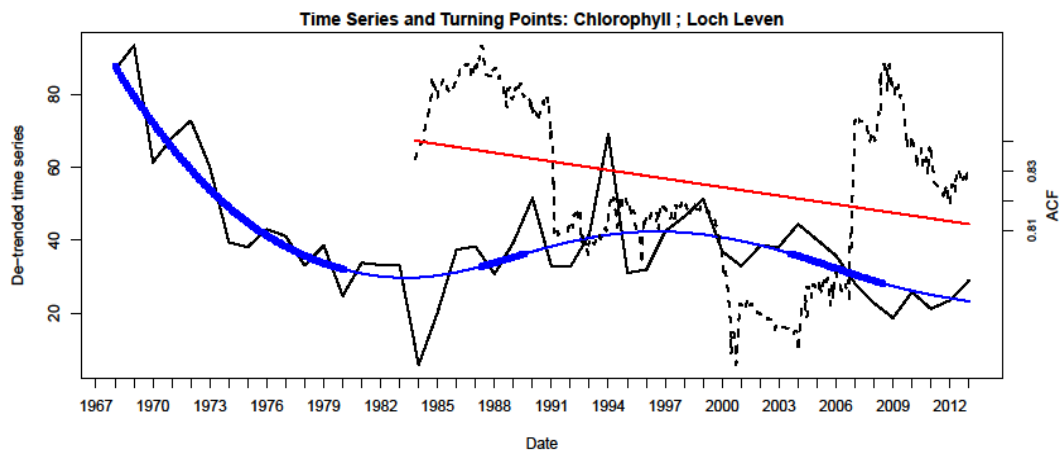
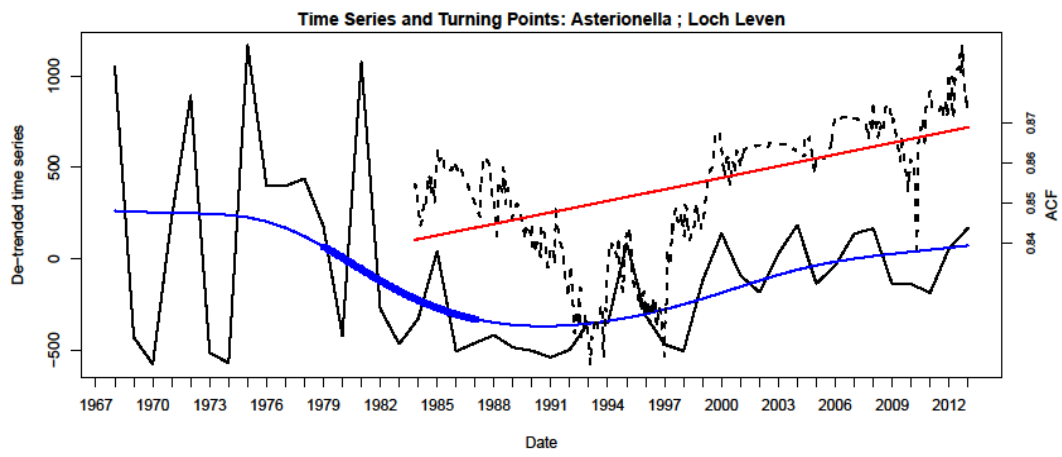


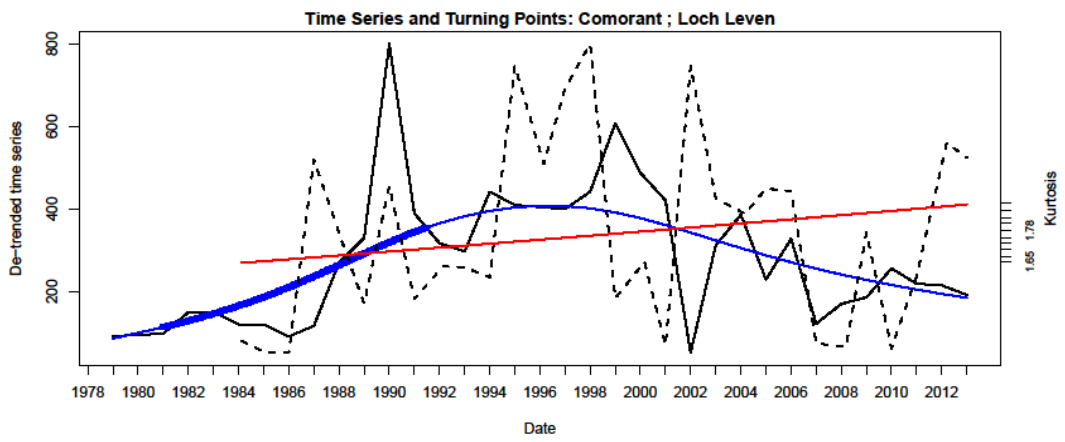
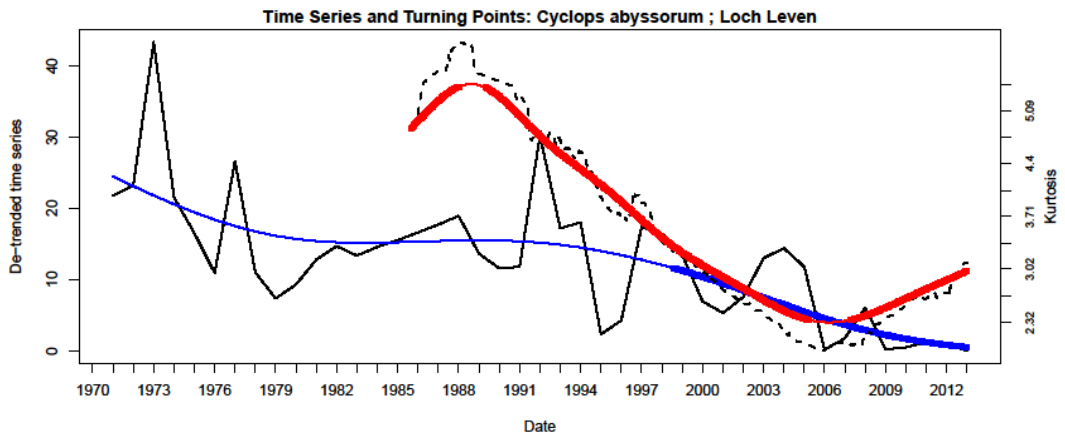
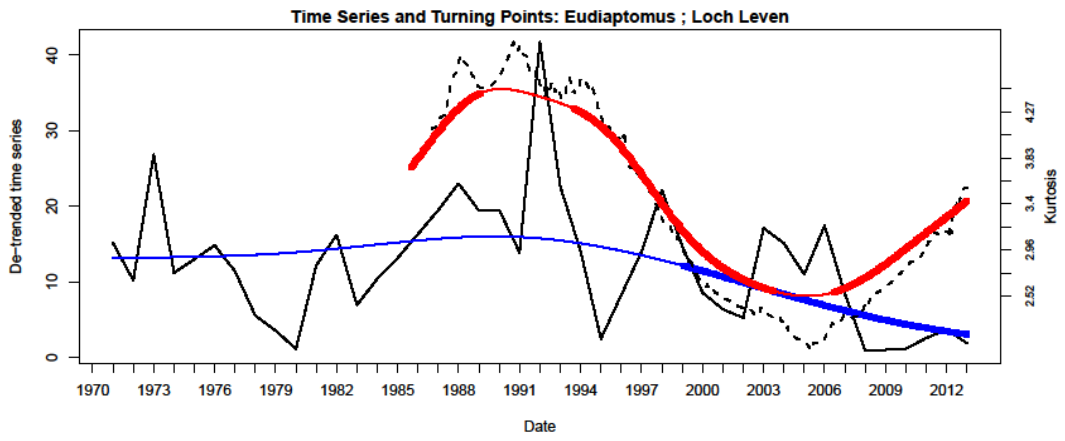


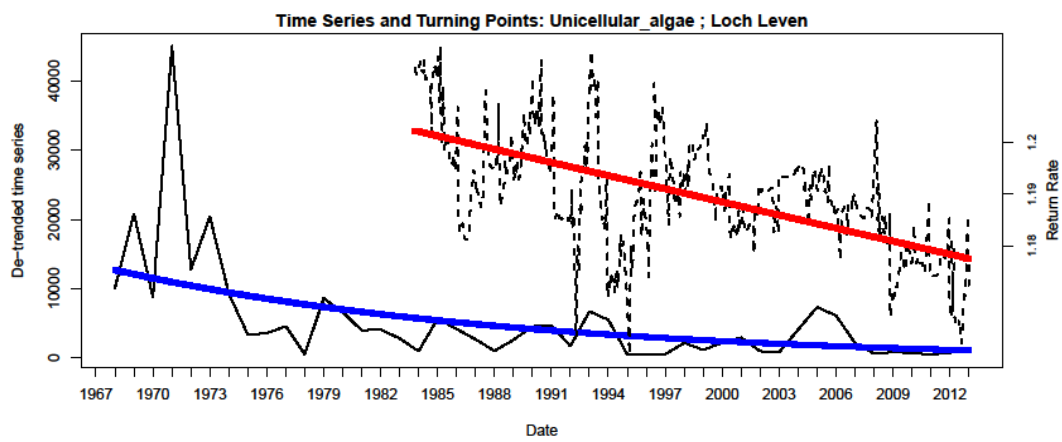
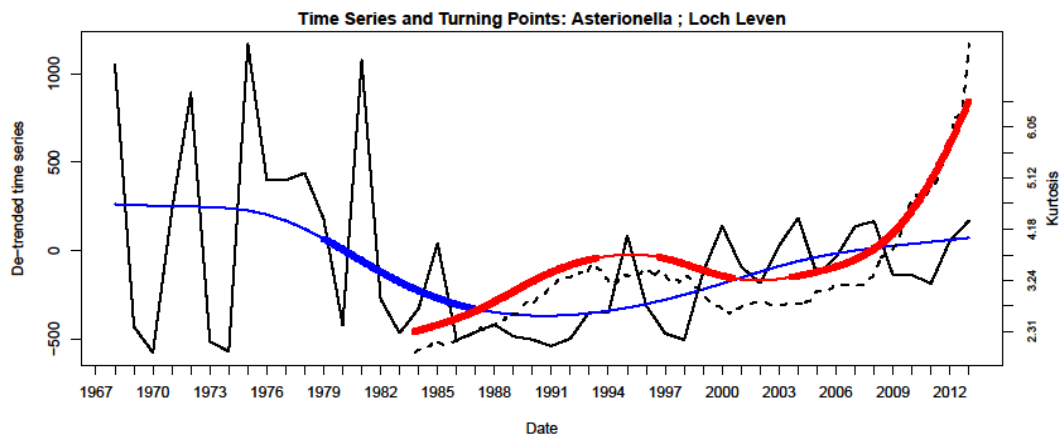
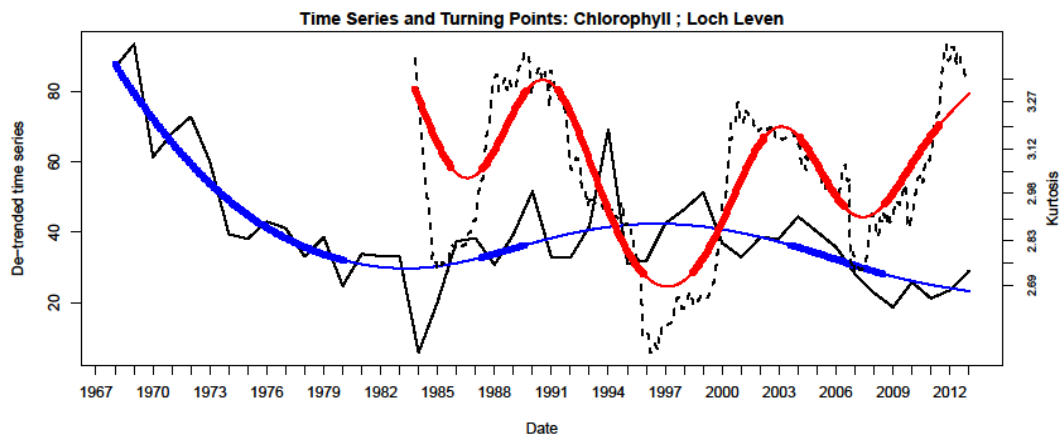


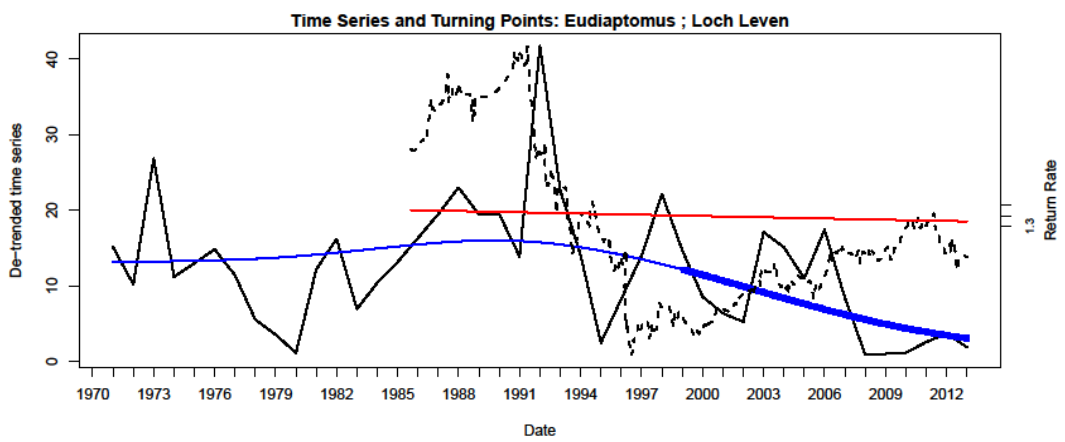
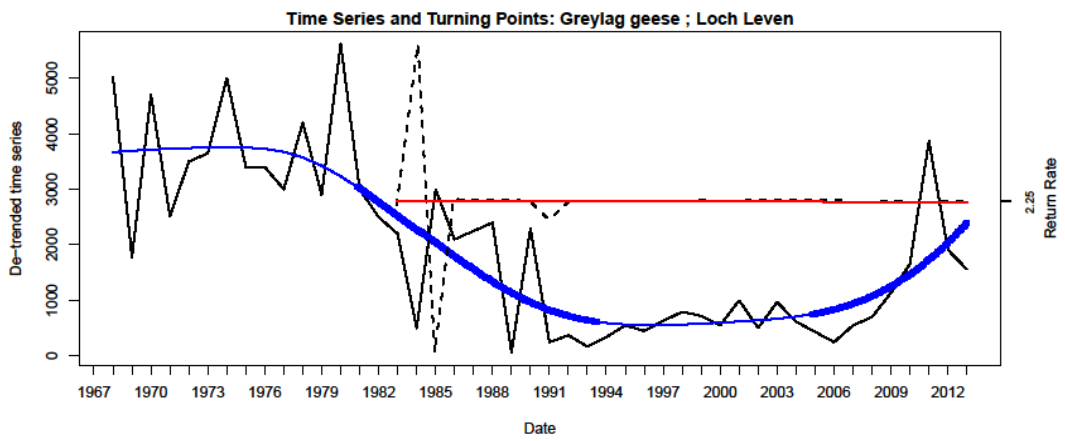
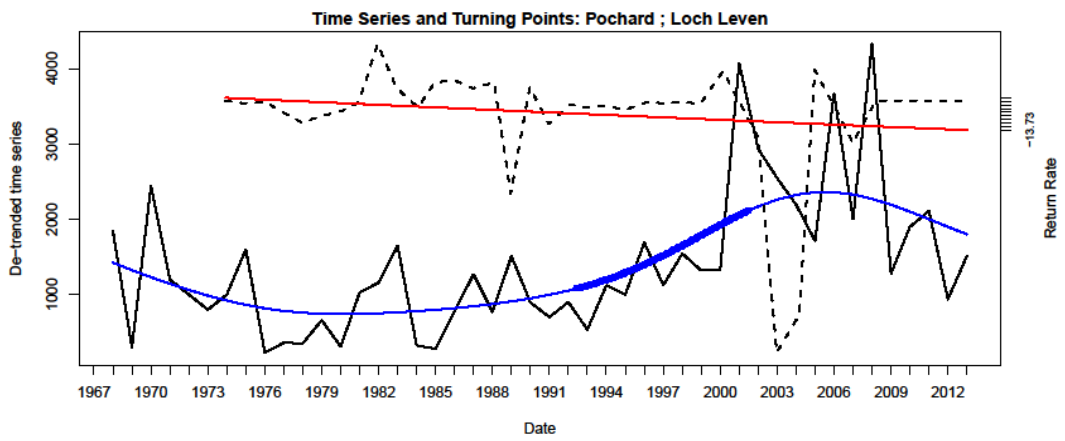


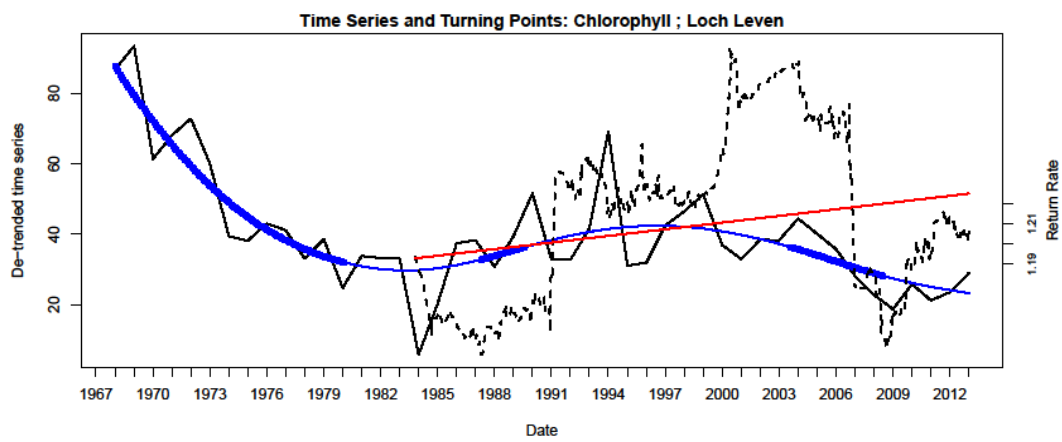
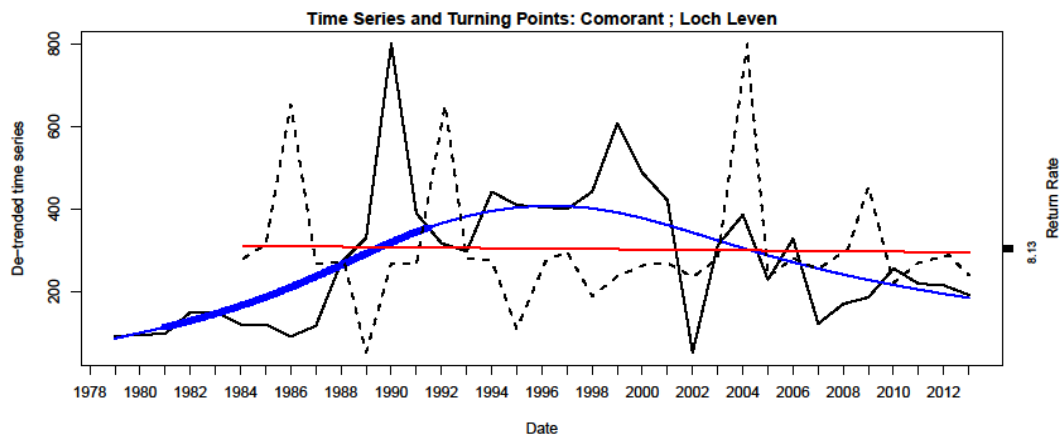
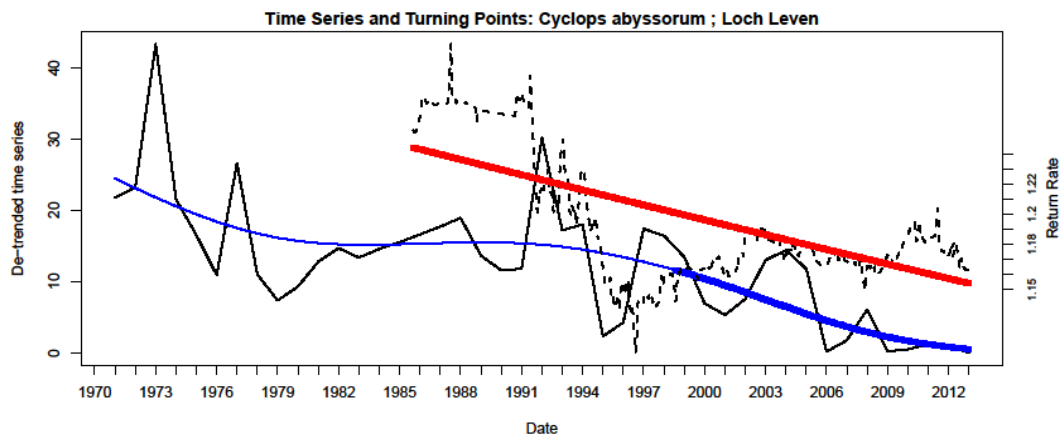


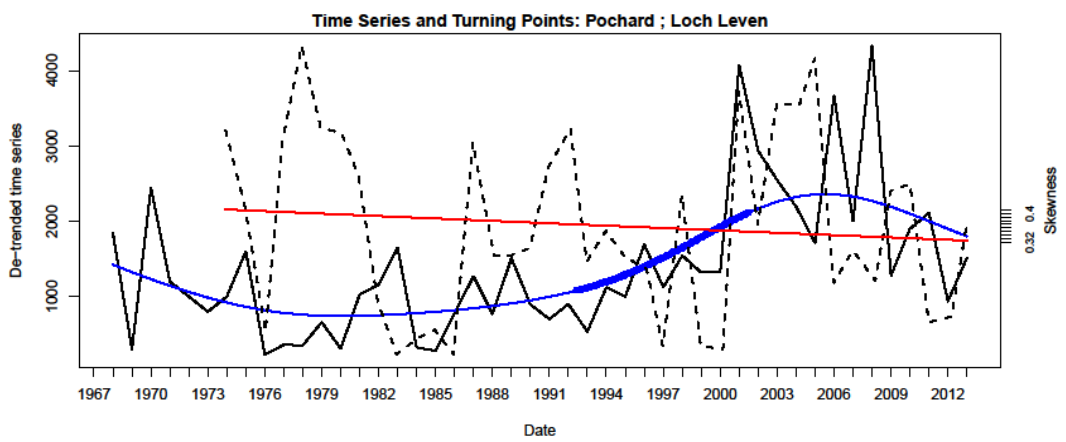
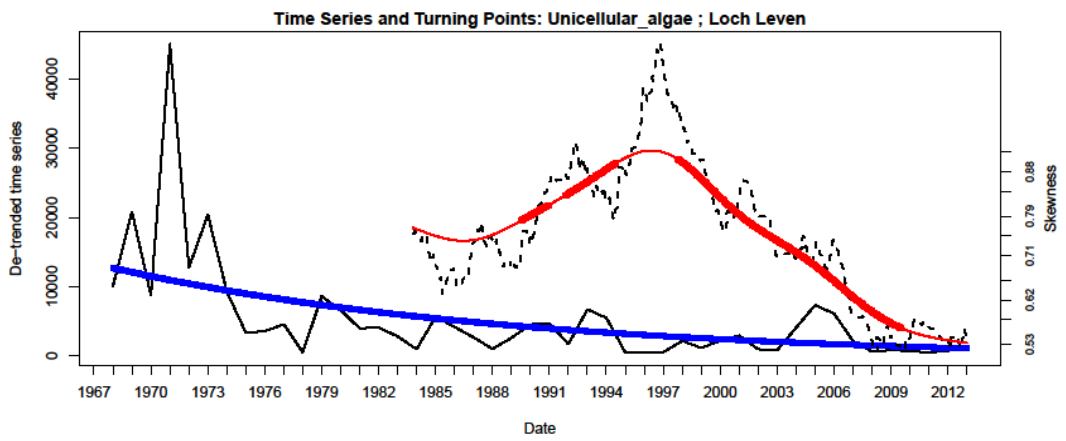
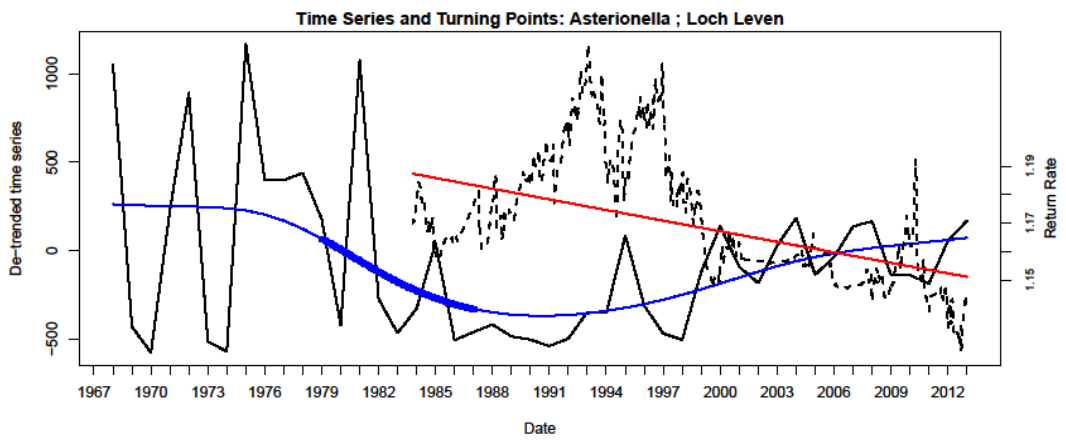


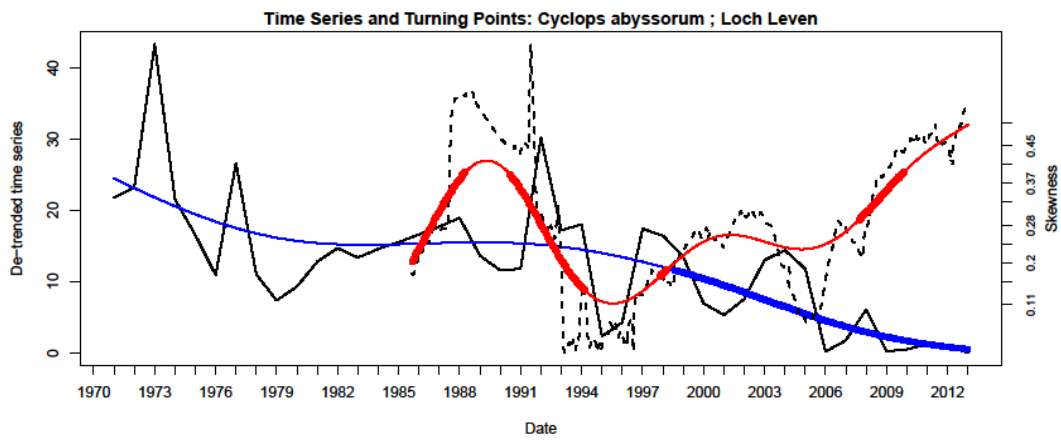
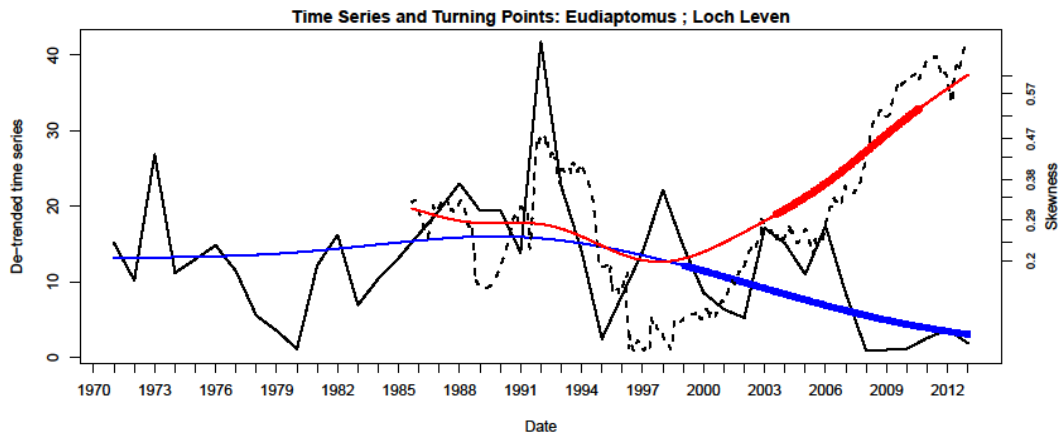
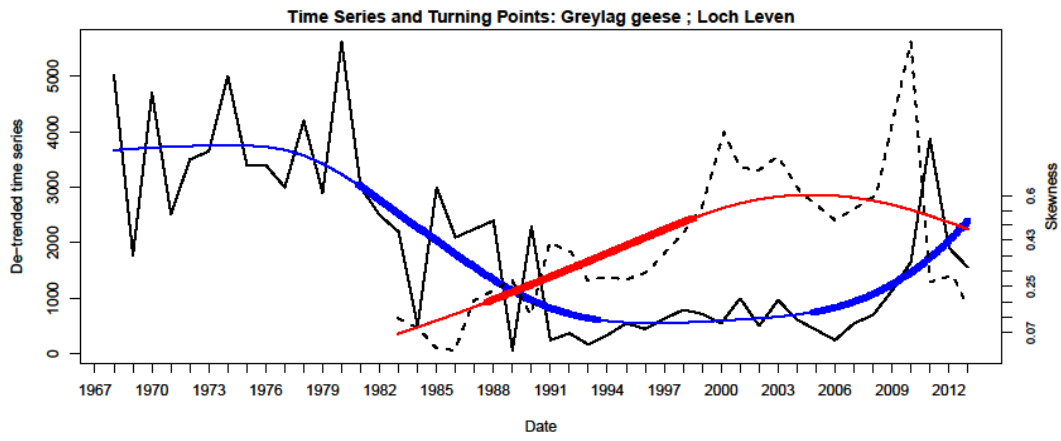


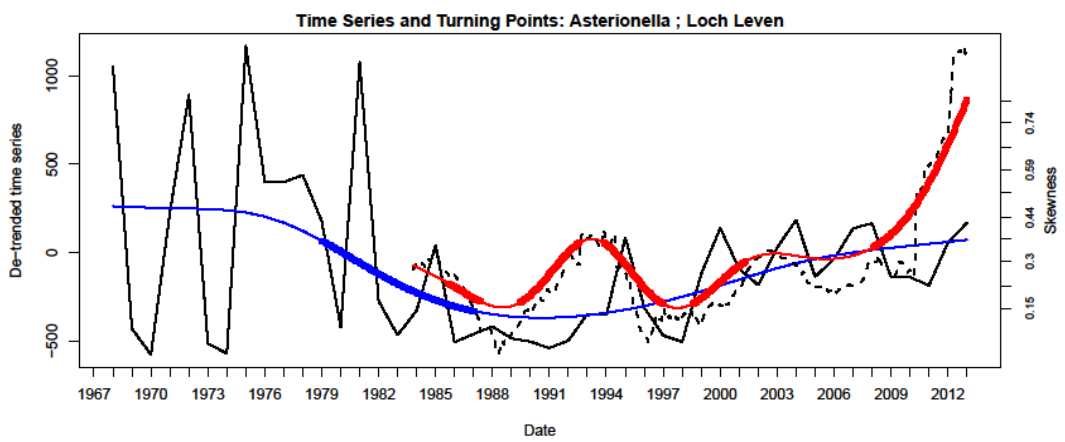
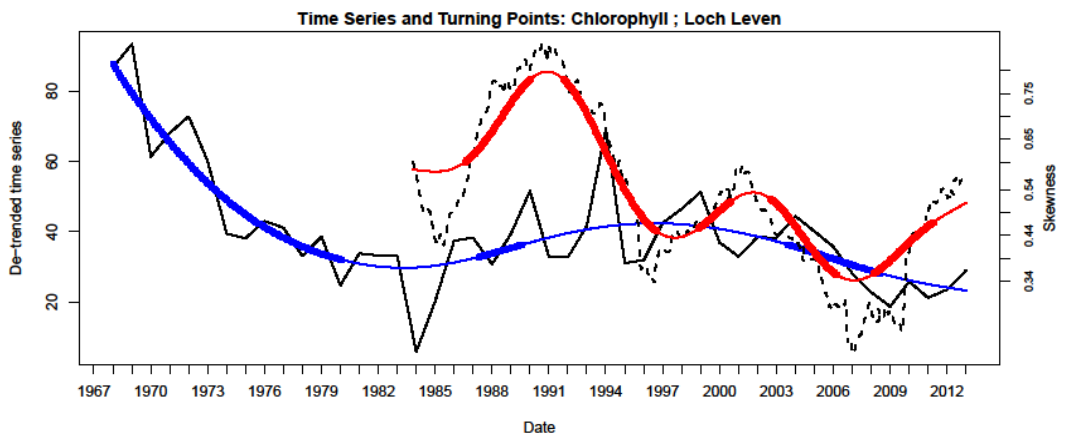
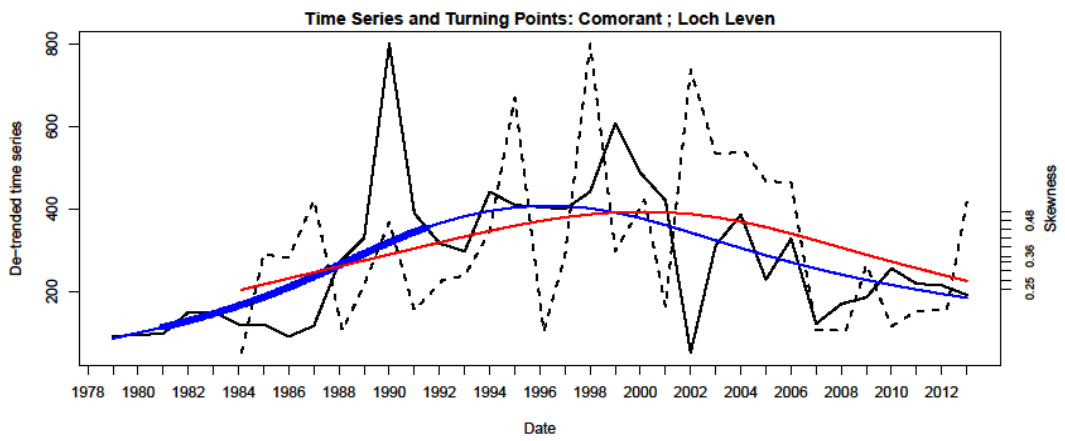


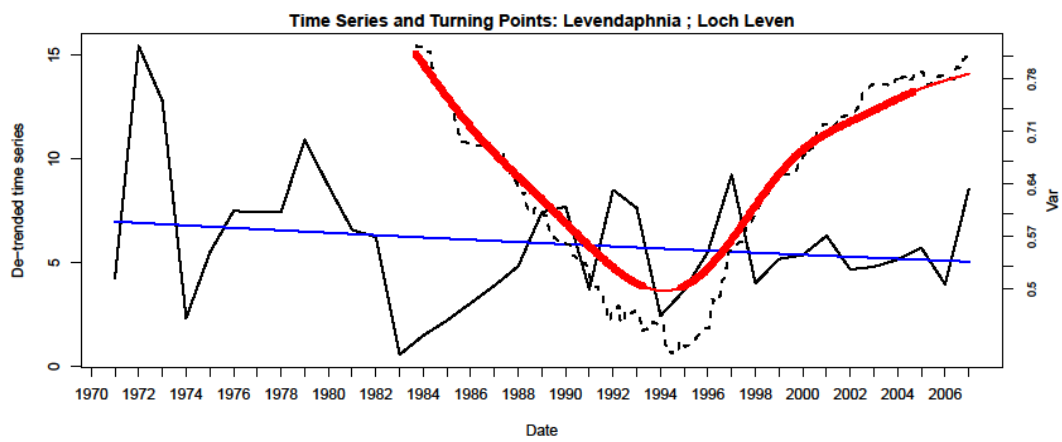
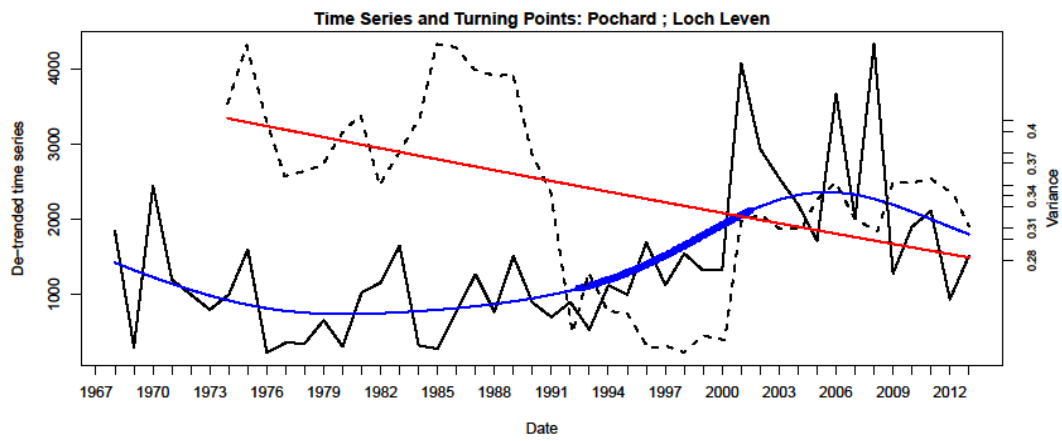
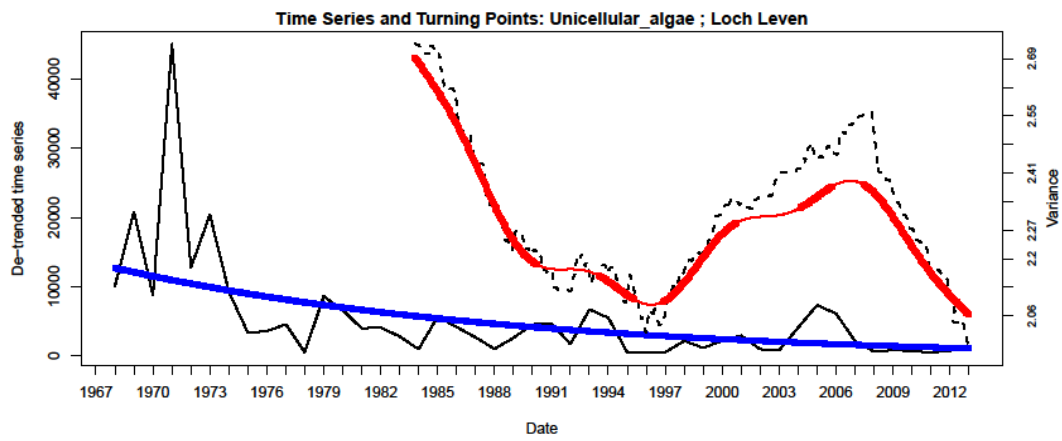


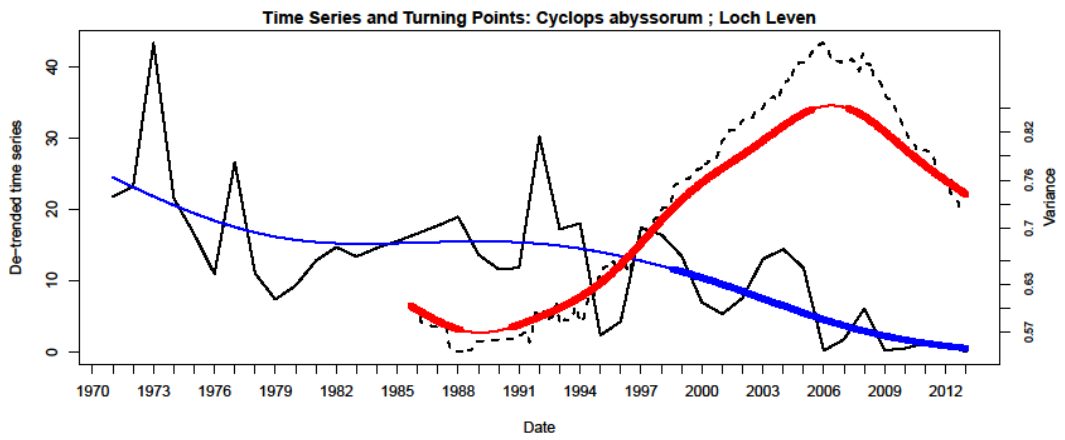
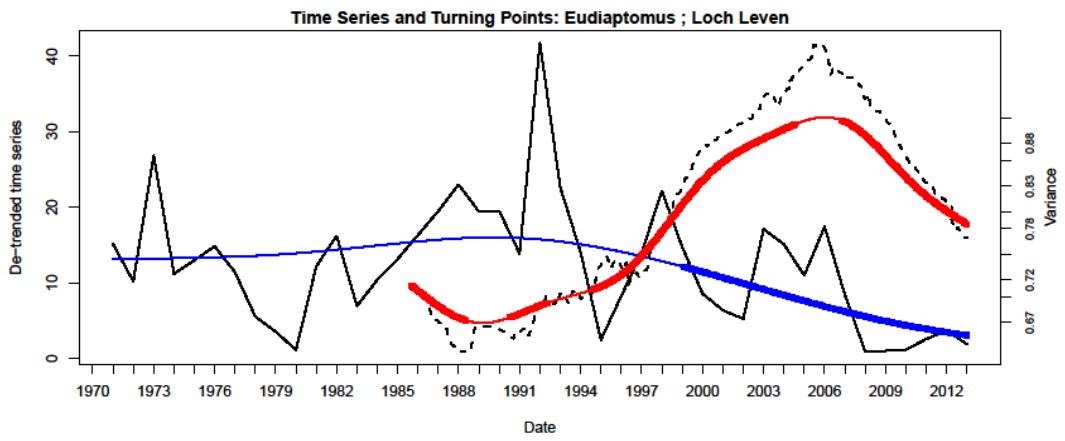
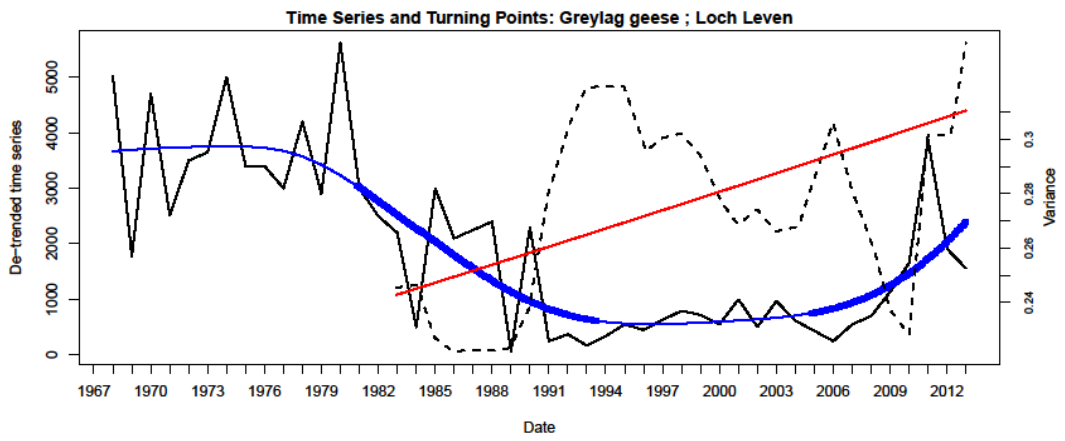


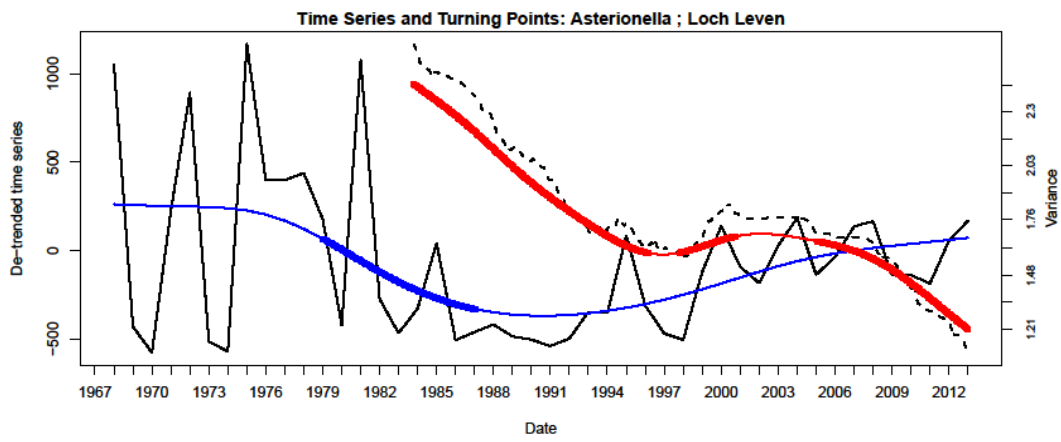
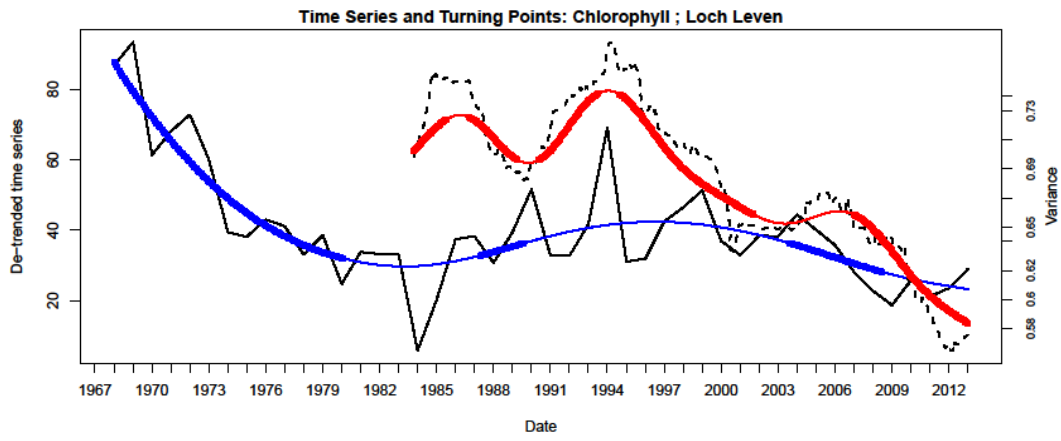
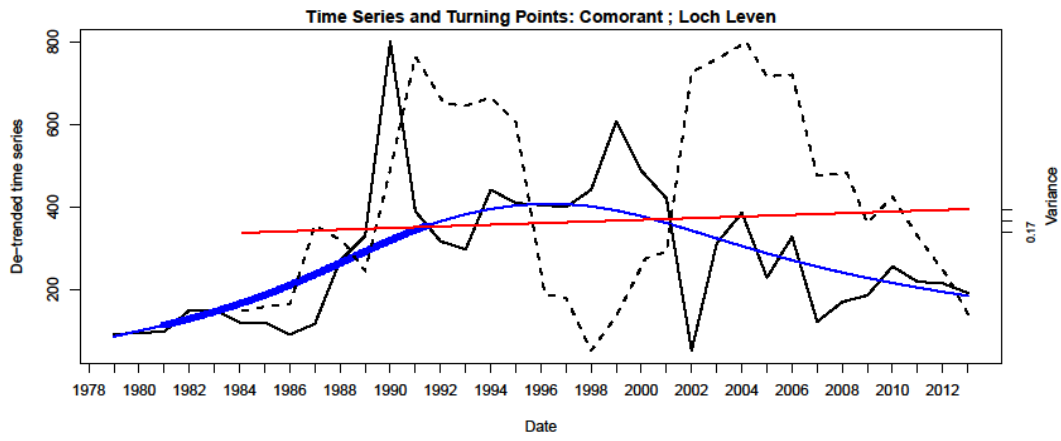


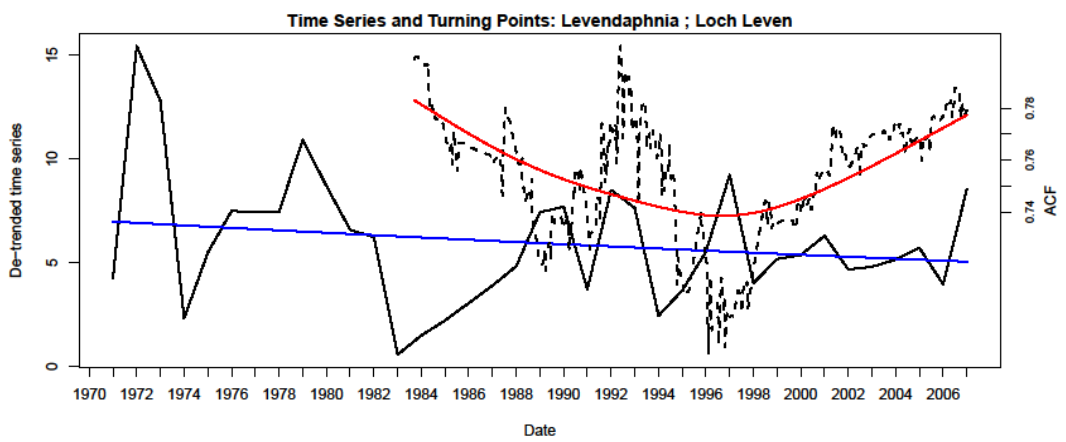
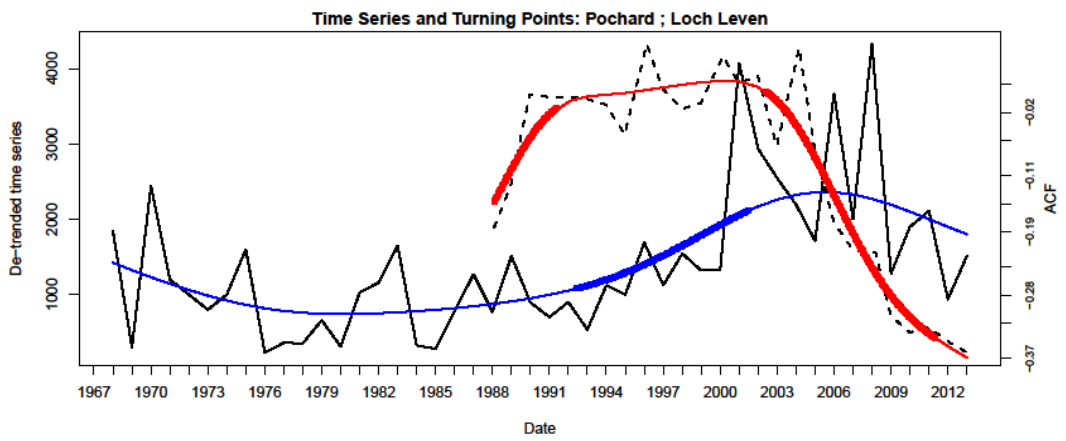
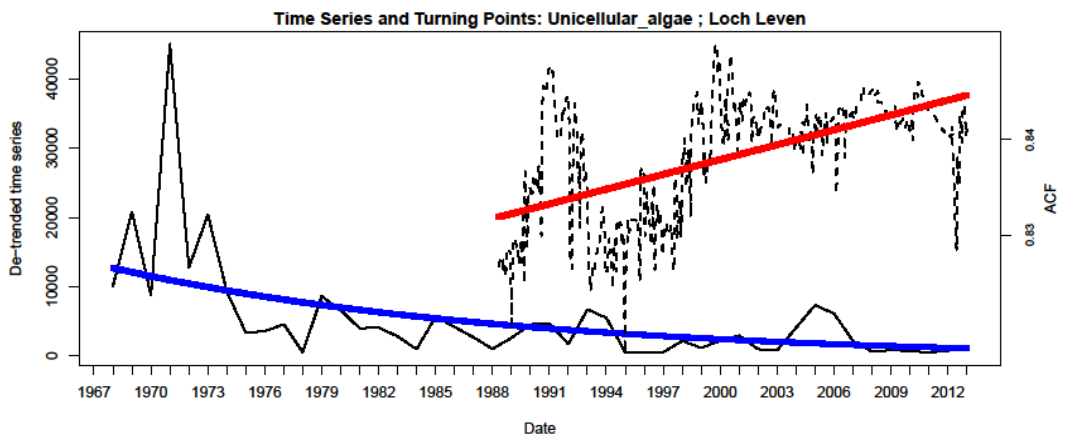


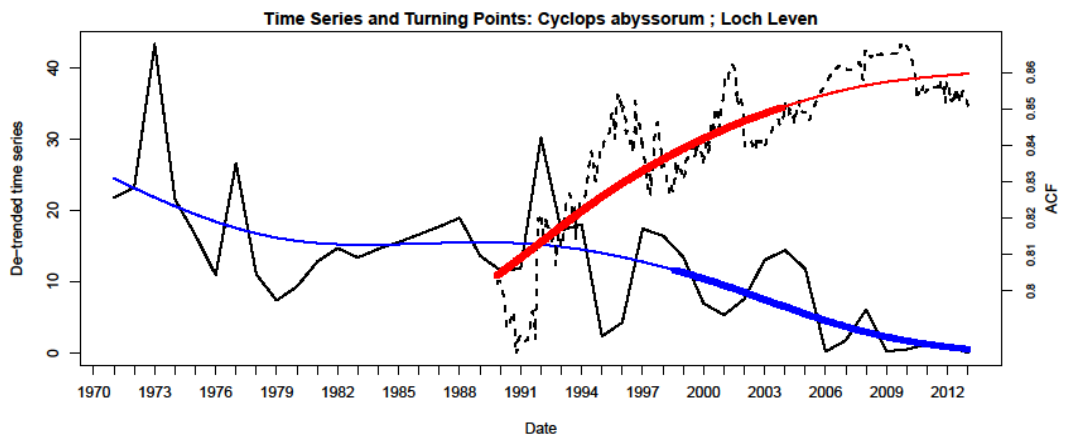
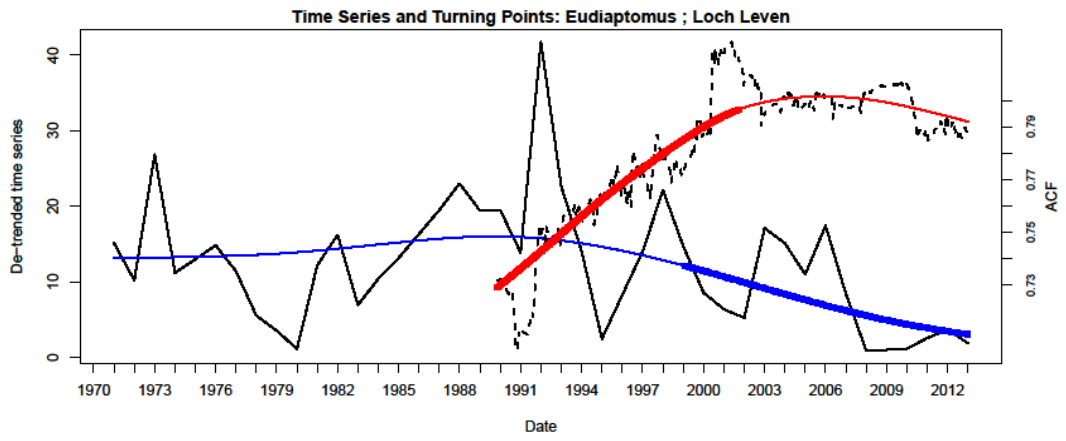
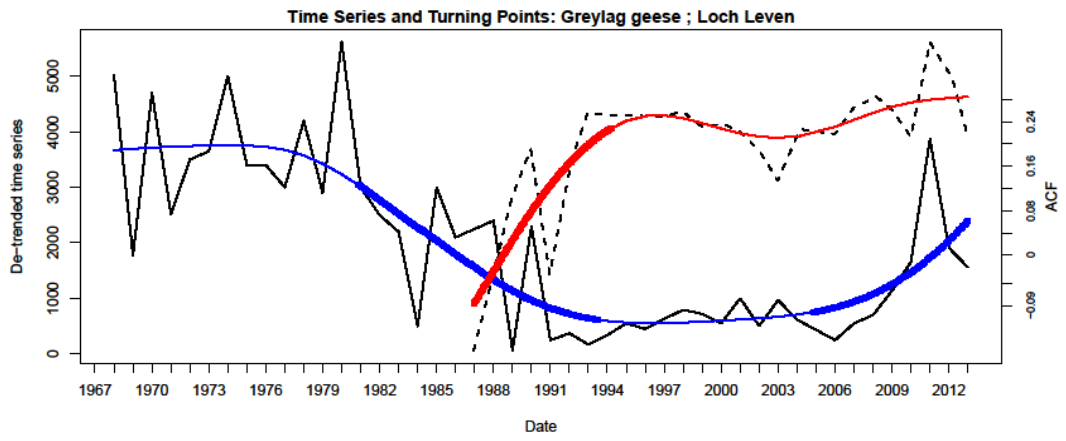


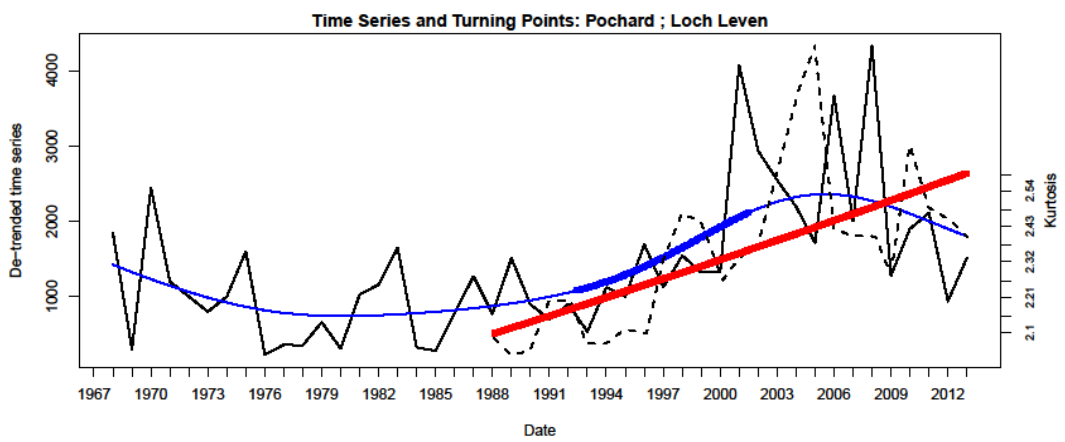
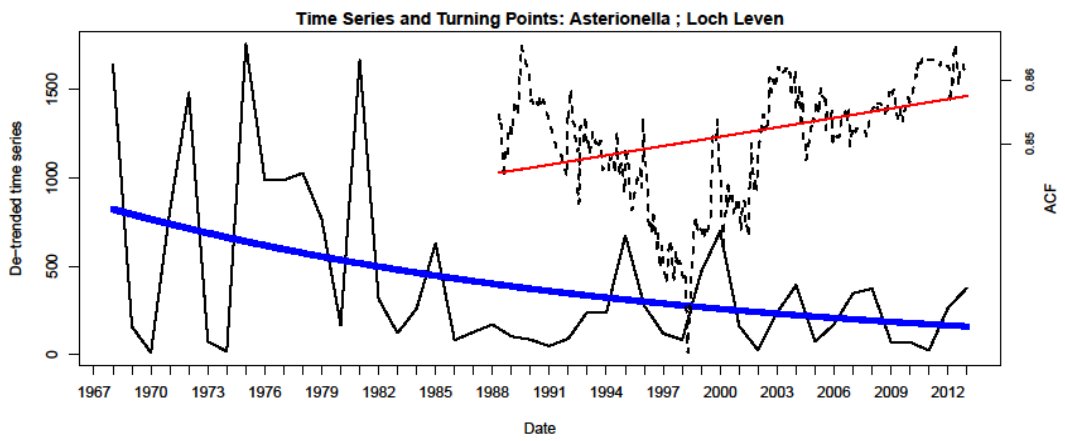
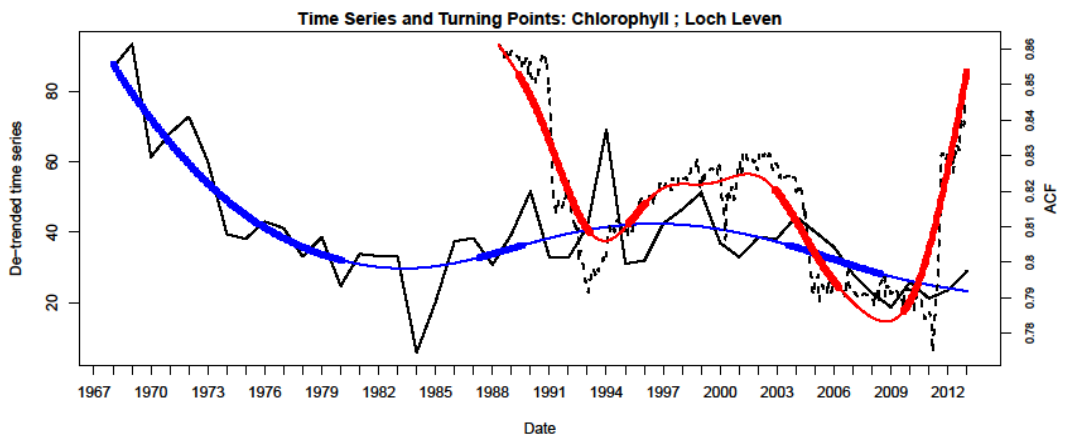


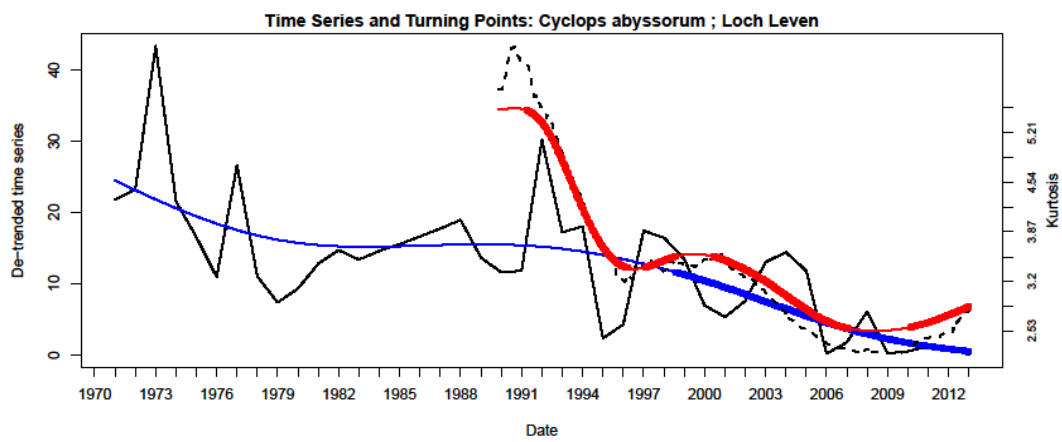
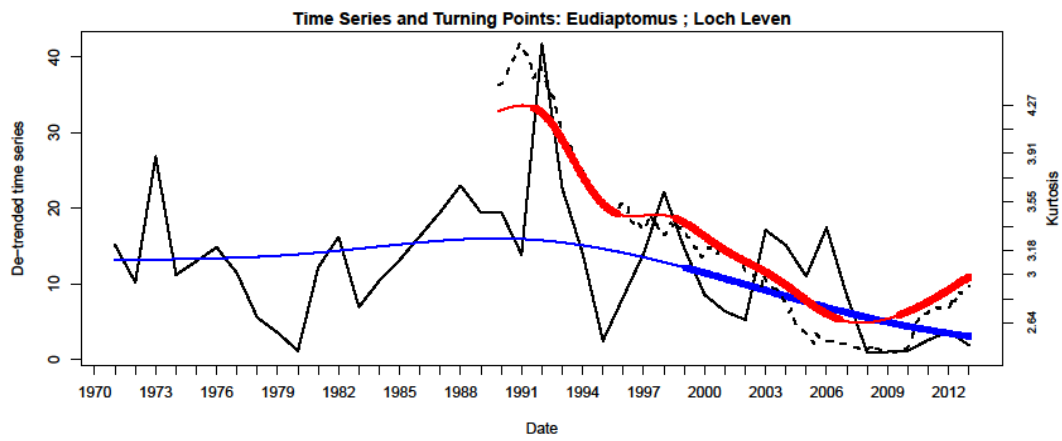
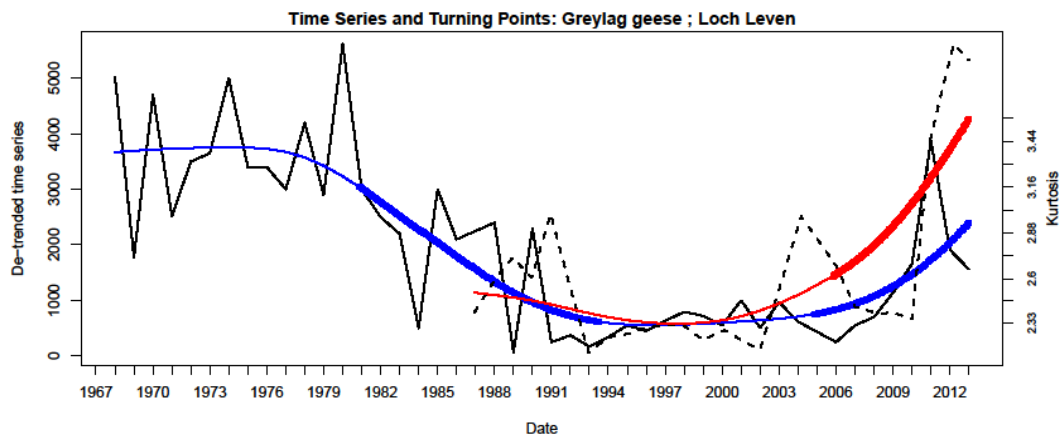


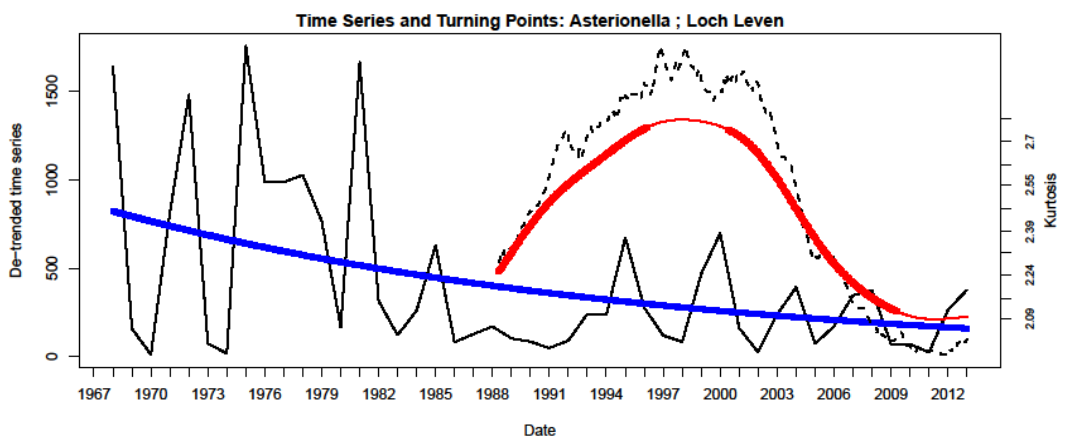
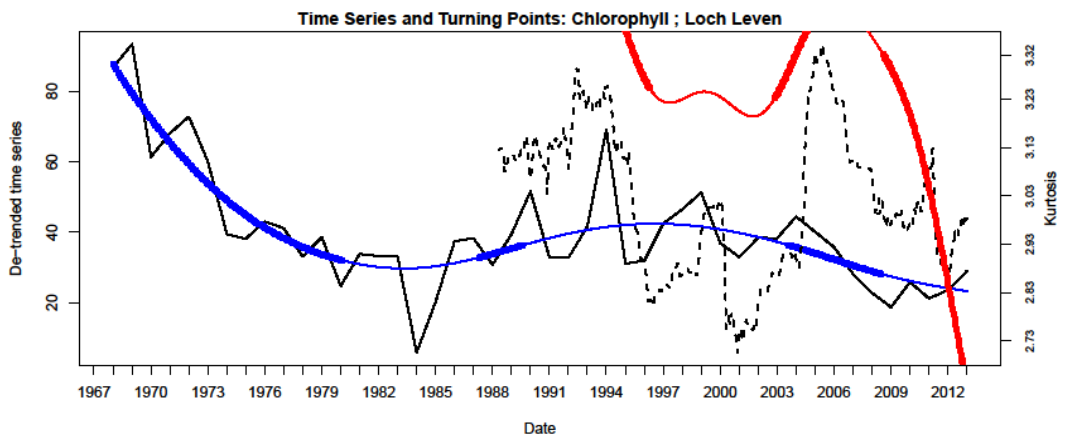
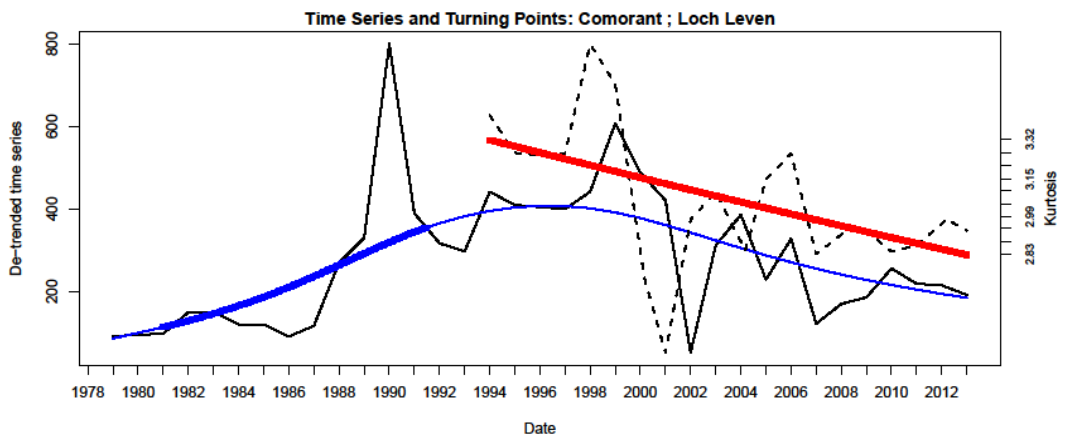


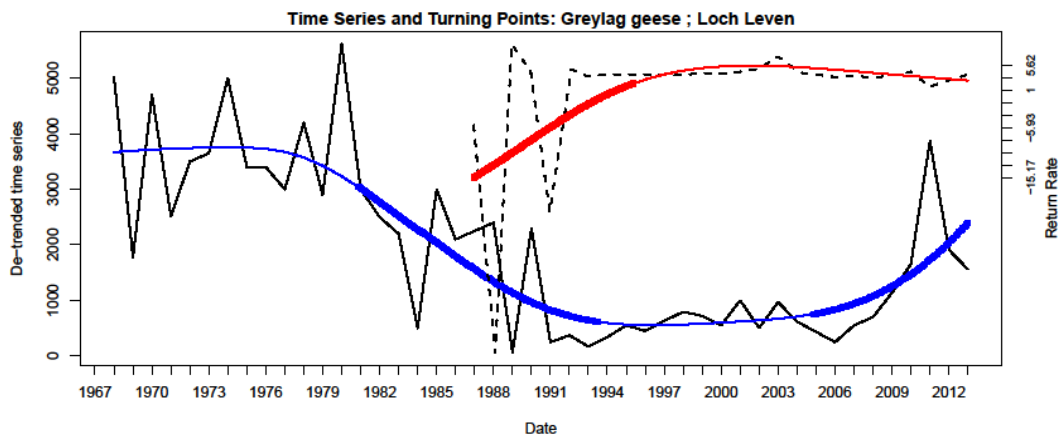
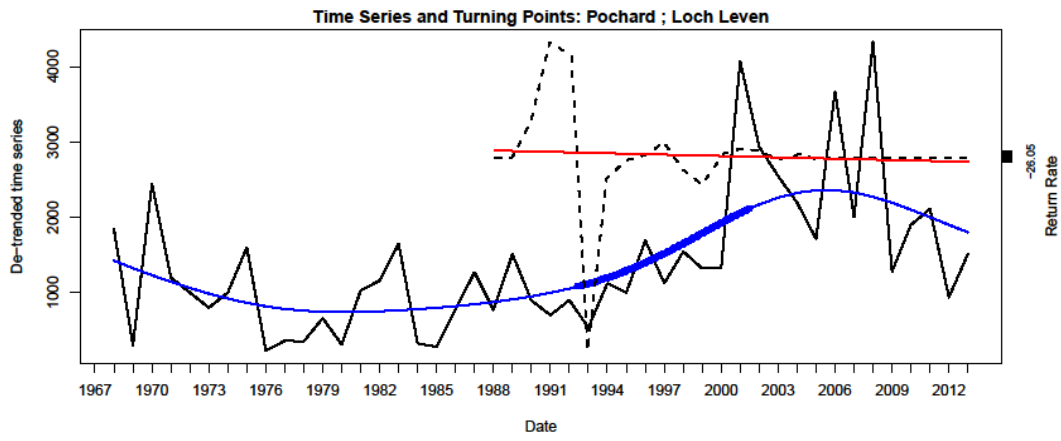
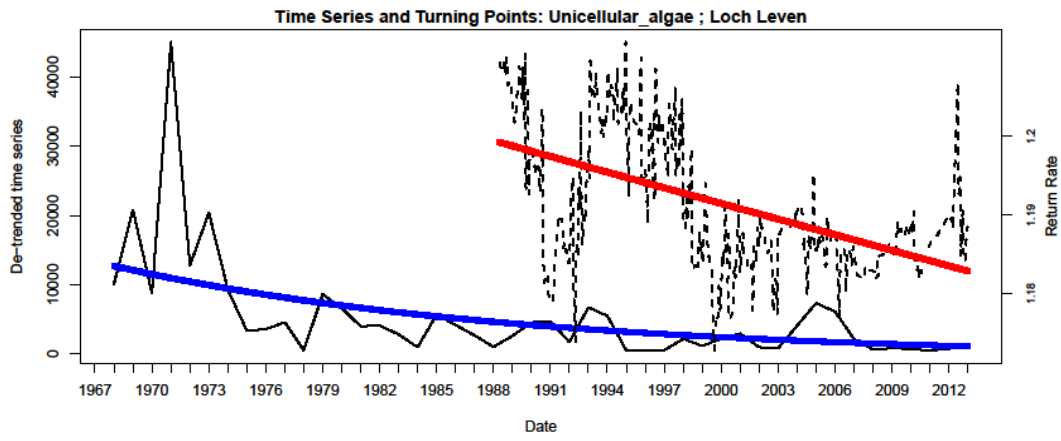


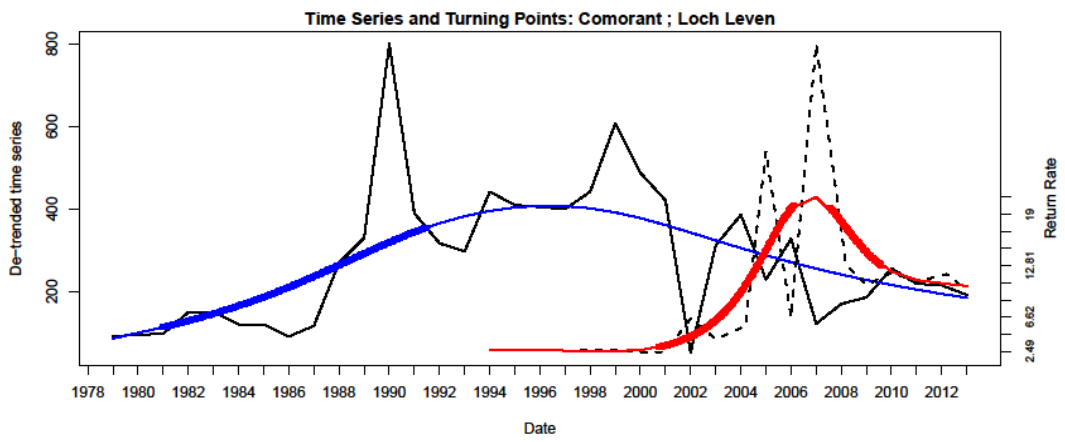
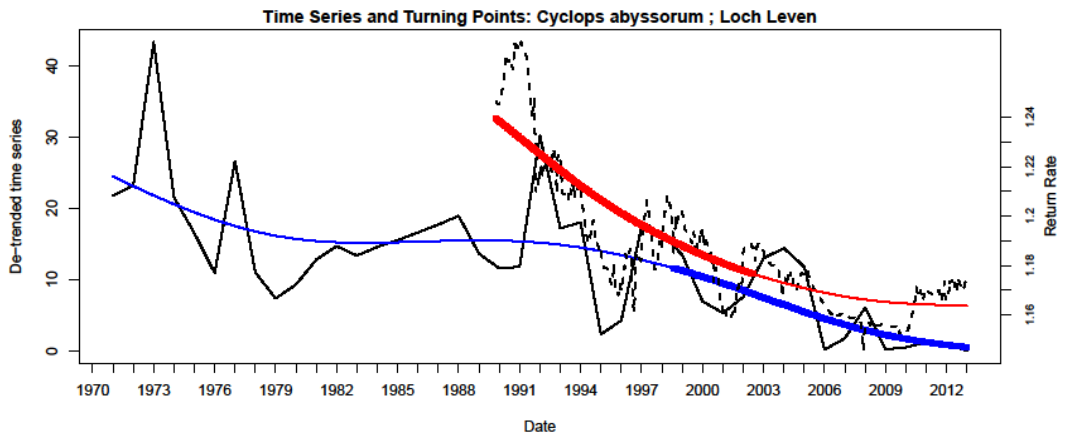
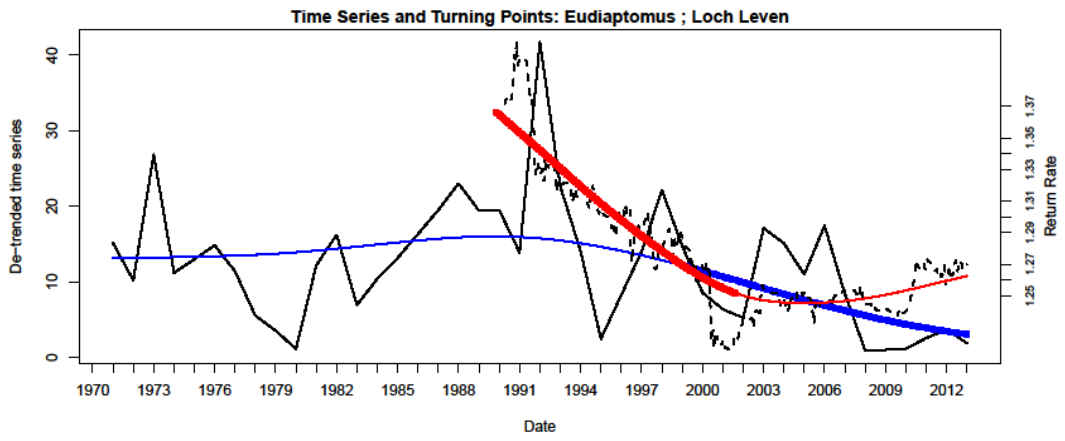


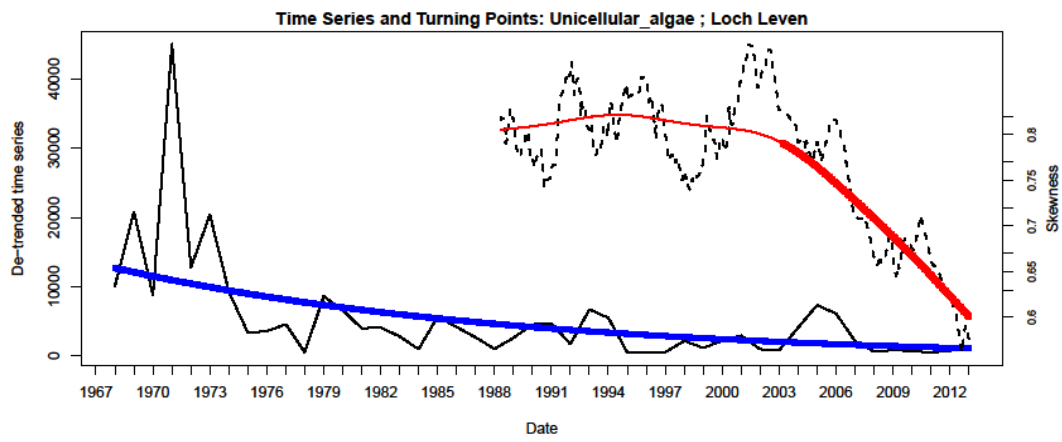
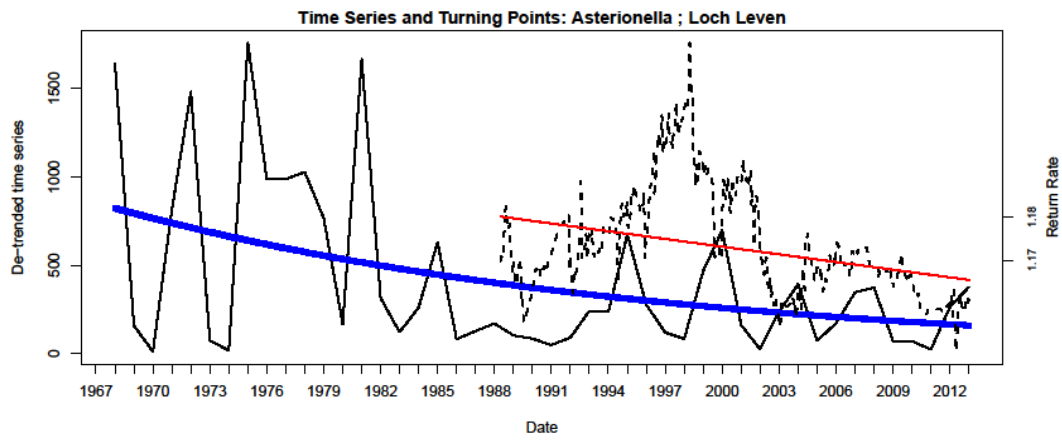
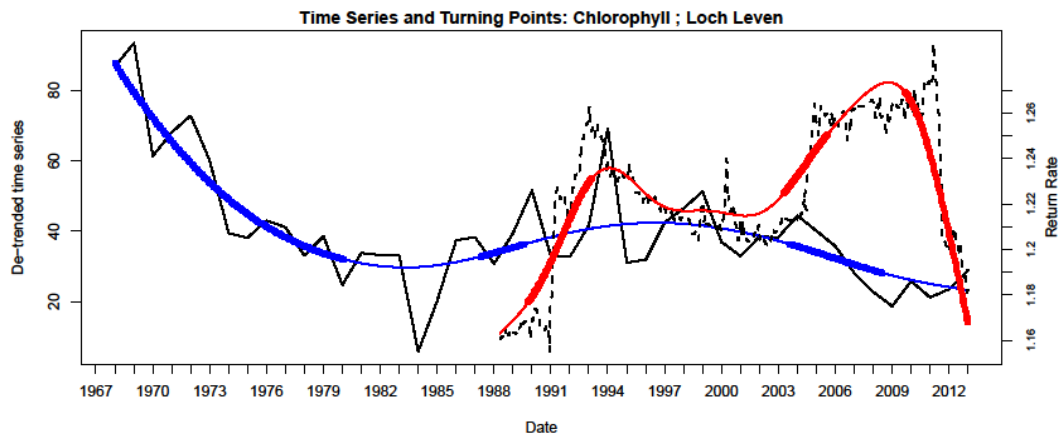


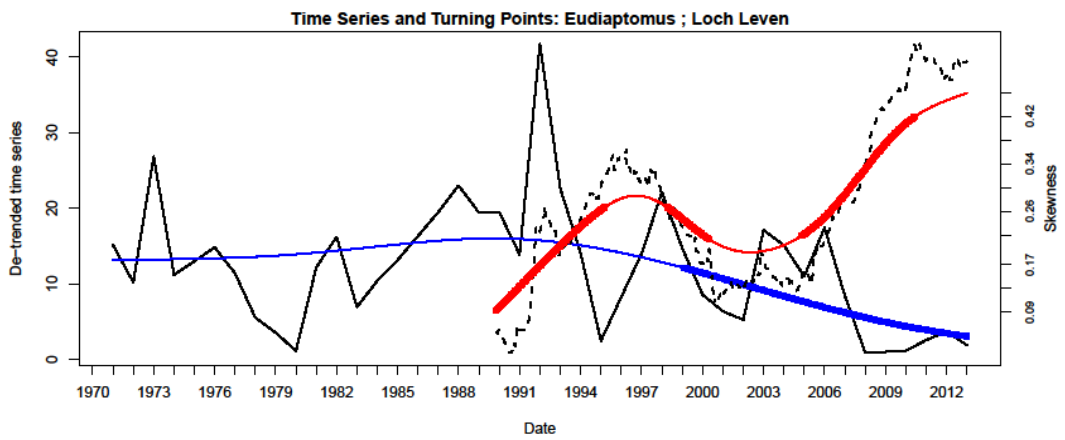
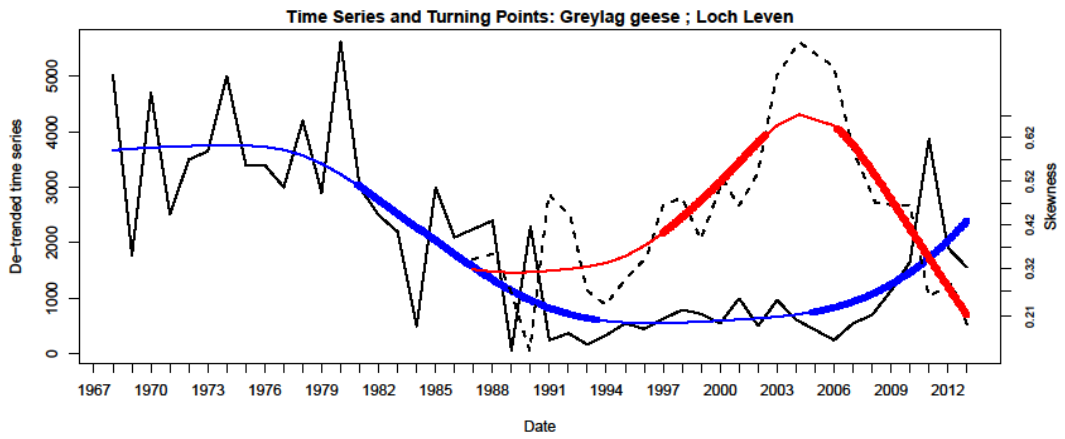
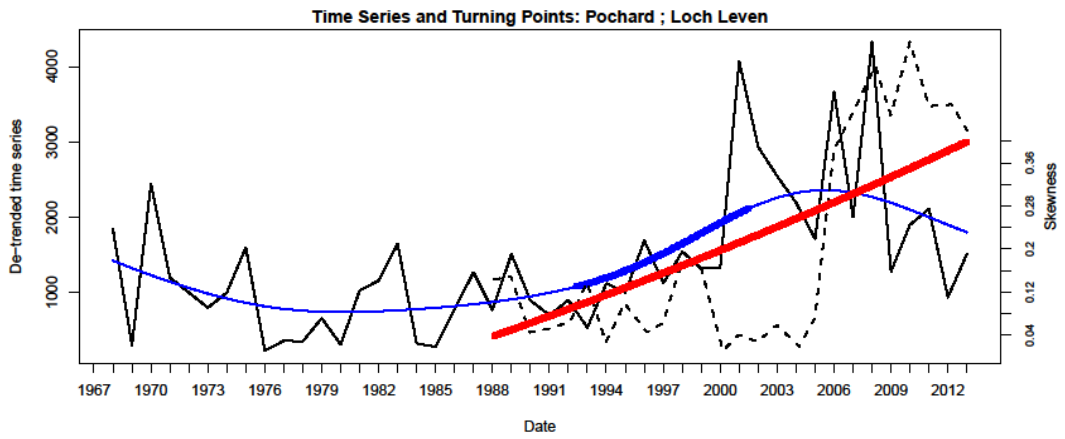


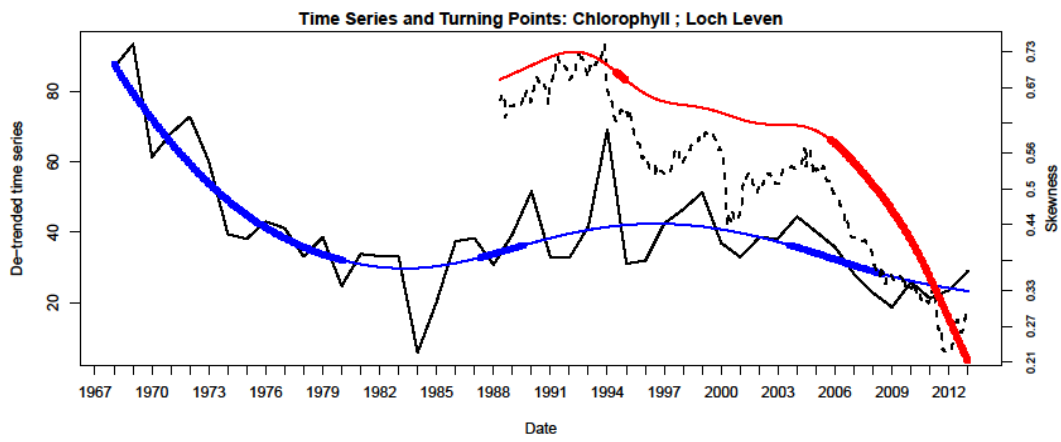
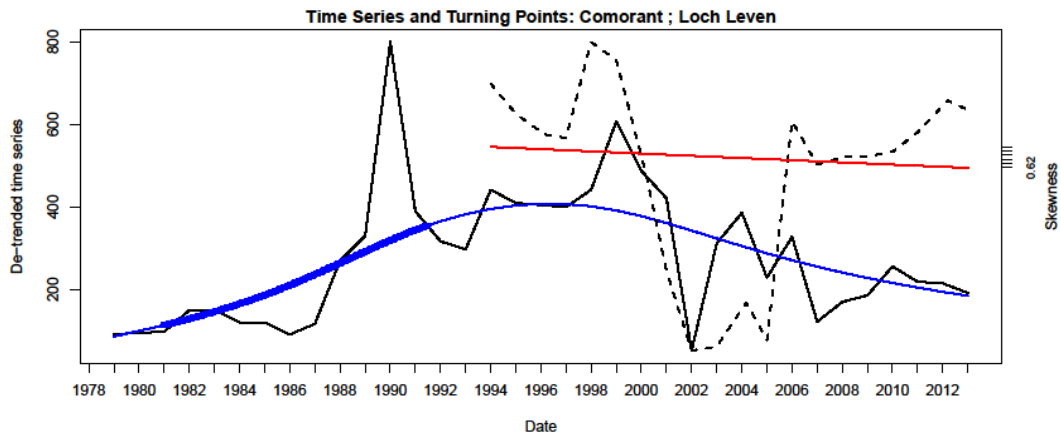
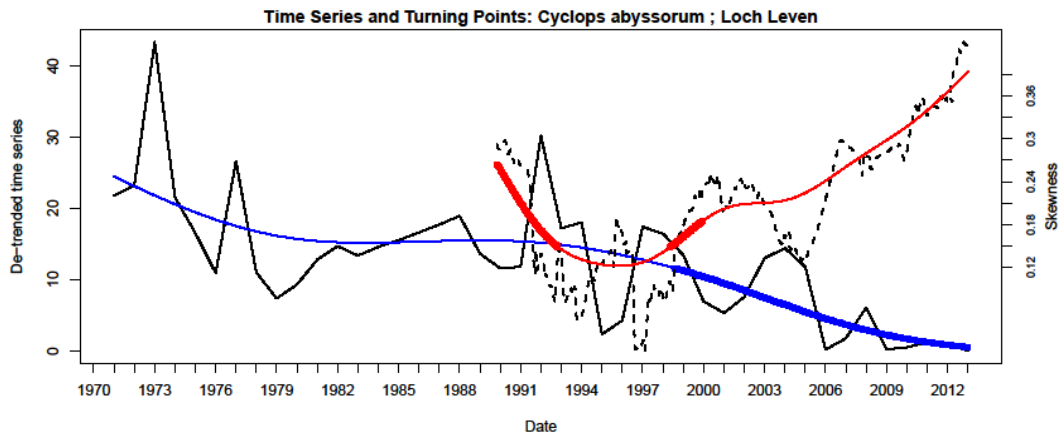


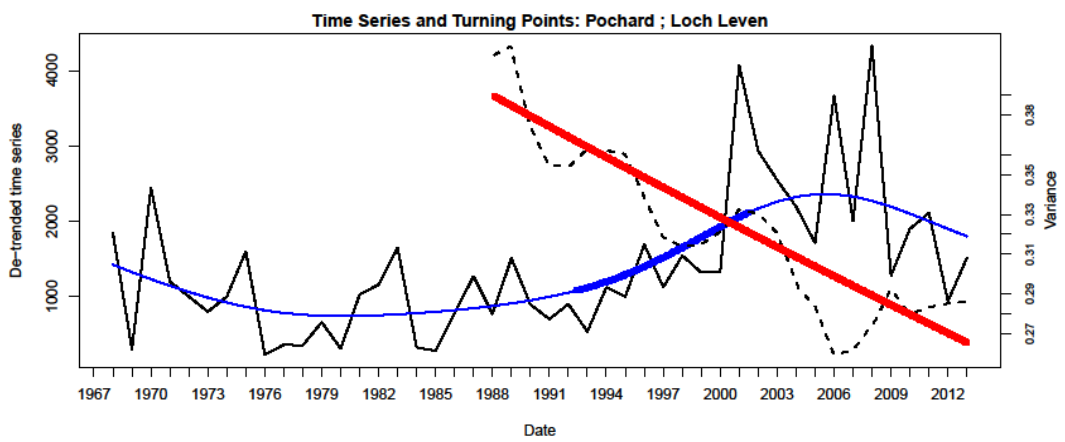
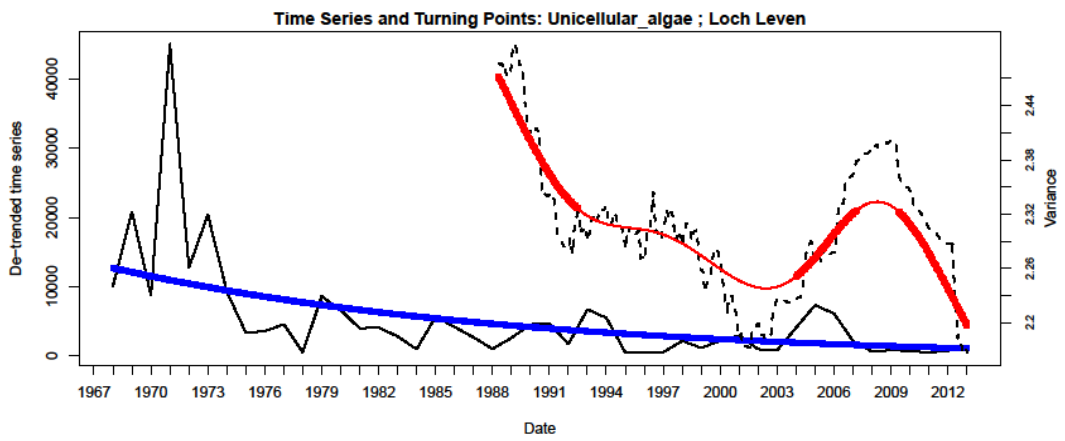
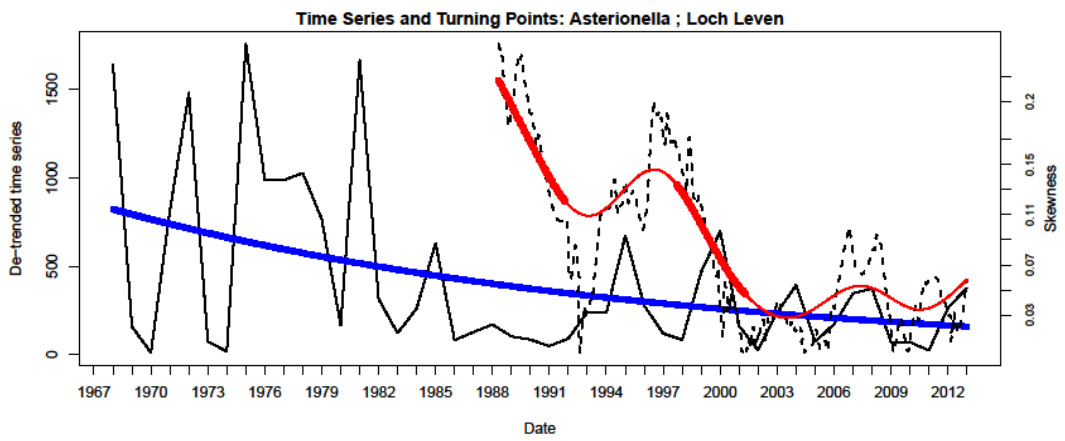


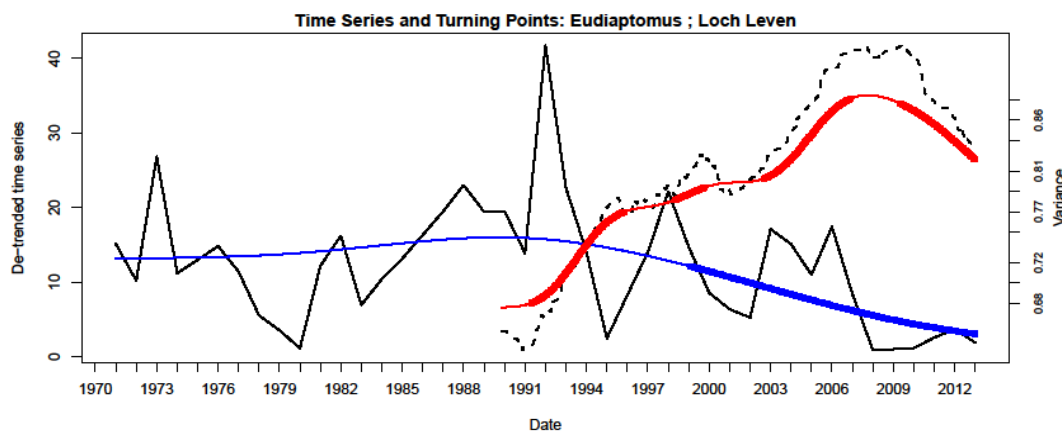
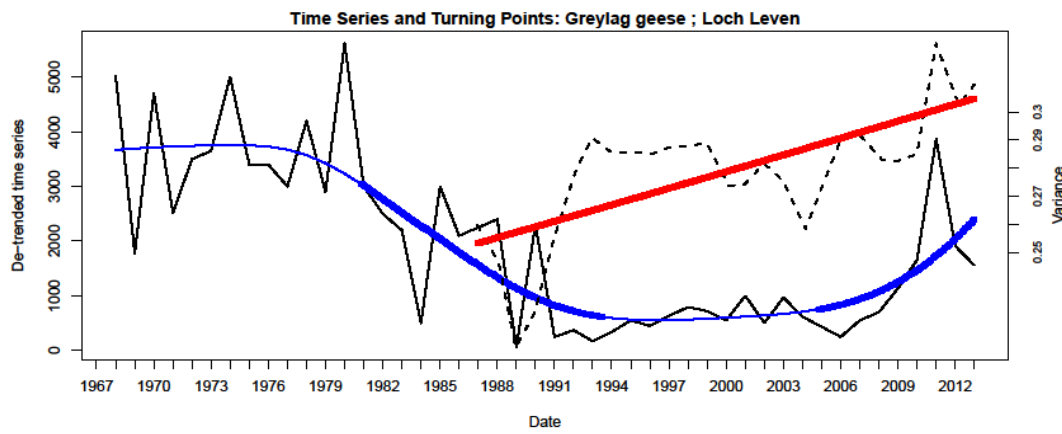
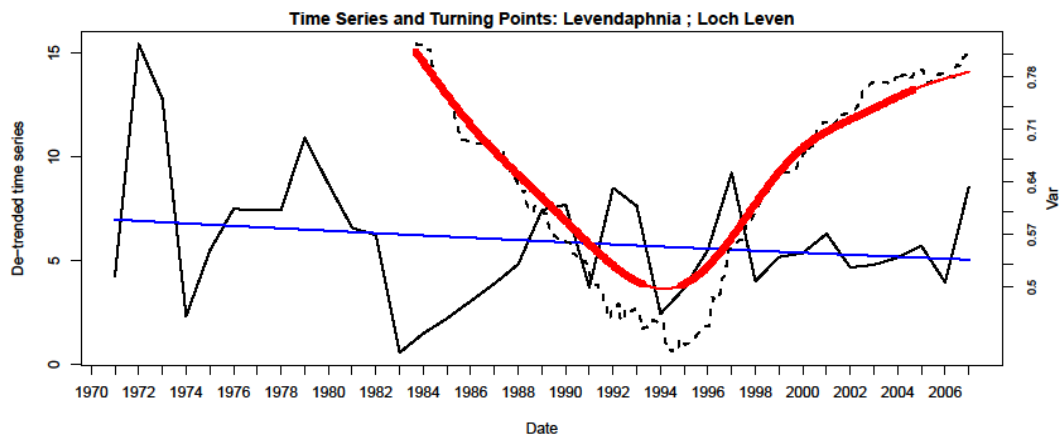


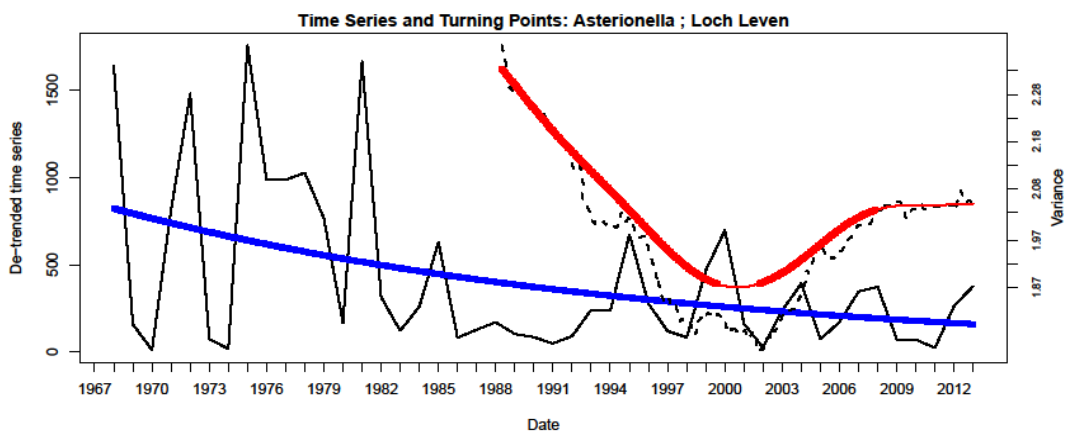
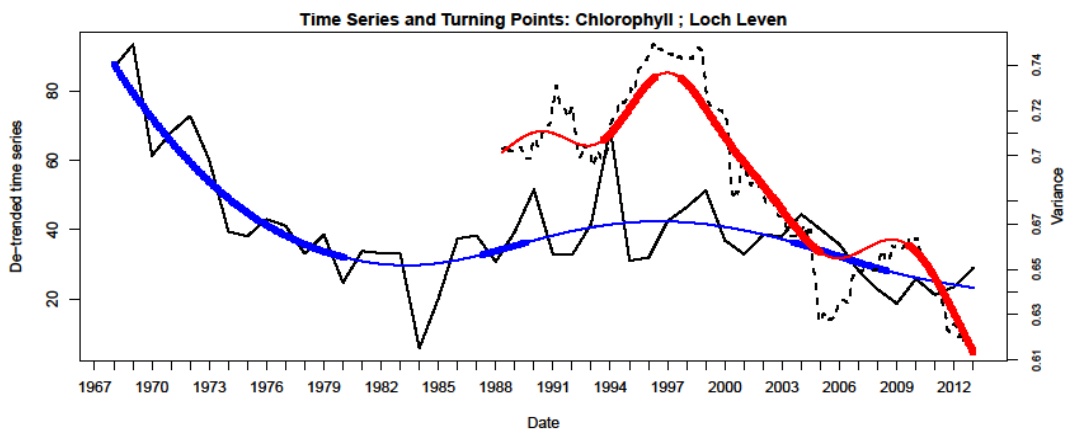
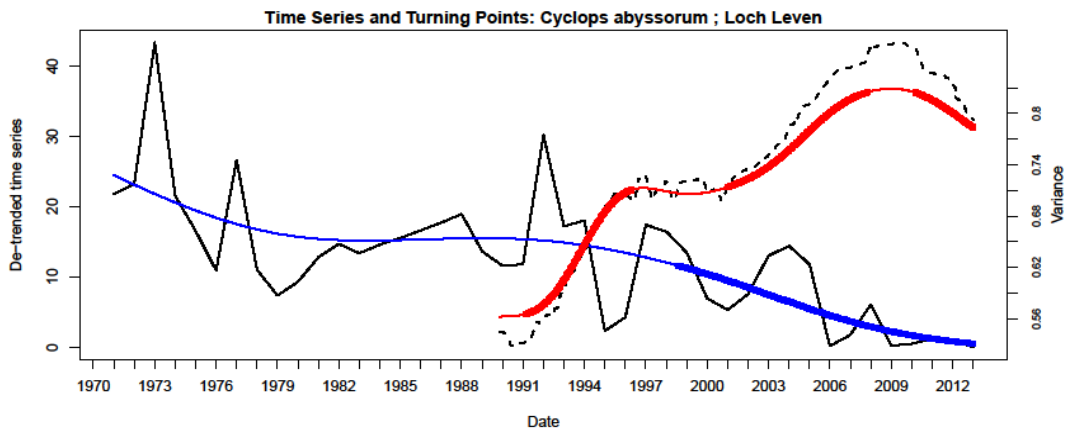


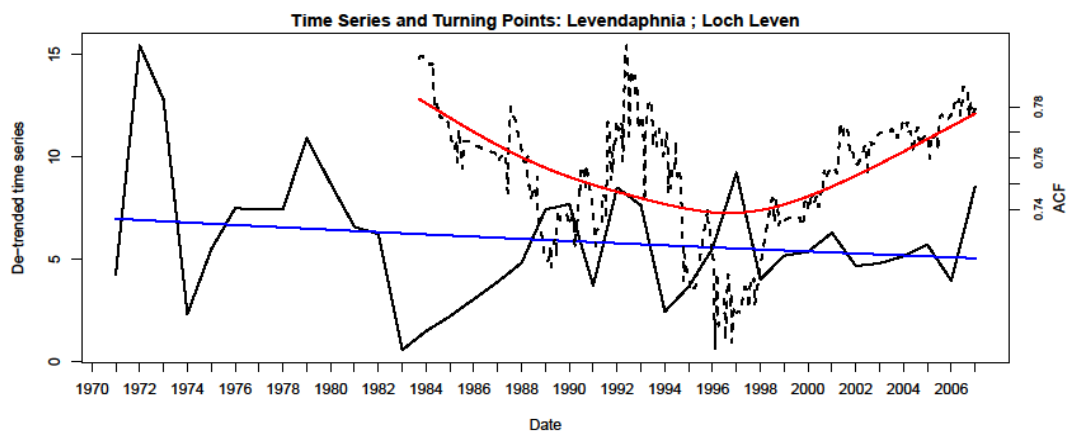
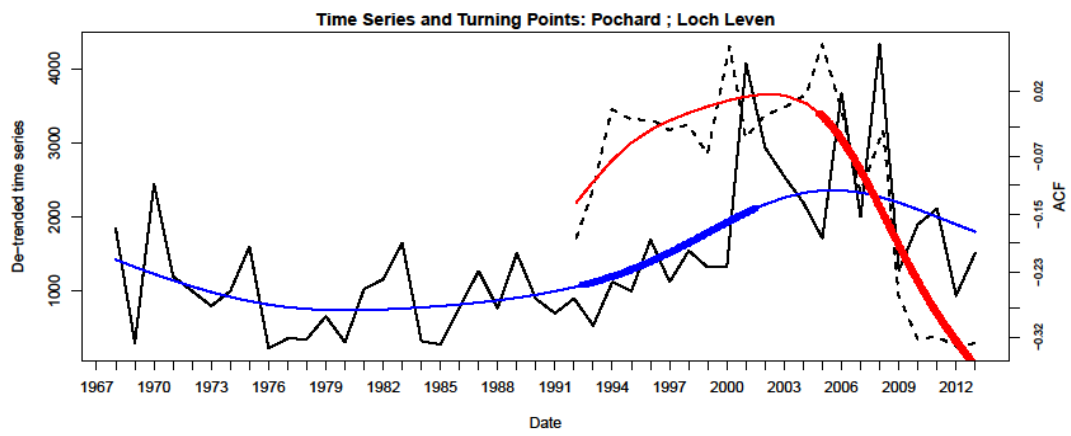
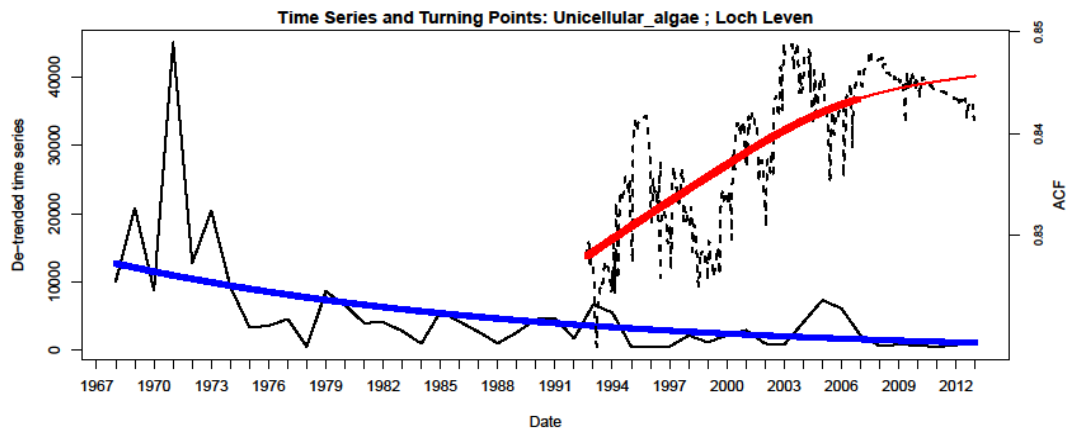


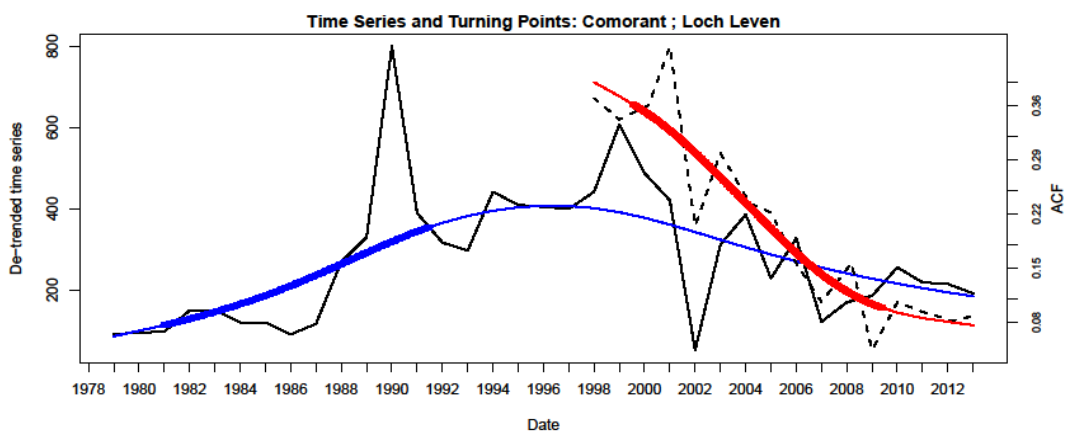
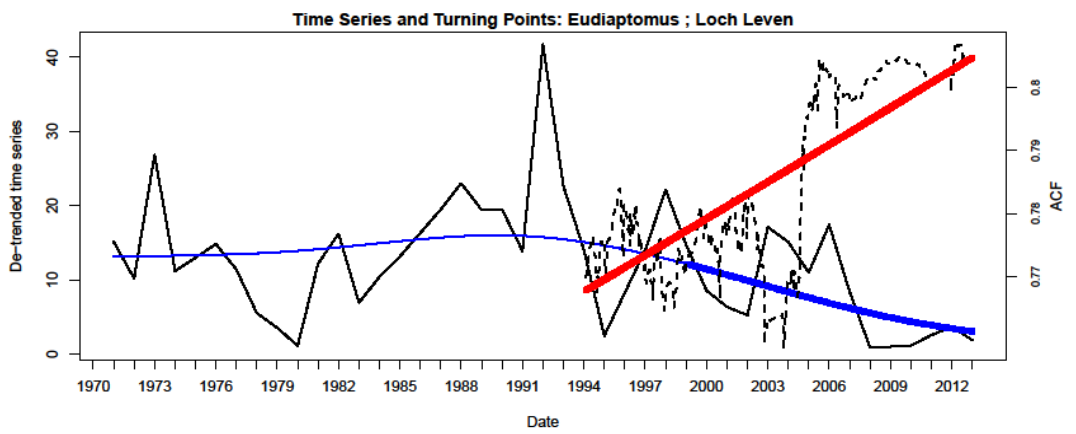
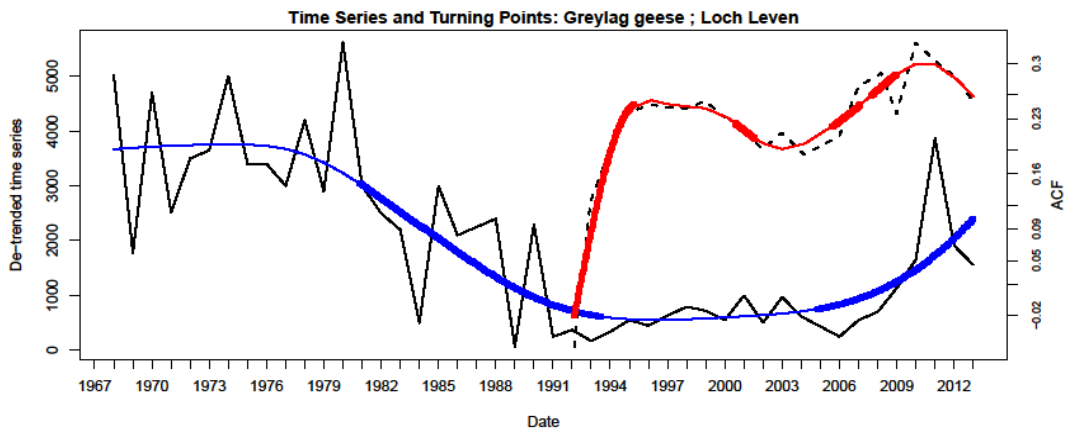


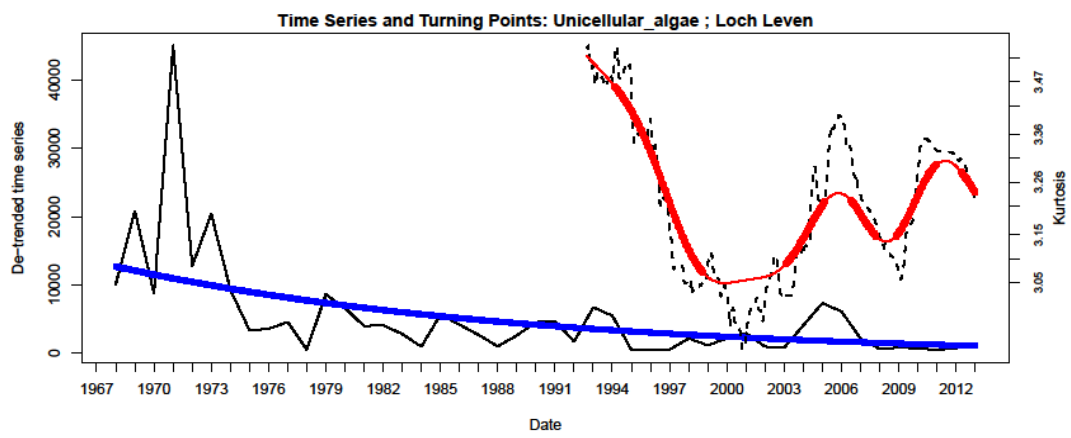
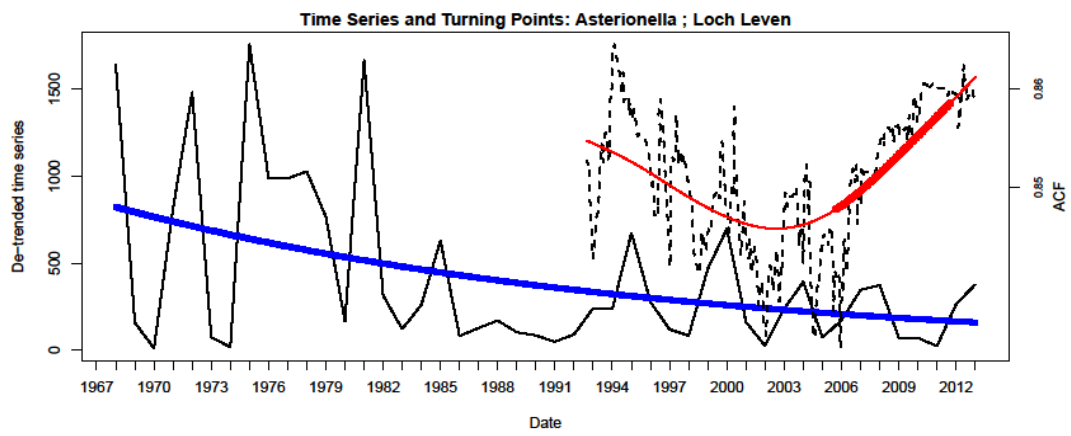
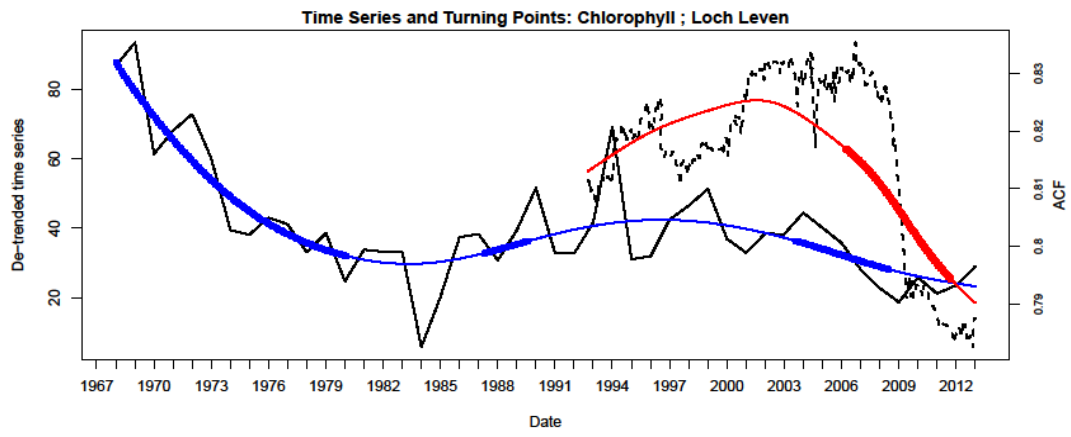




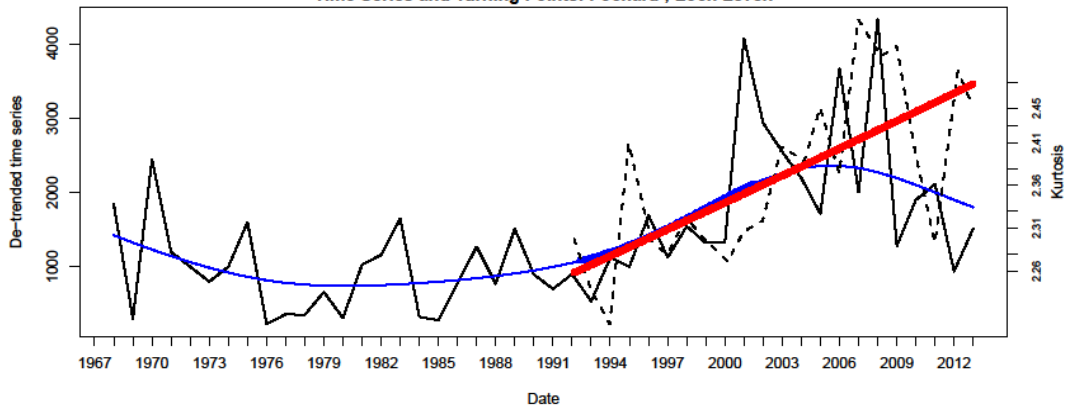




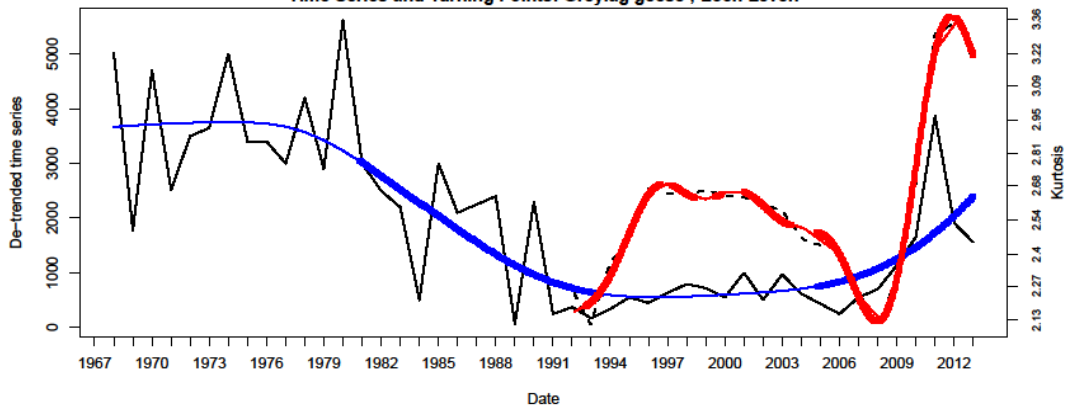




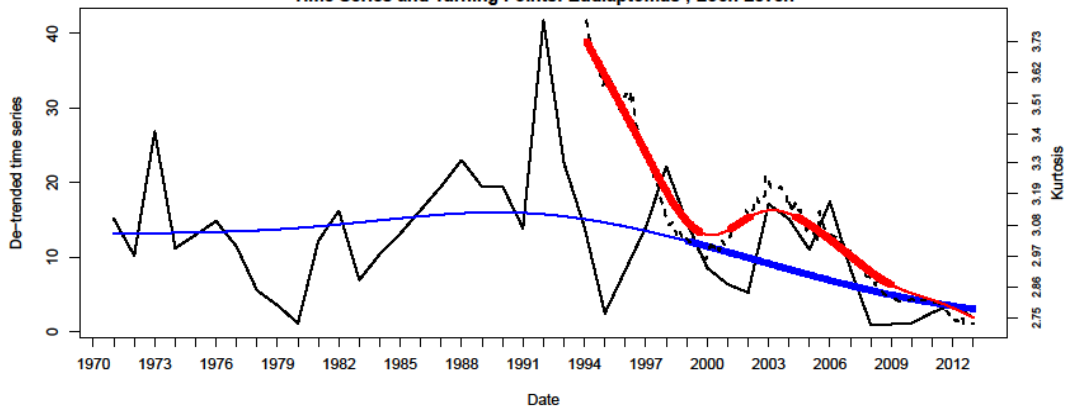
Time Series and Turning Points: Pochard ; Loch Leven

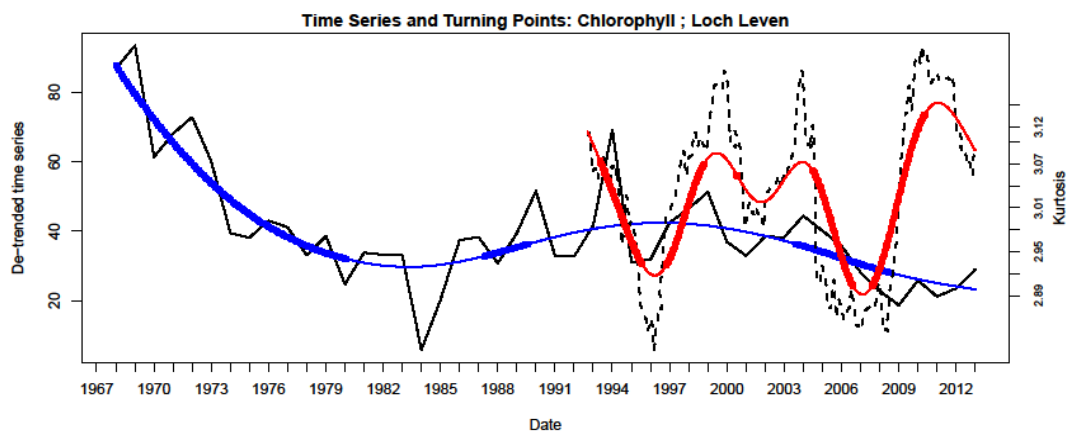
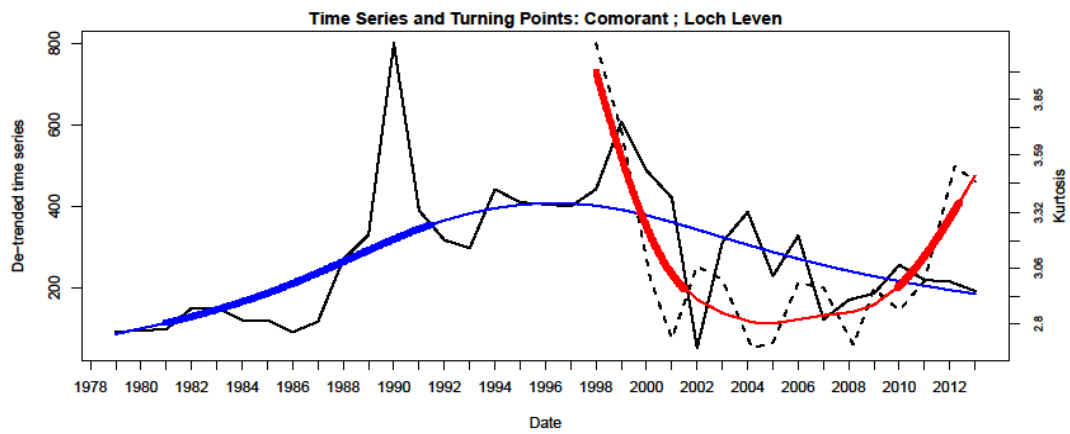
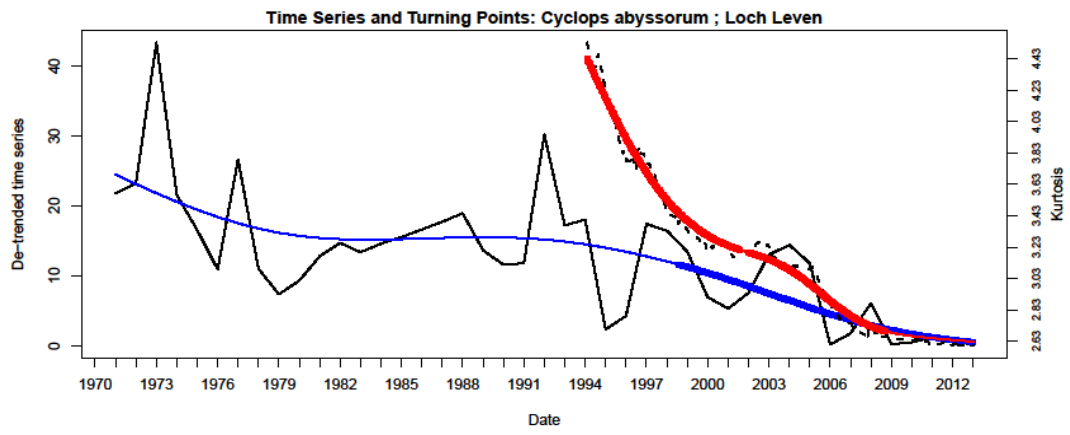


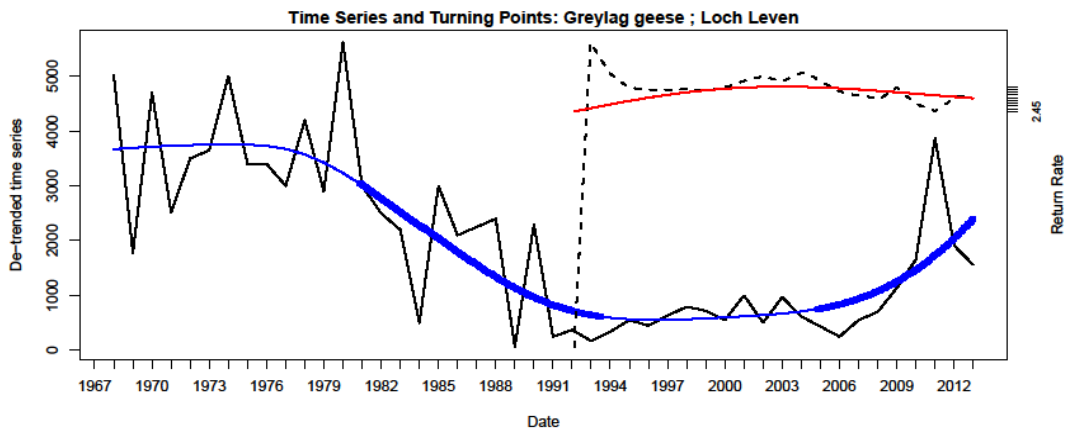
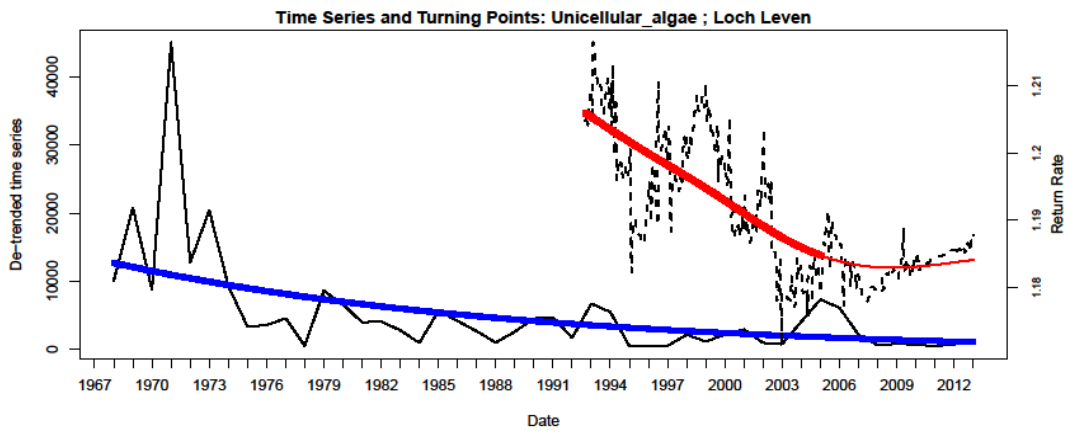
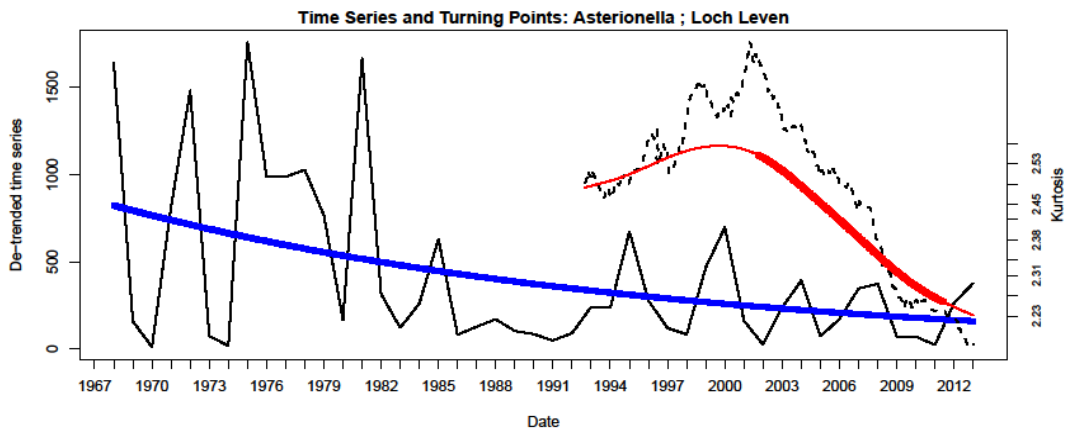
Time Series and Turning Points: Greylag geese ; Loch Leven

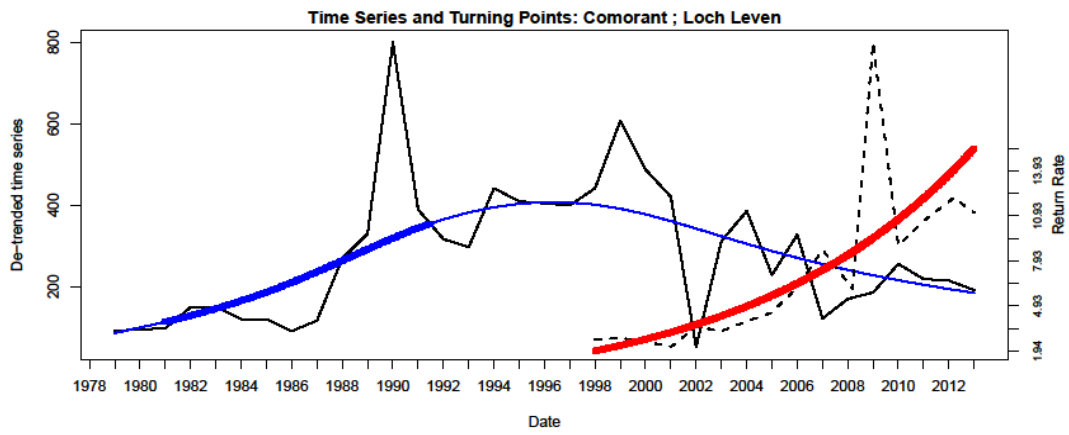
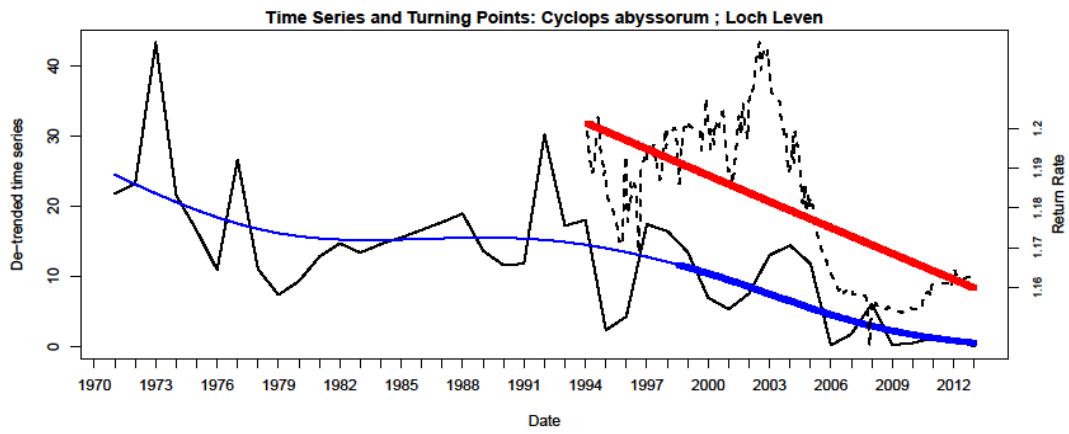
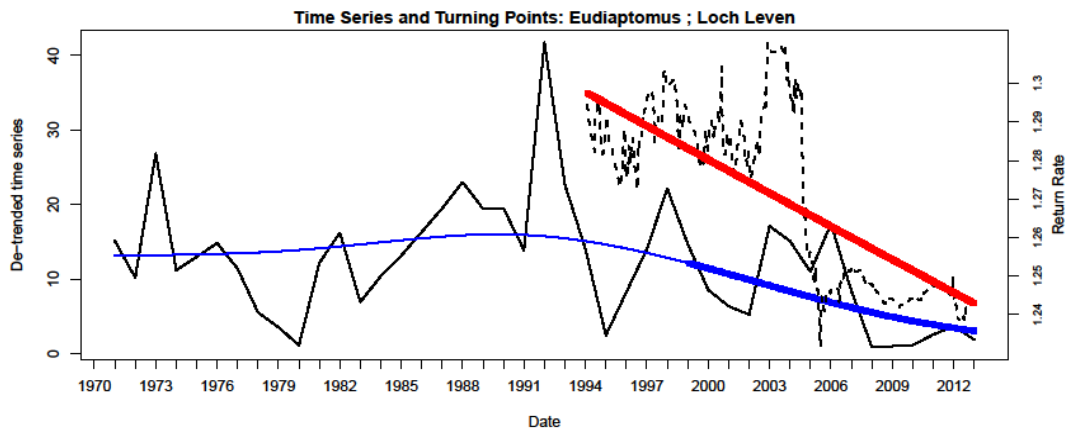


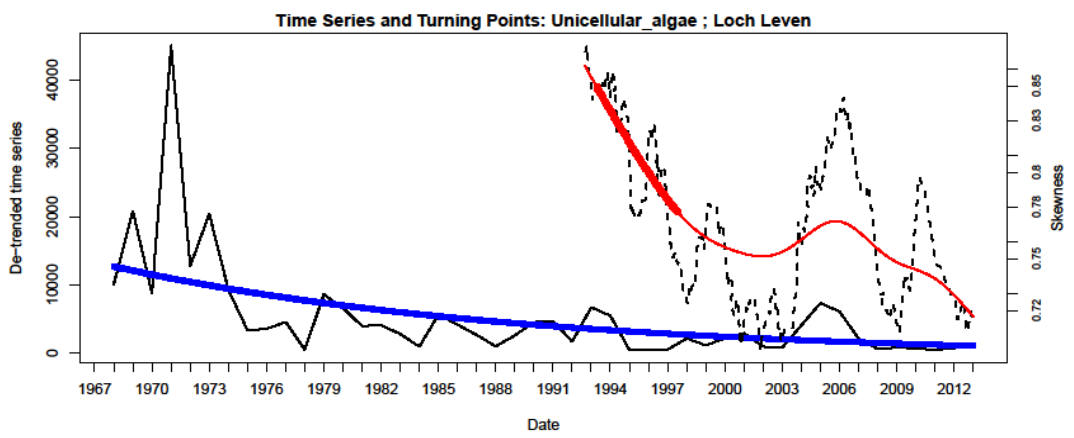
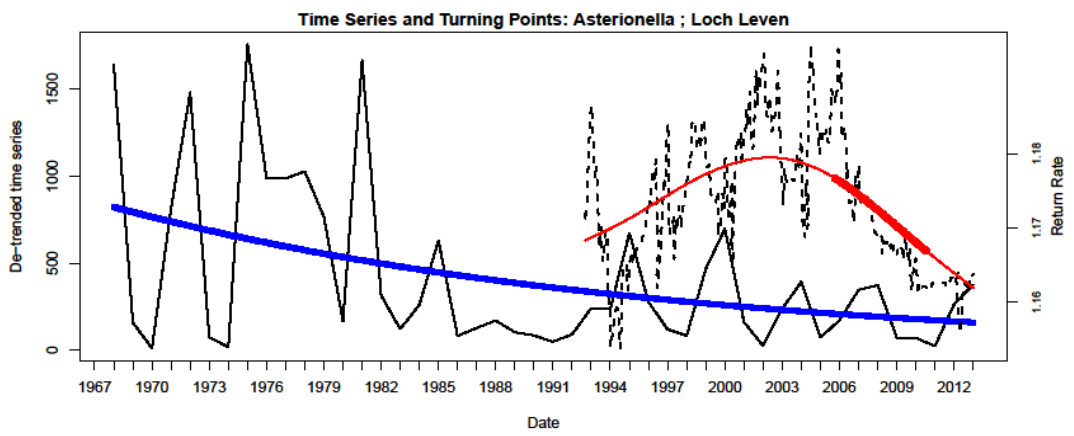
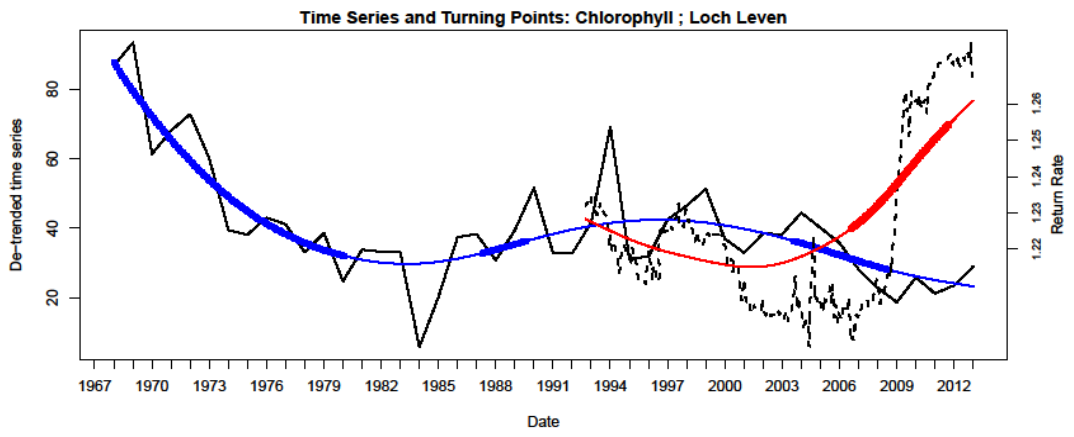
Time Series and Turning Points: Eudiaptomus ; Loch Leven

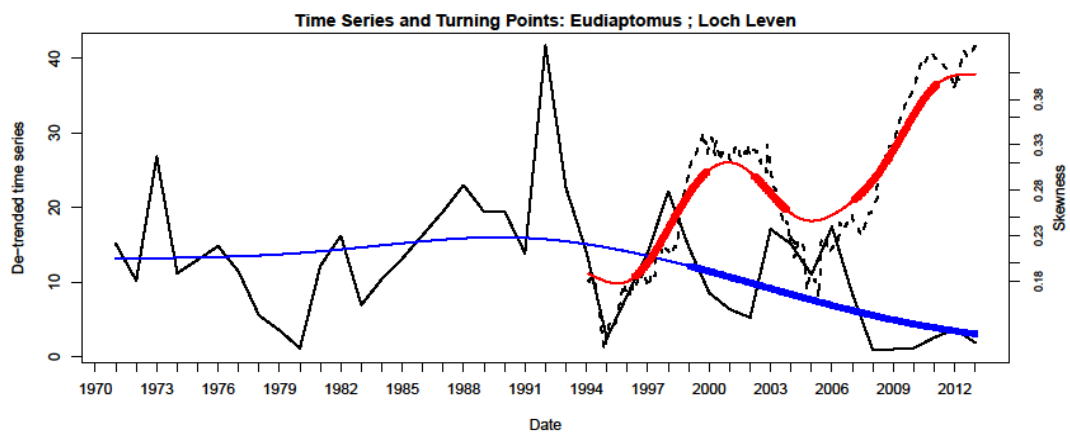
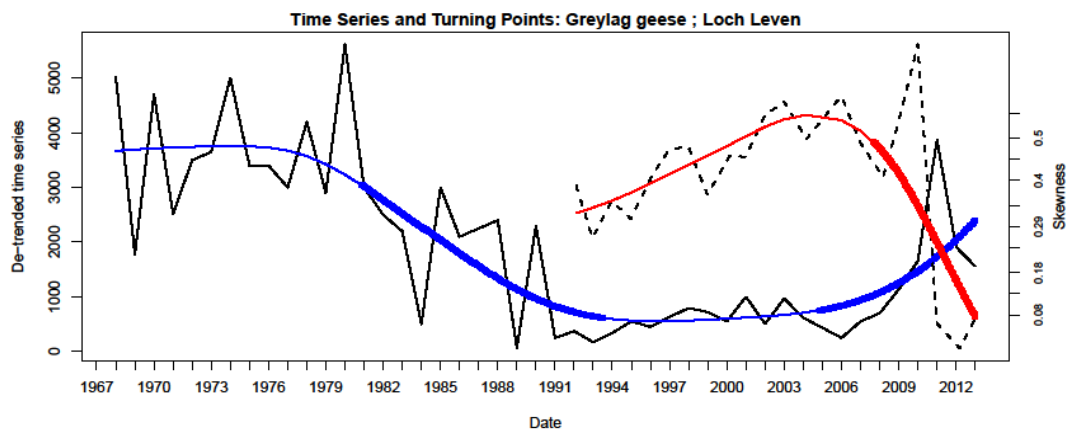
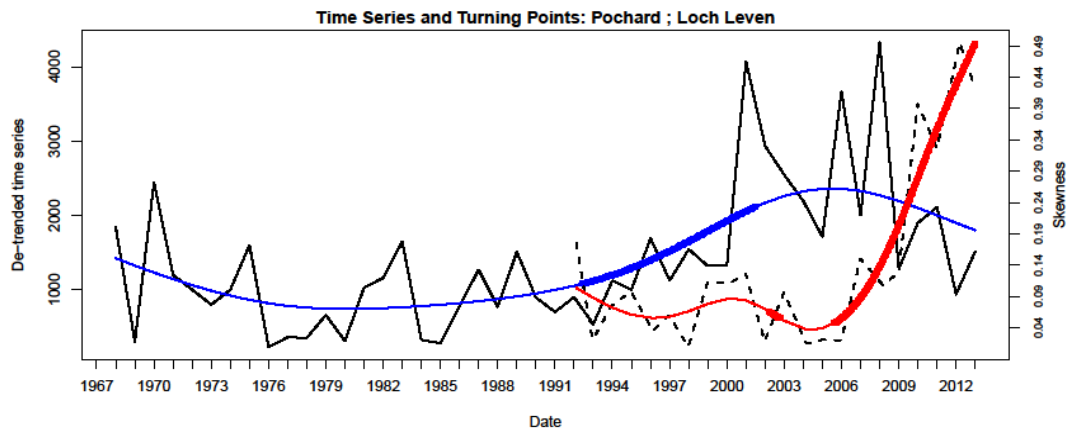


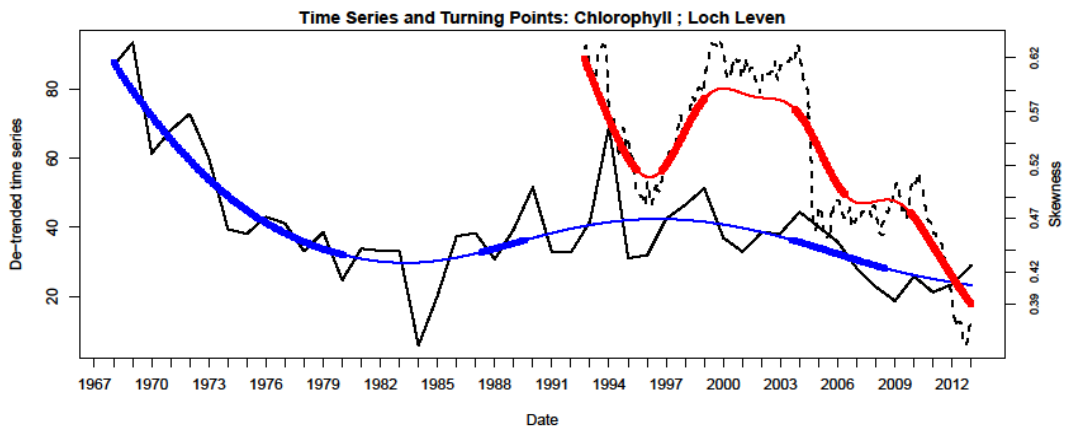
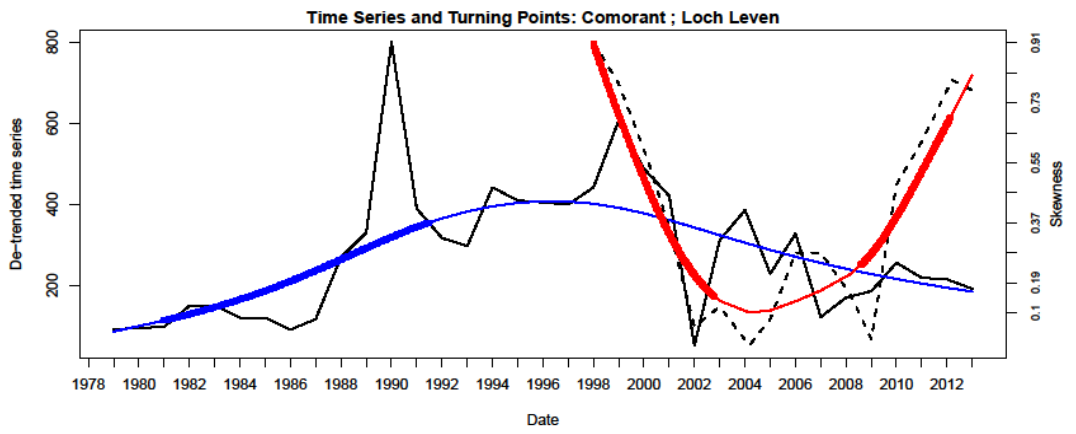
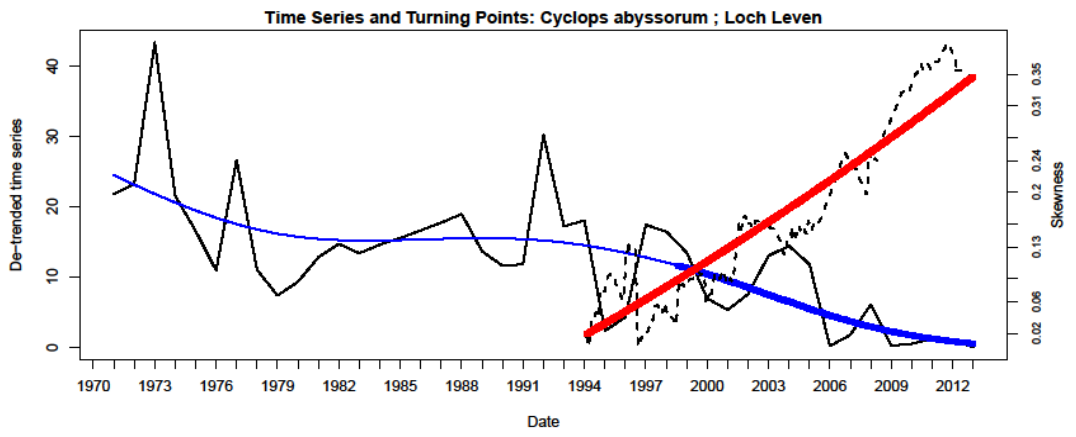


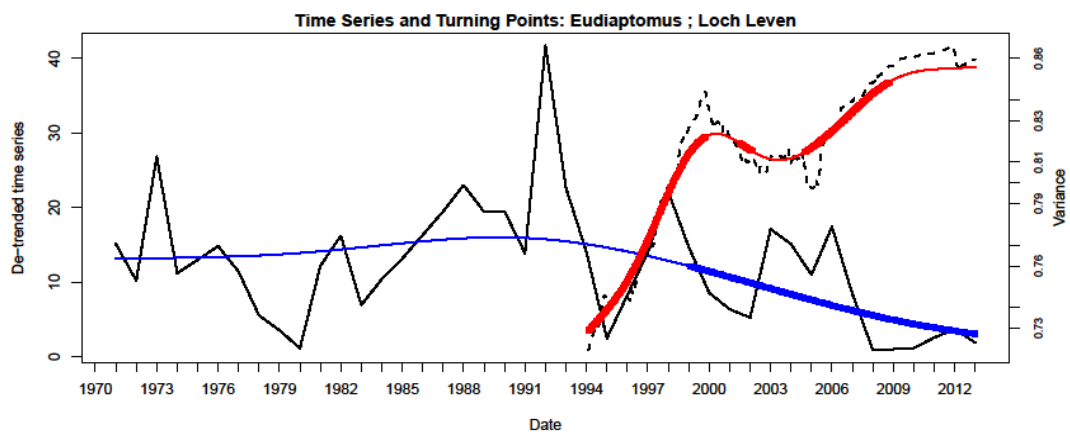
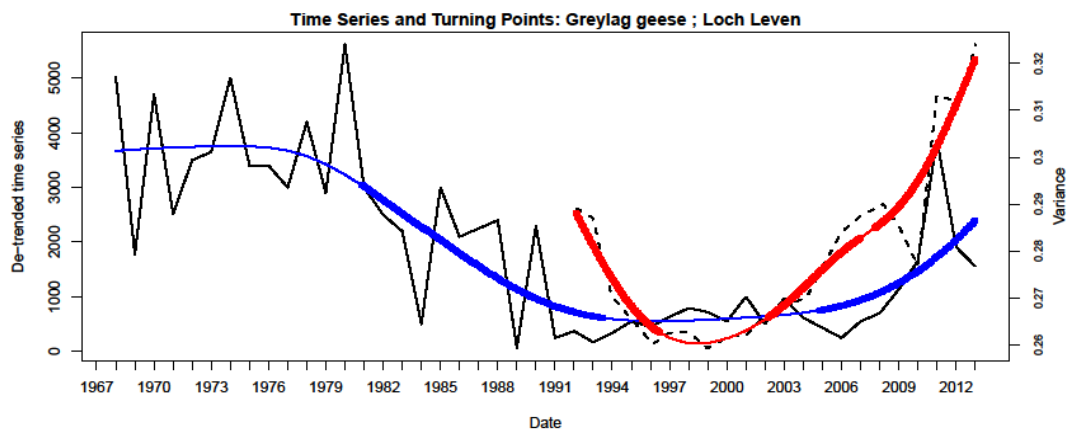
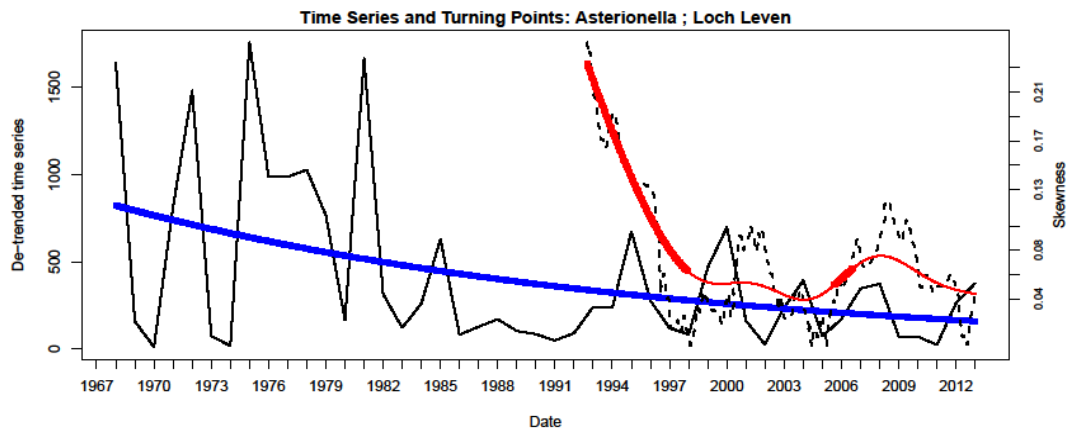


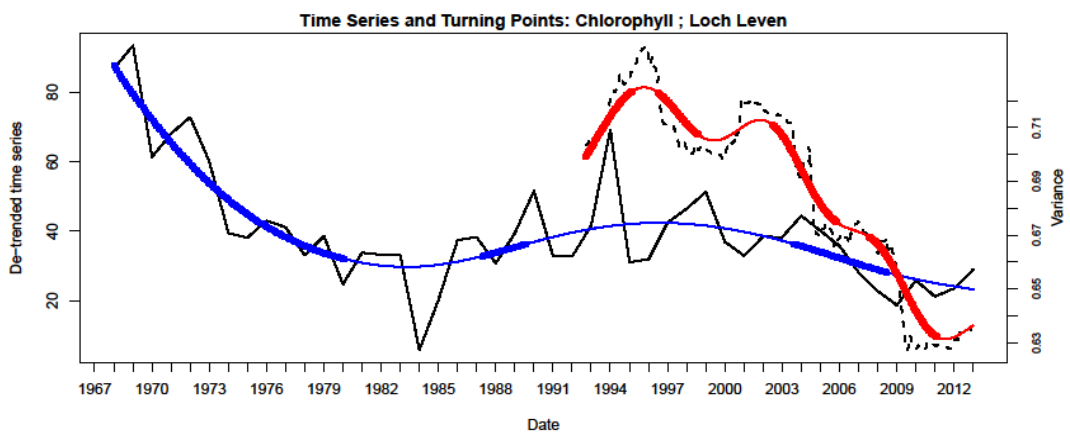
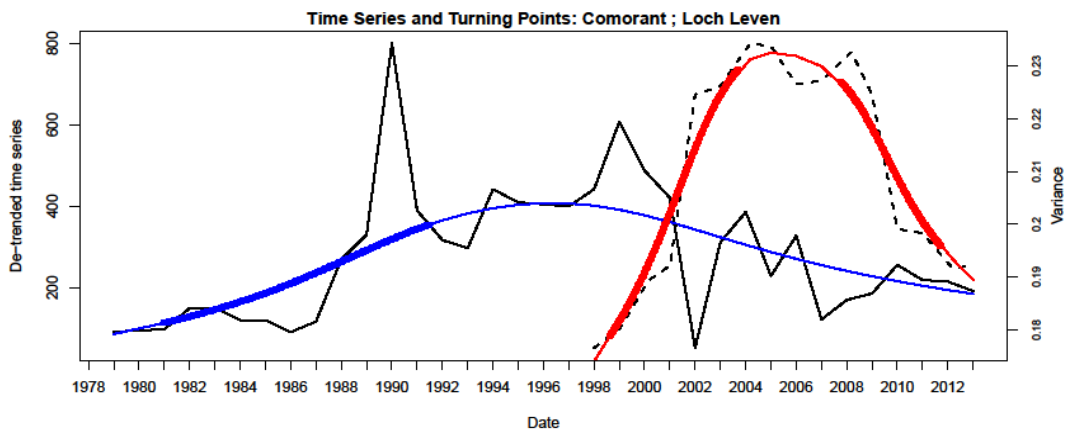
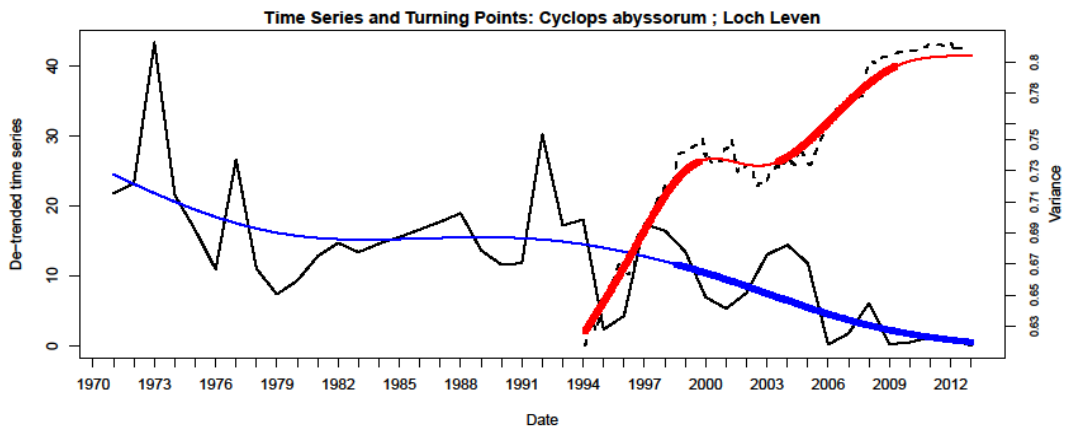


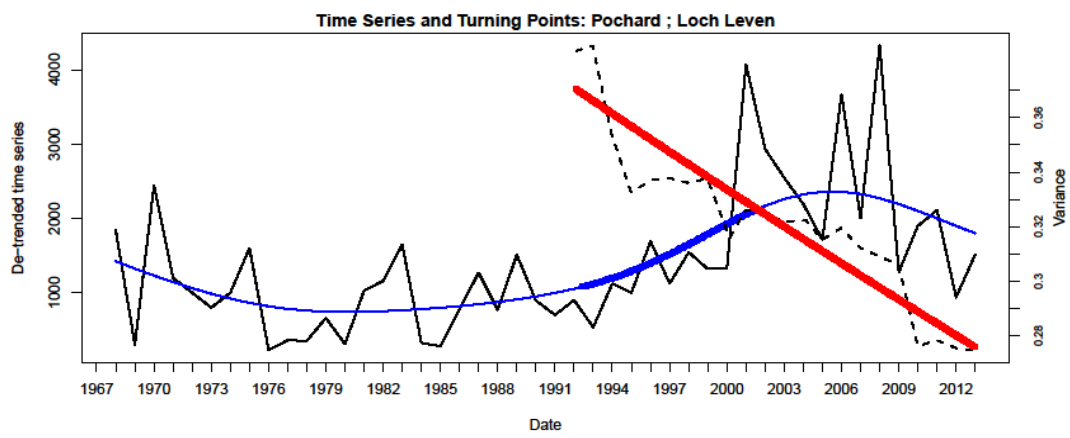
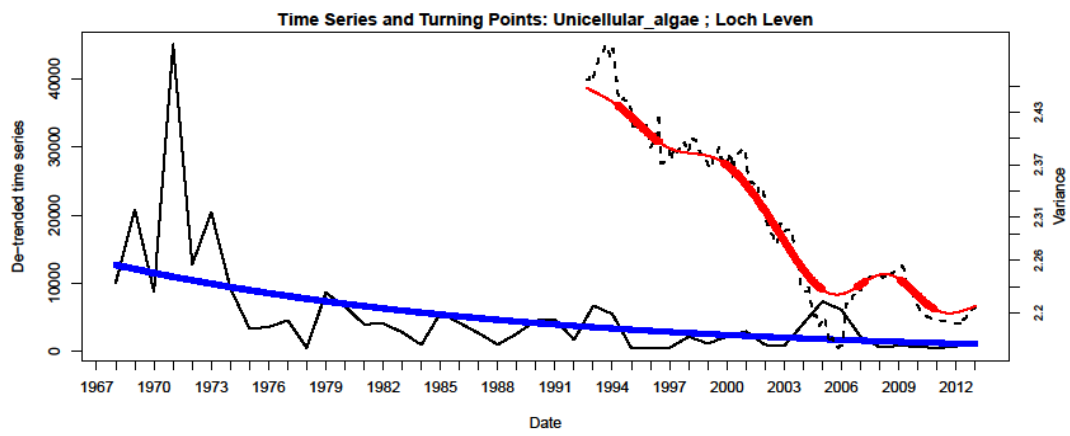
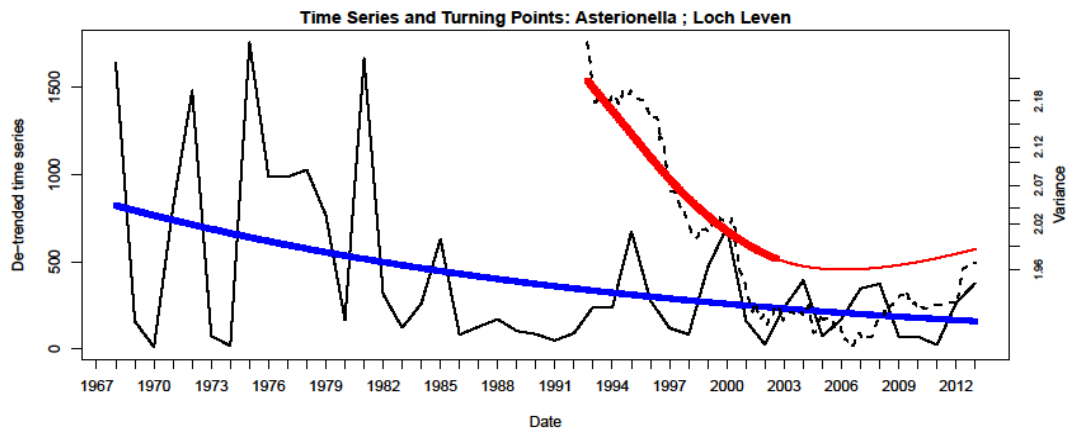


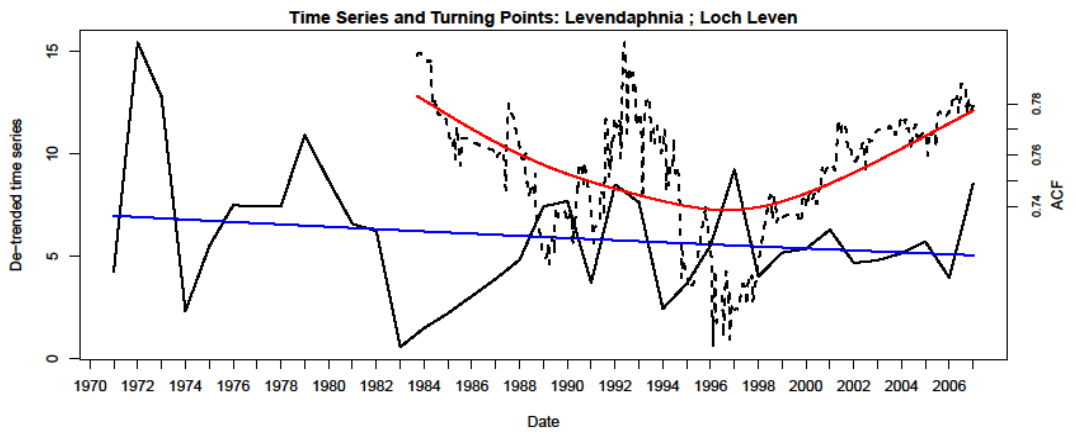
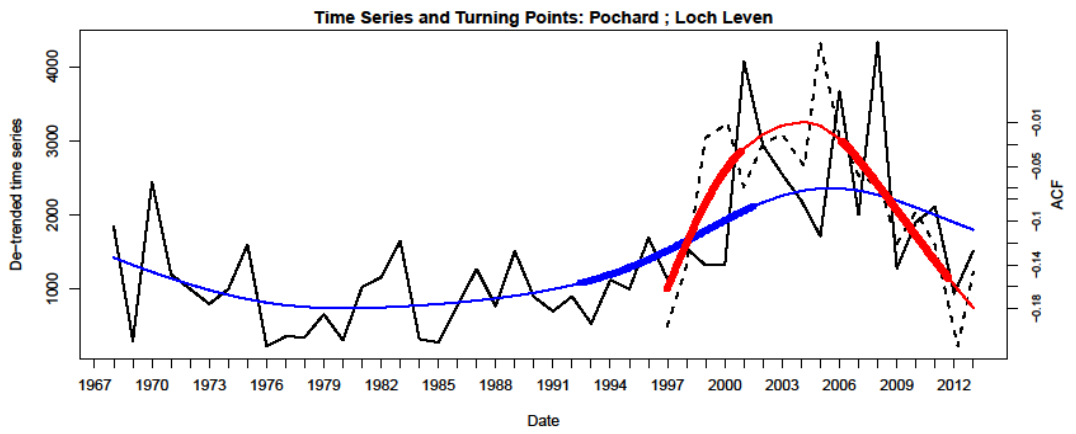
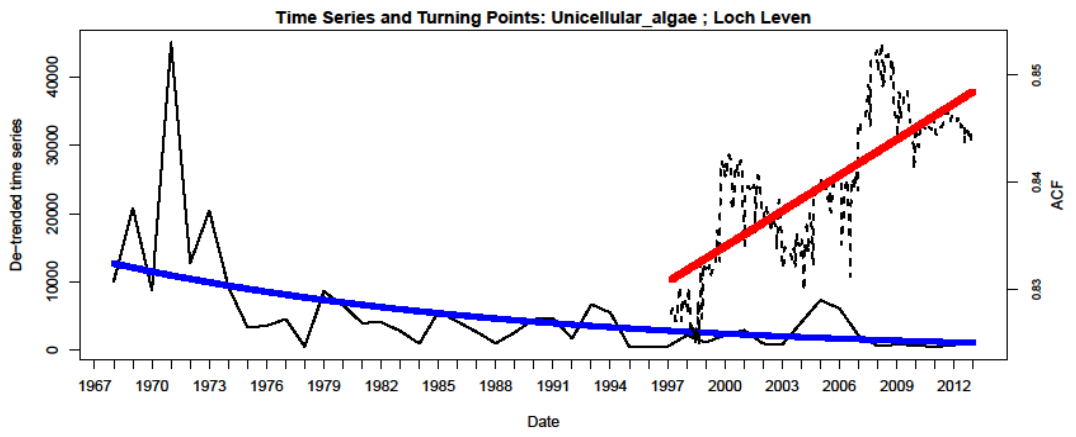


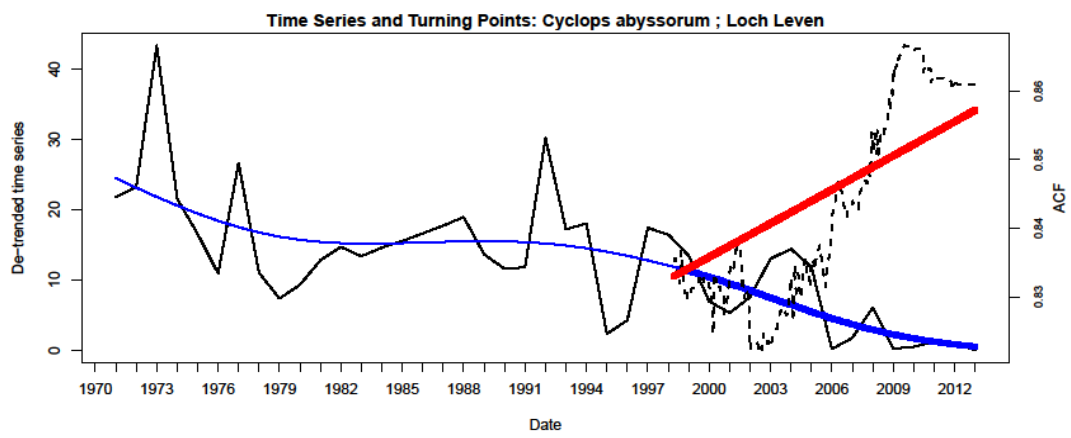
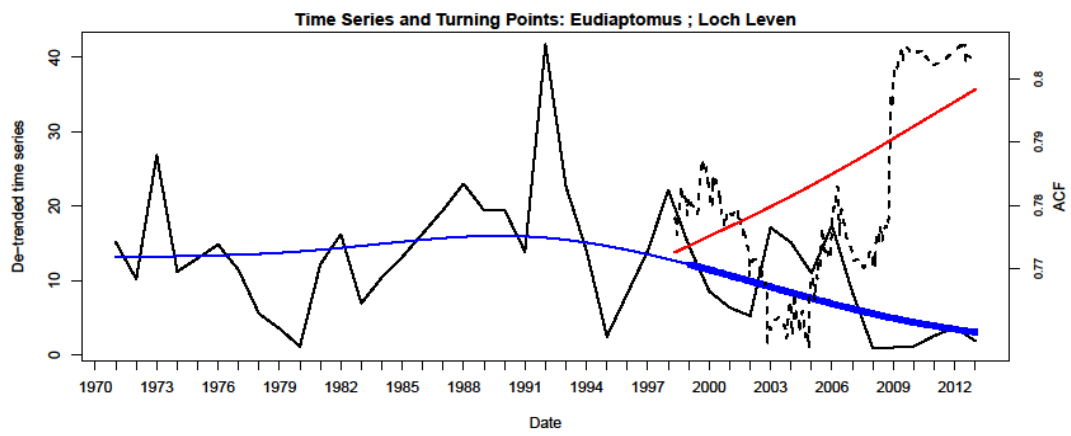
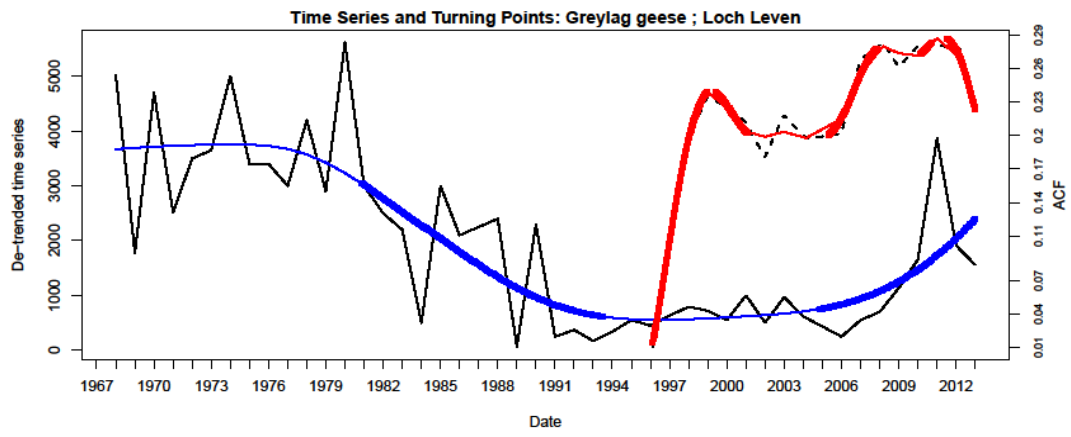


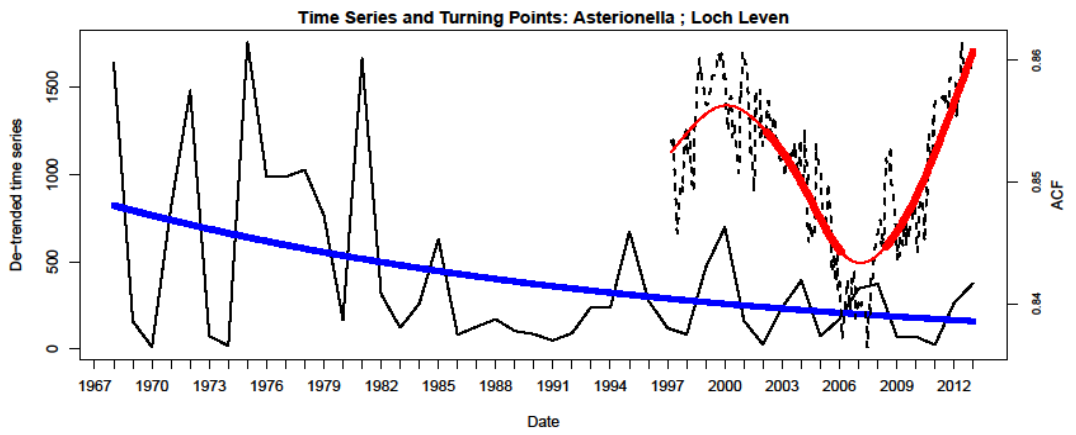
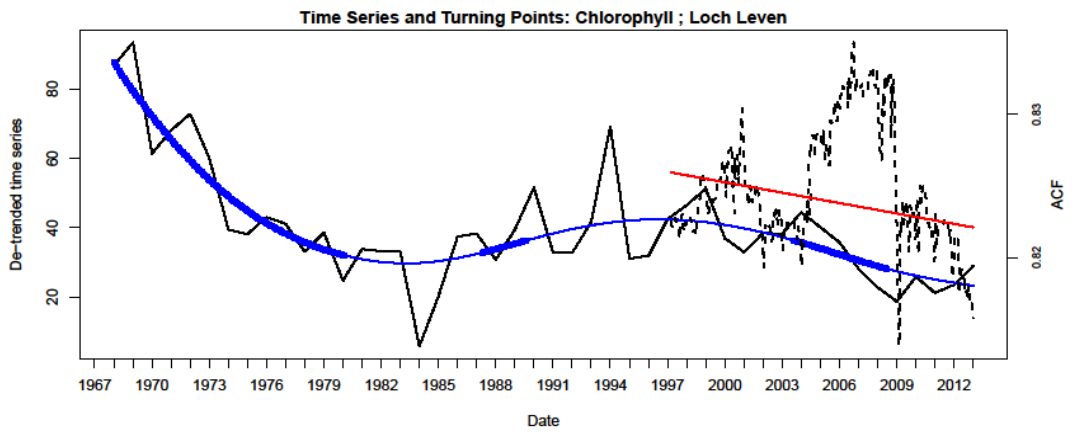
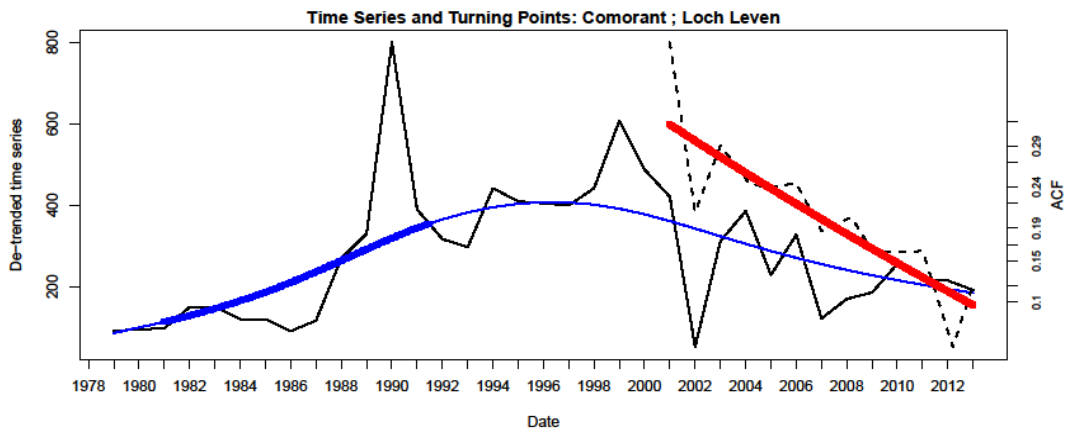


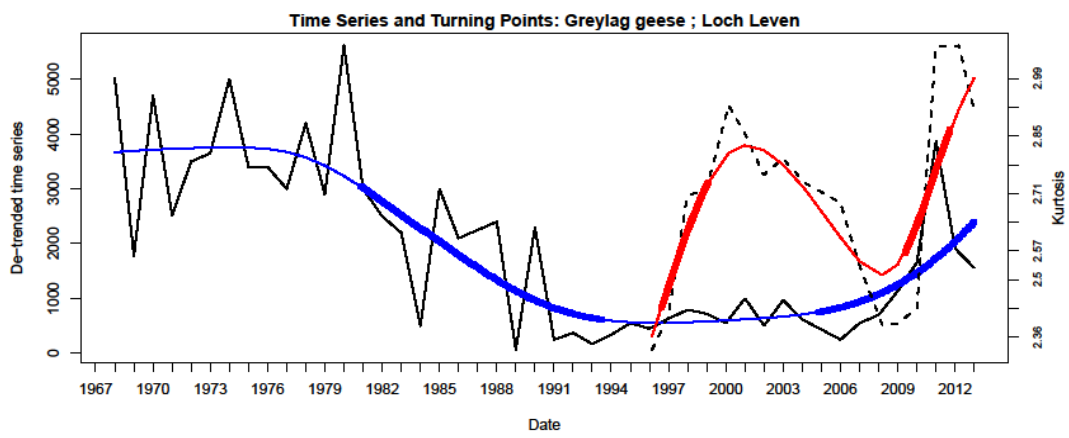
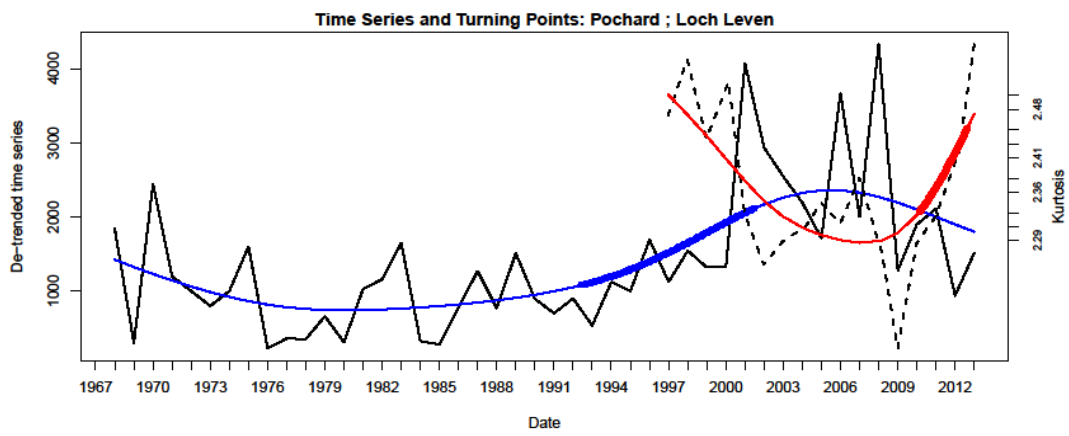
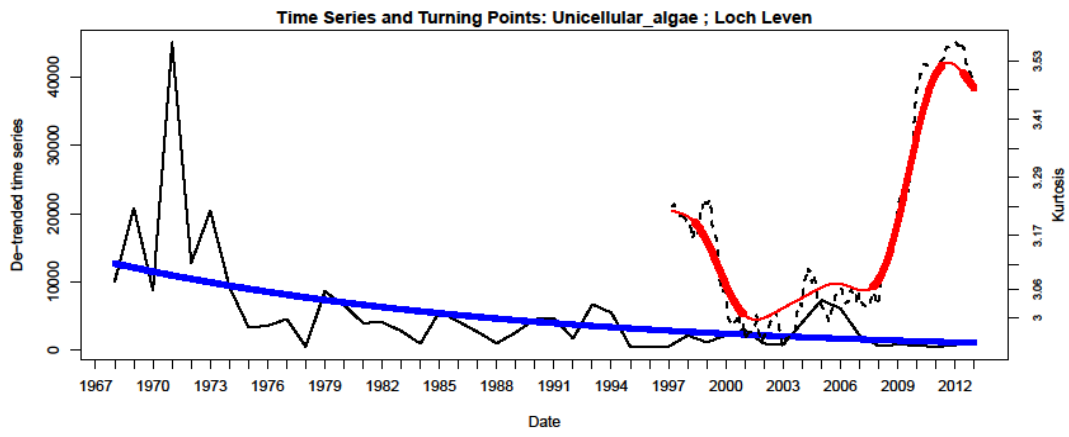


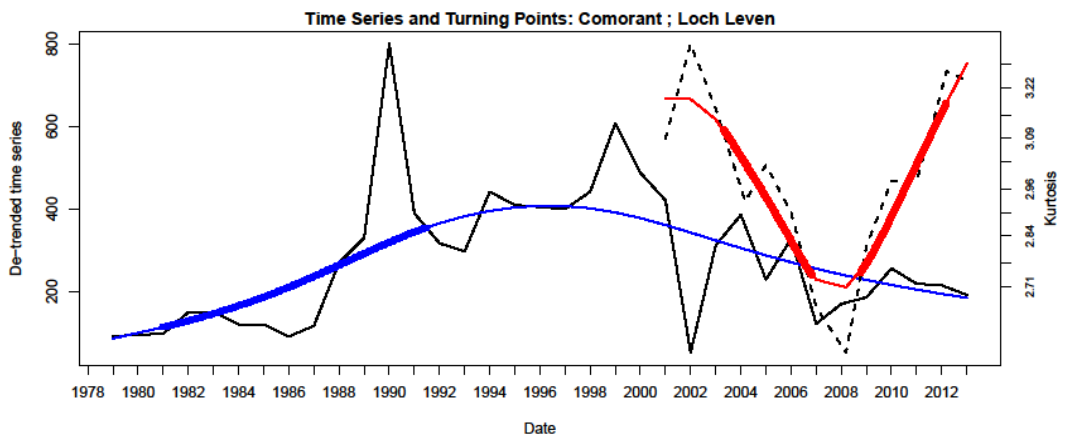
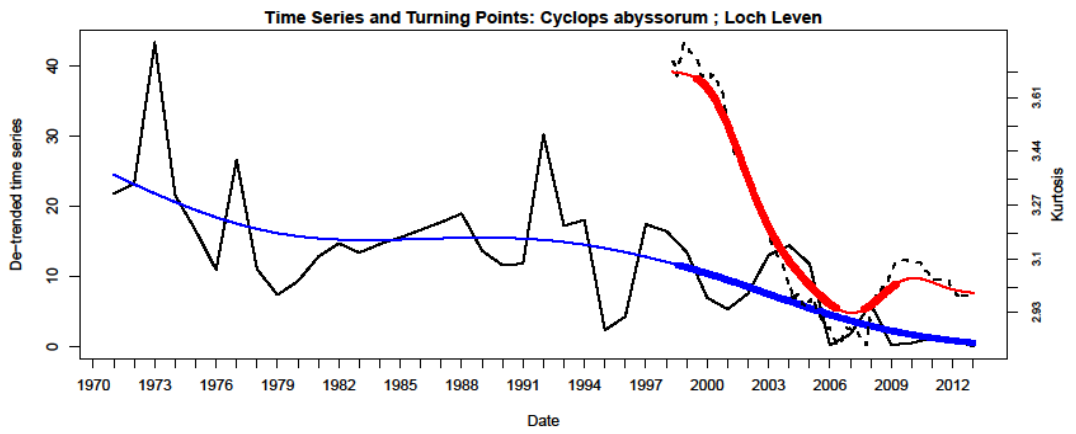
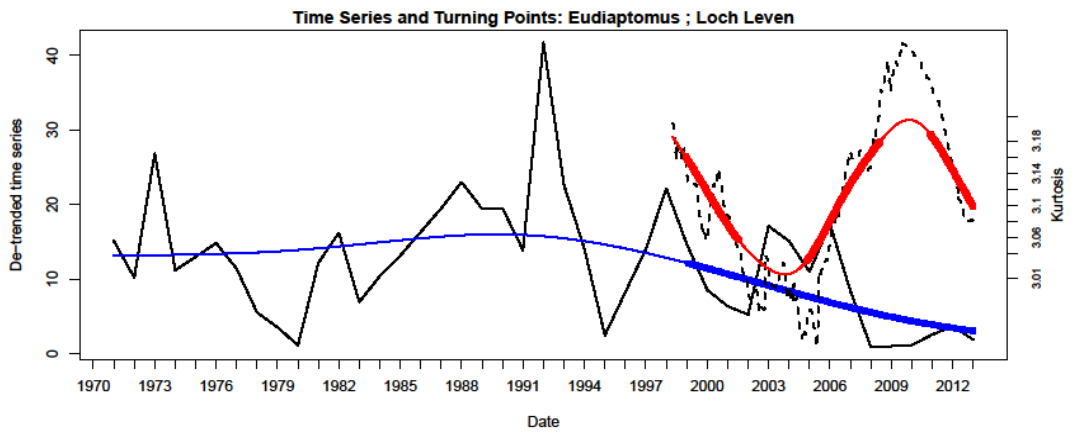


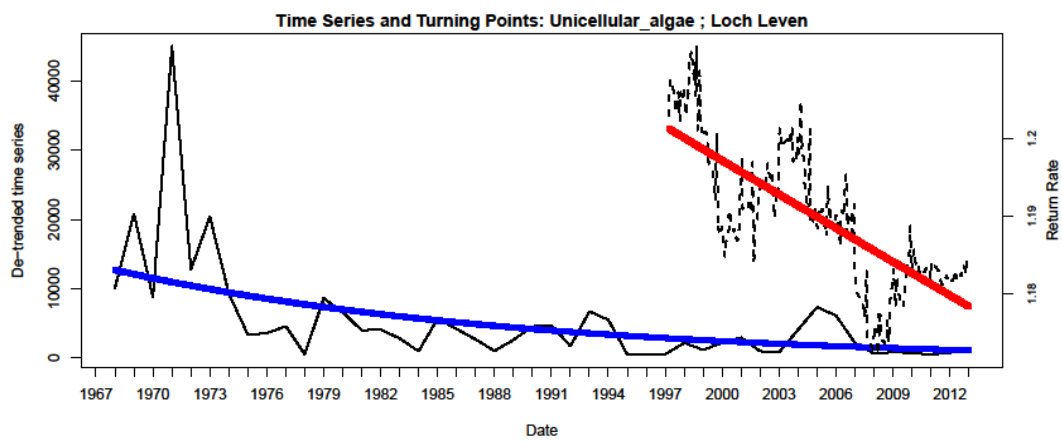
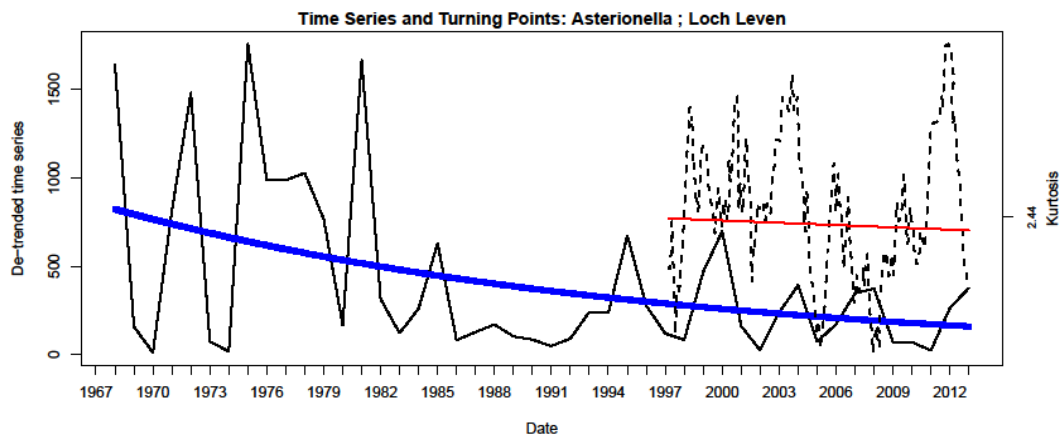
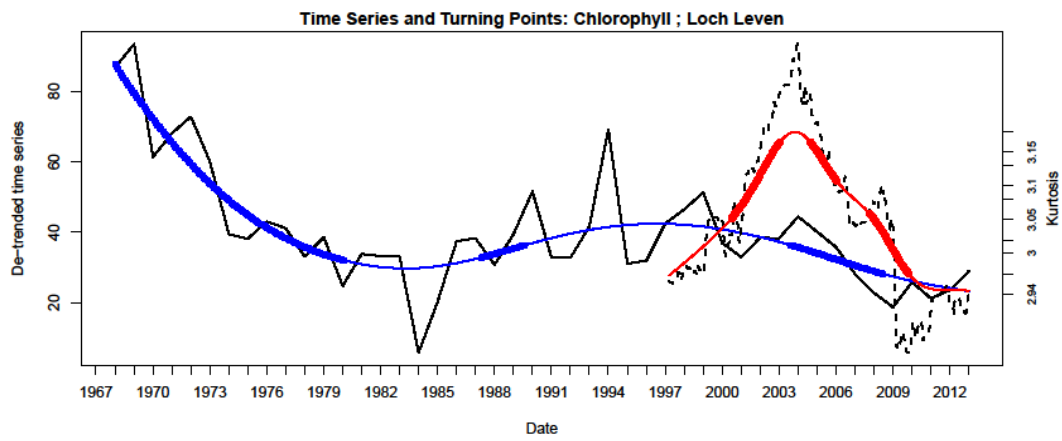


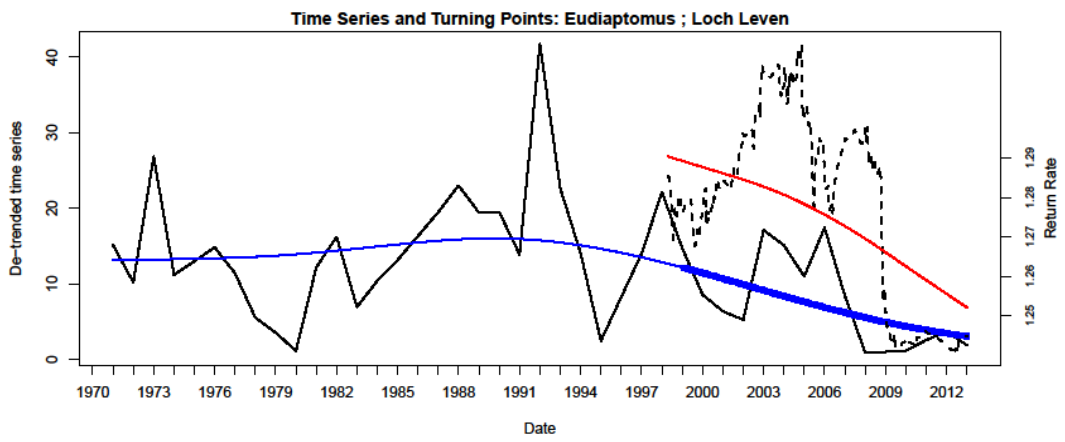
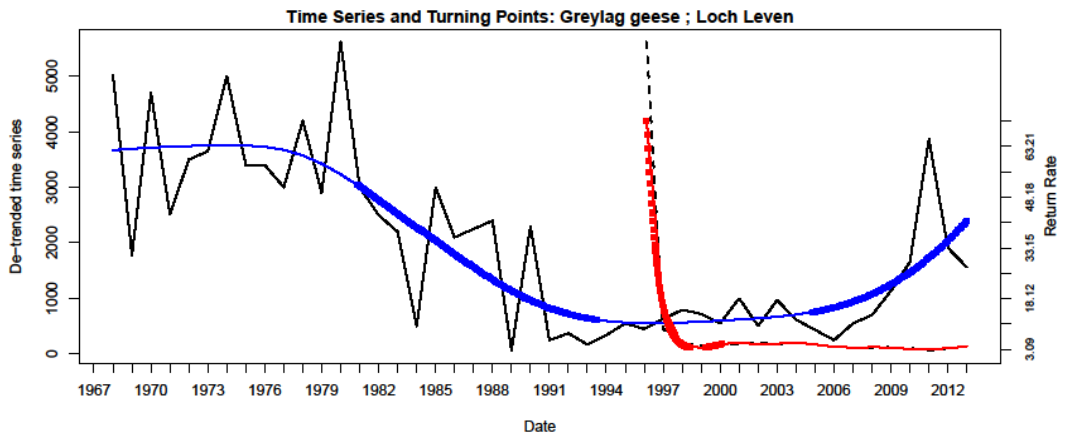
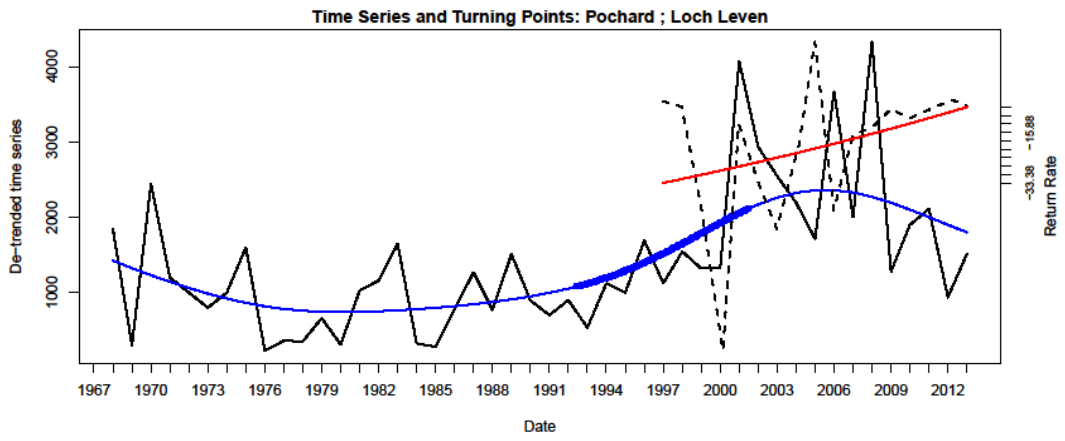


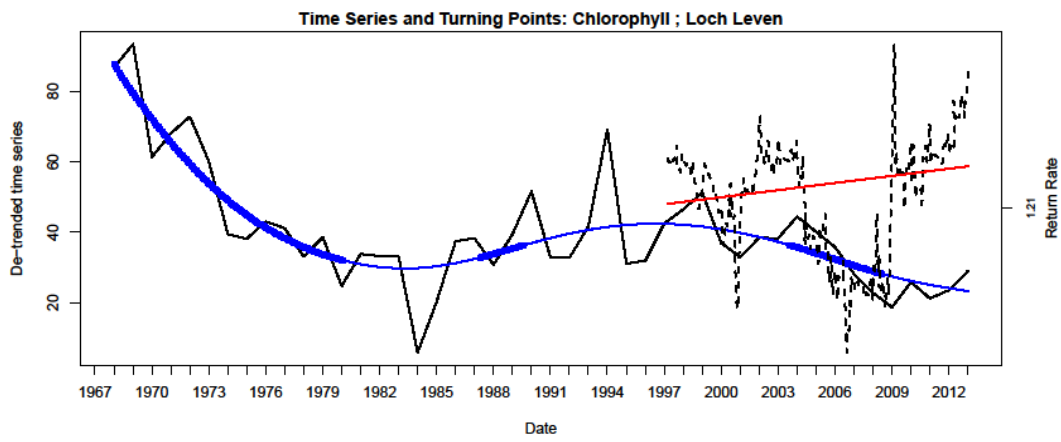
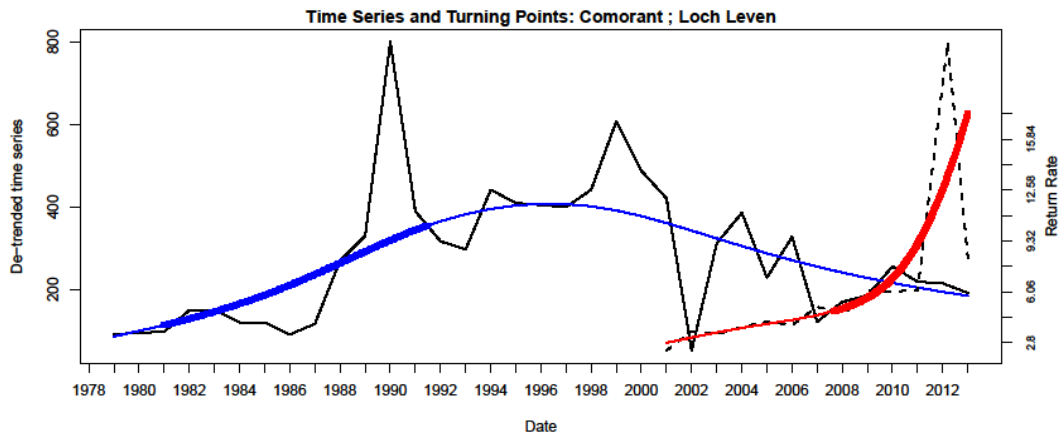
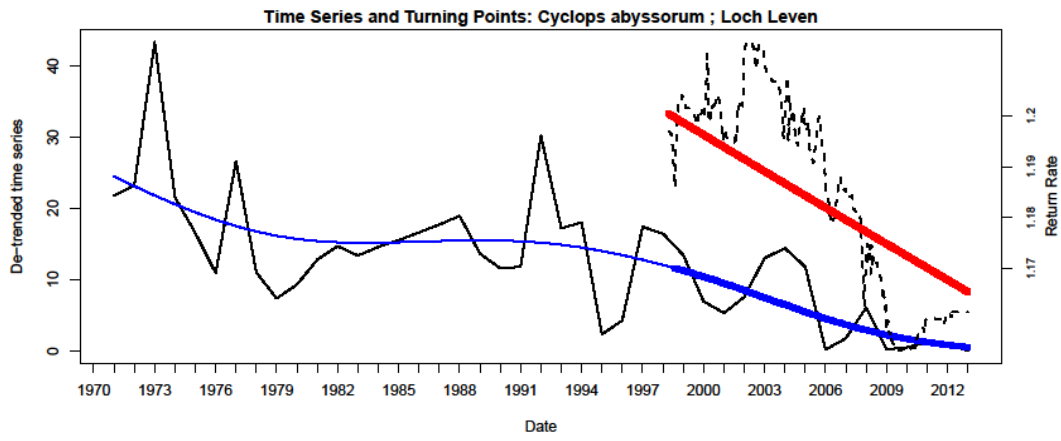


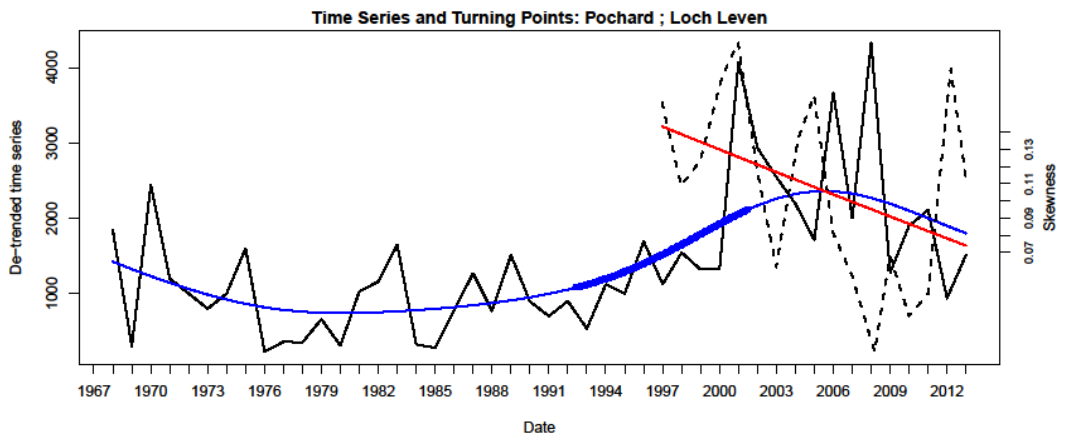
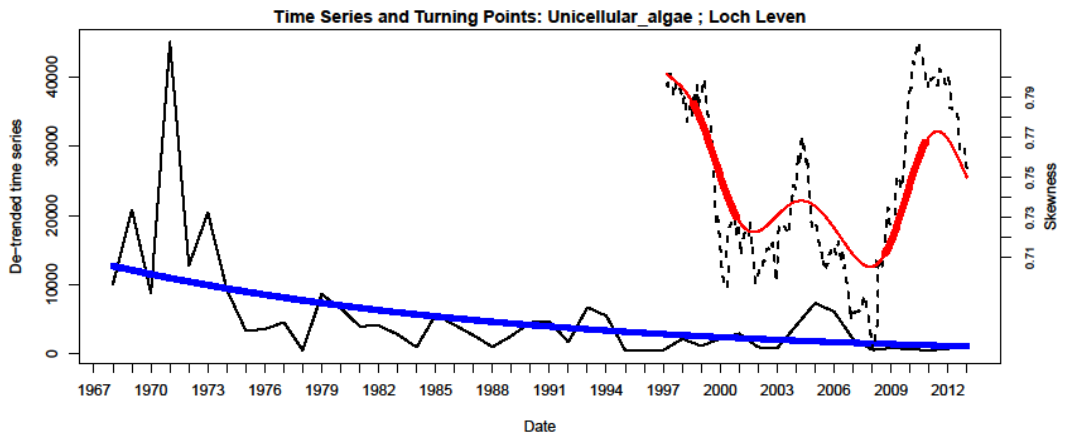
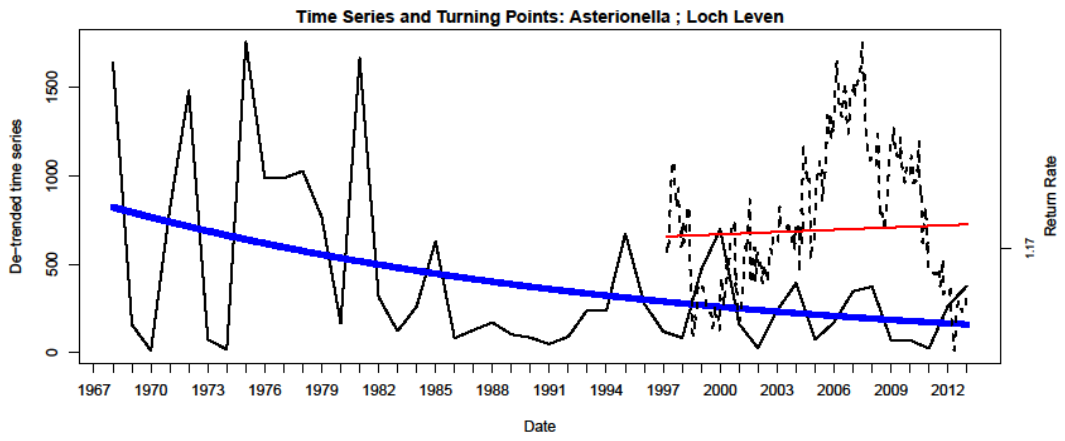


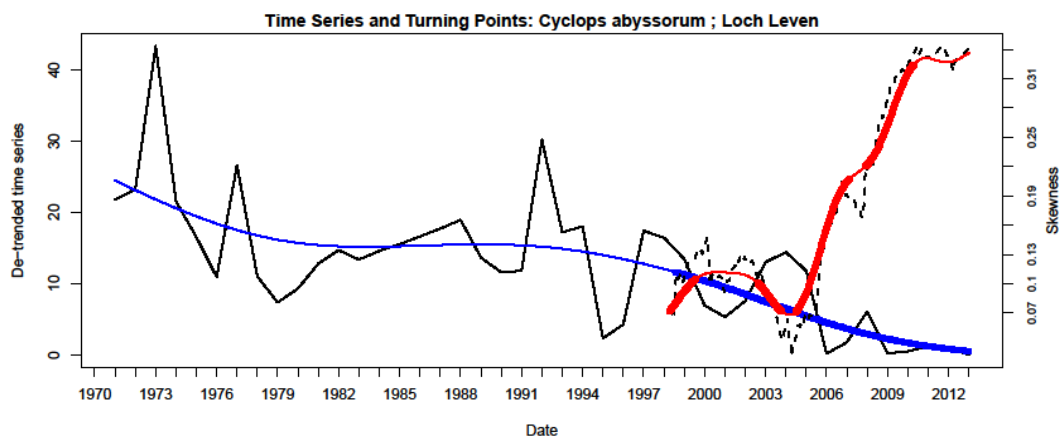
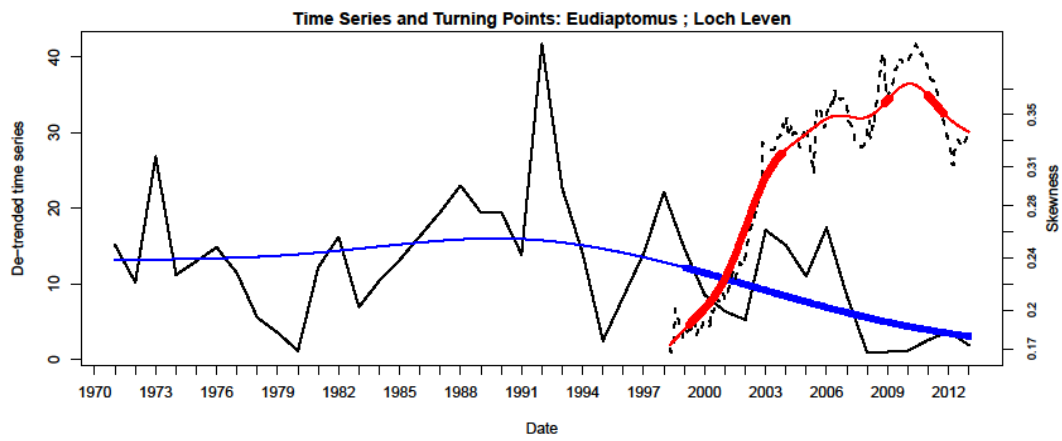
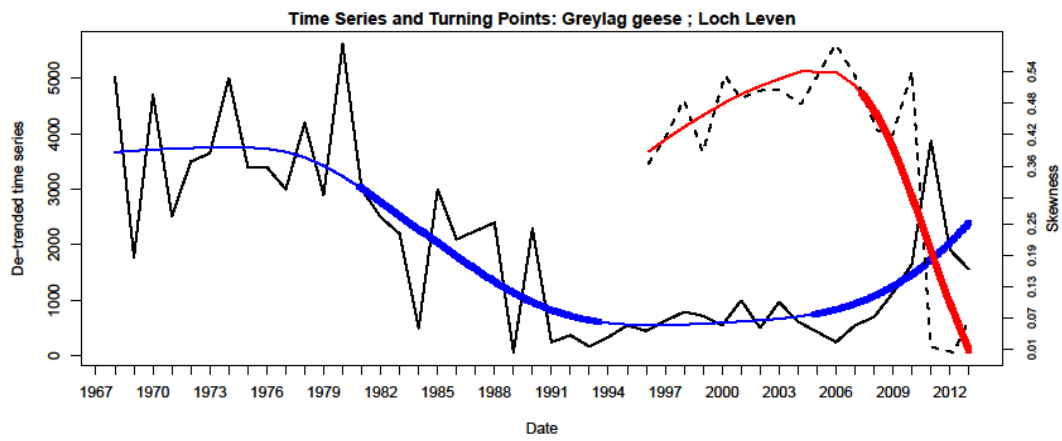


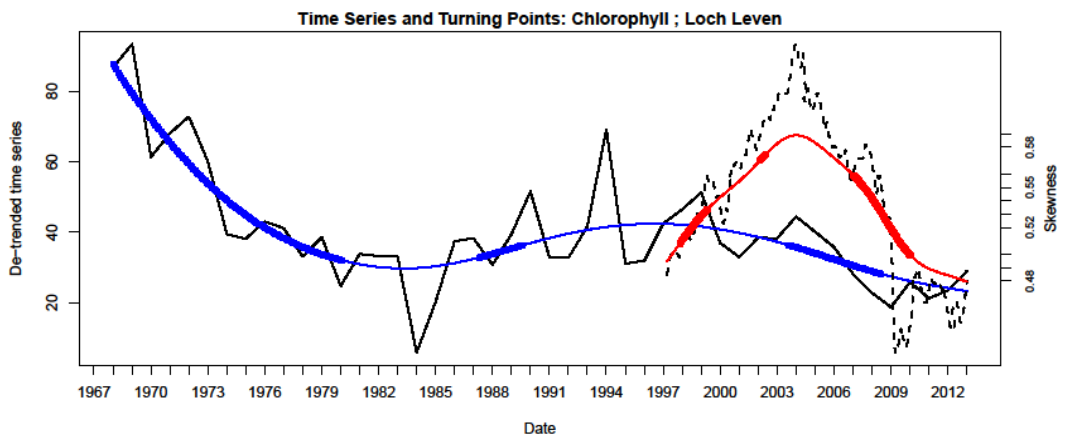
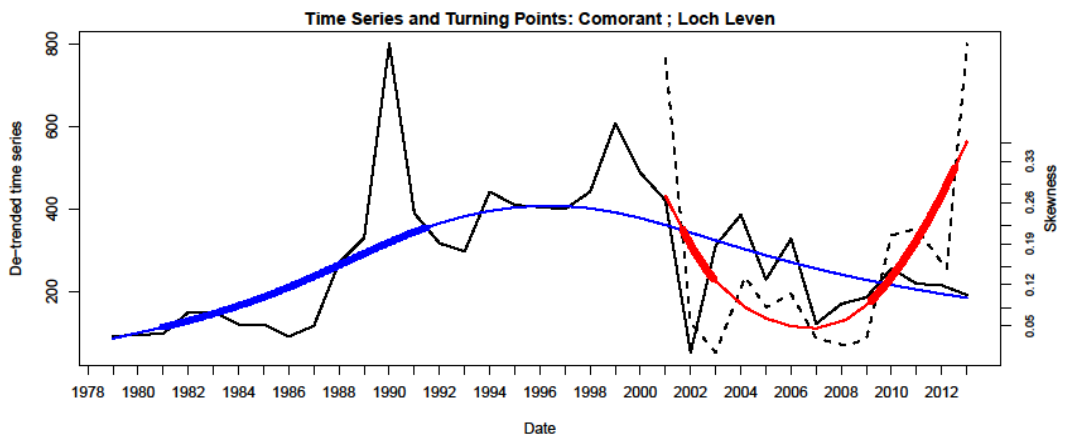


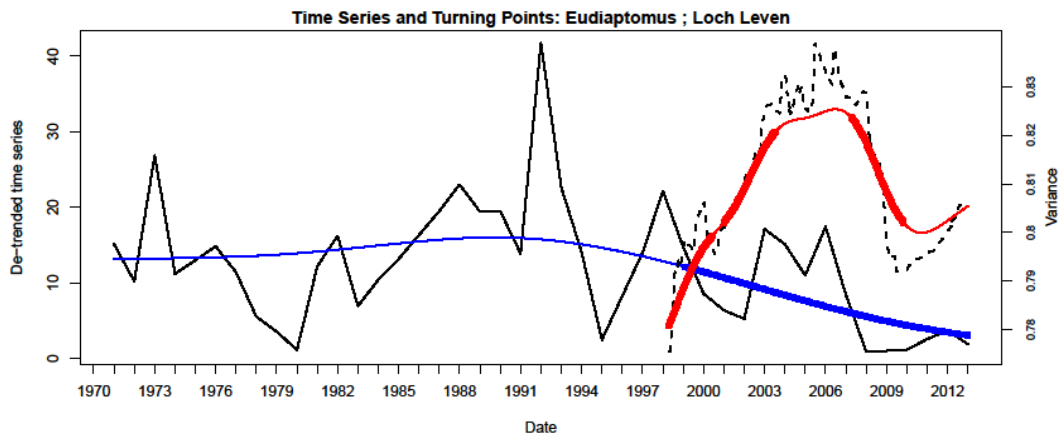
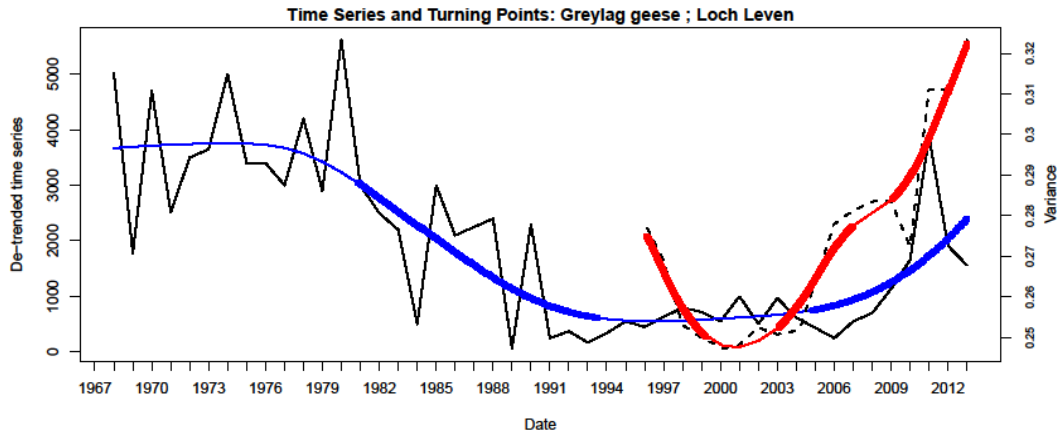
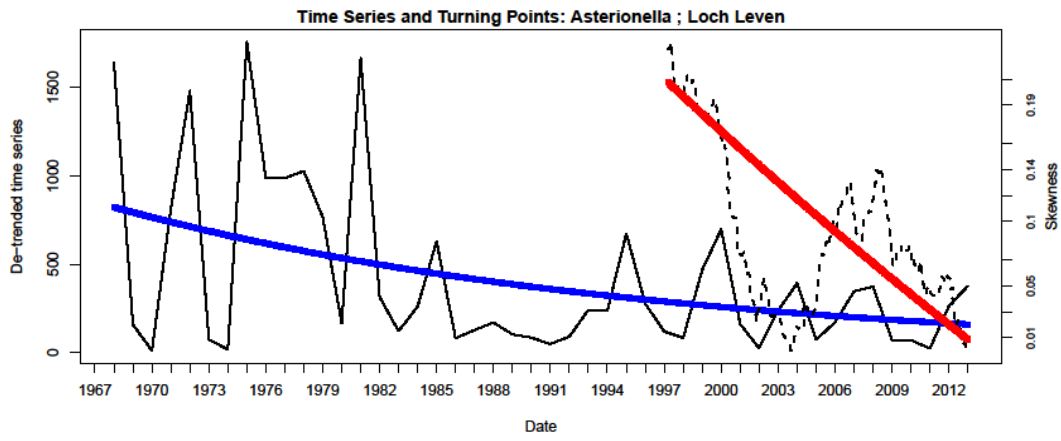


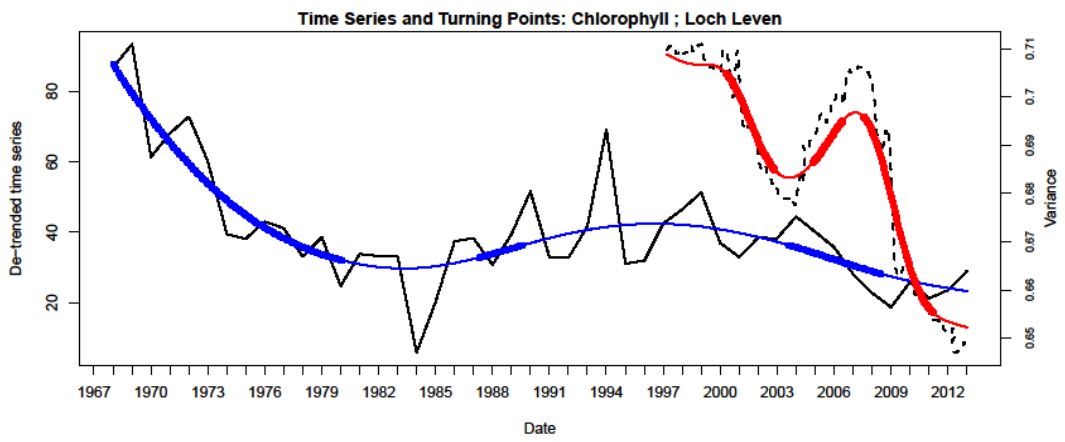
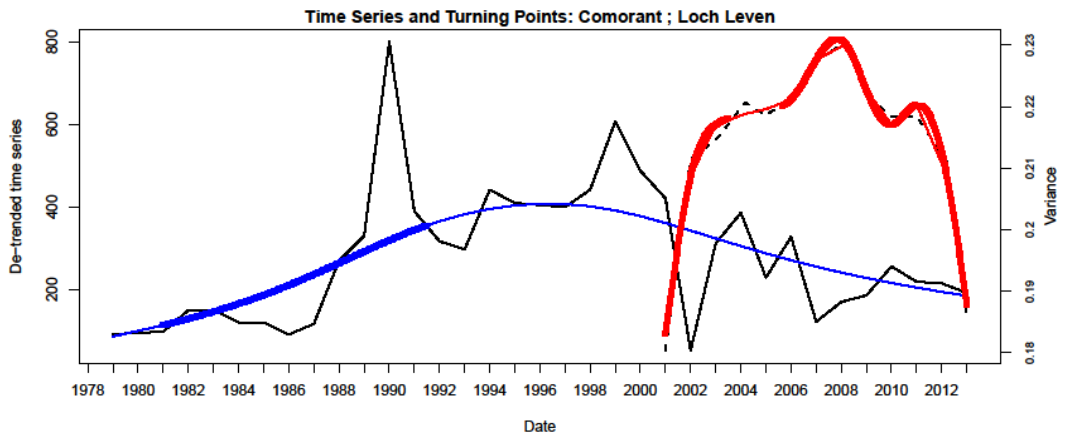
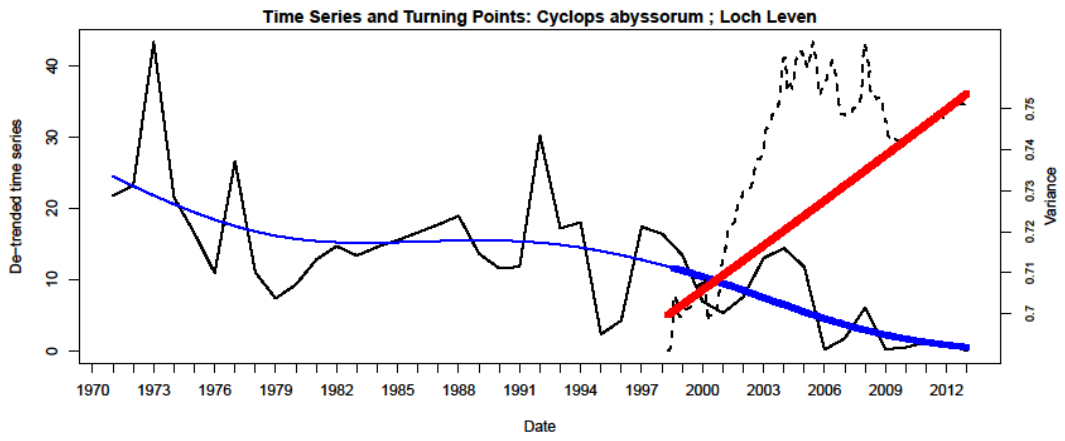


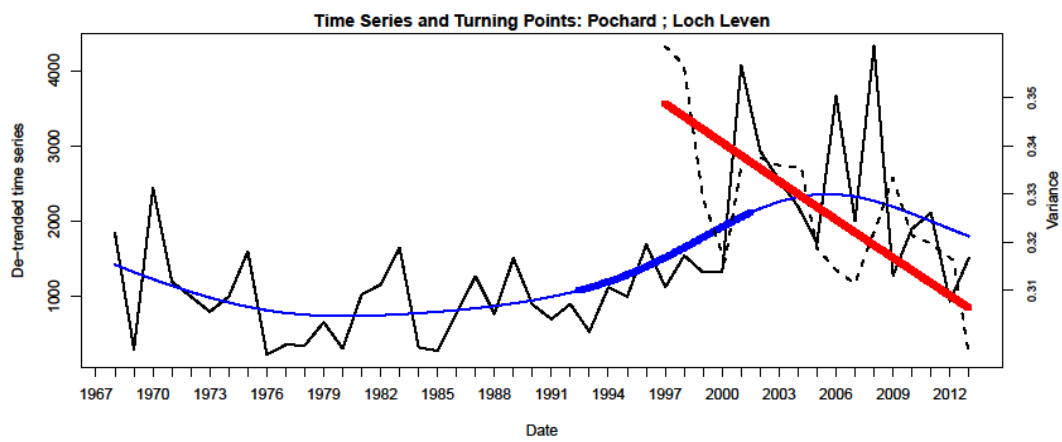
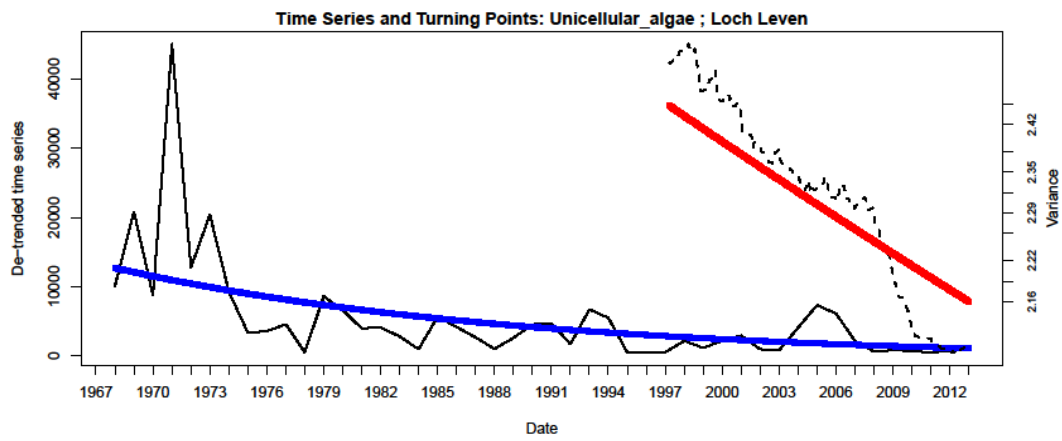
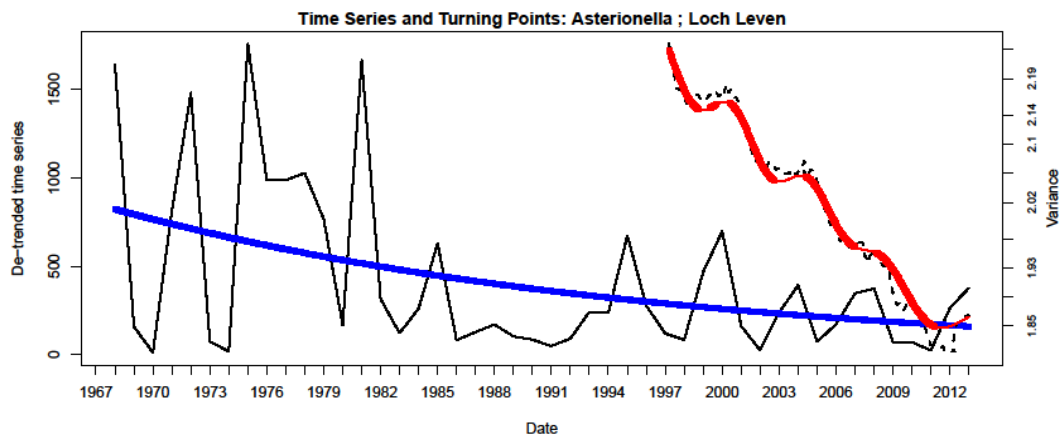












1 Appendix B

2

3

4 **Effective management of ecological resilience – are we there yet?**

5

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9

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21

22

23 Running head: Resilience-based environmental management

24 **Summary**

- 25 1. Ecological resilience is developing into a credible paradigm for policy development and
26 environmental management for preserving natural capital in a rapidly changing world.
27 However, resilience emerges from complex interactions, limiting the translation of theory into
28 practice.
- 29 2. Main limitations include: (i) difficulty in quantification and detection of changes in ecological
30 resilience; (ii) a lack of empirical evidence to support preventative or proactive management
31 and (iii) difficulties in managing processes operating across socio-ecological systems that vary
32 in space and time.
- 33 3. We highlight recent research with the potential to address these limitations including new
34 and/or improved indicators of resilience and tools to assess scale as a driver of resilience.
- 35 4. *Synthesis and applications.* Effective resilience-based management must be adaptive in
36 nature. To support this we propose an operational model using resilience-based iterative
37 management actions operating across scales.

38
39 **Key-words:** Resilience, preventative, policy, research, society, ecosystem, management

40 INTRODUCTION

41

42 Environmental change threatens the complex ecological systems humanity relies upon at local,
43 regional and global scales. To support a 'resource-efficient, green and competitive low-carbon
44 economy' (European Environment Agency 2014), society must reduce pressures degrading
45 ecosystems. To achieve this, managers must reduce pressures and/or manipulate components of
46 ecosystems to achieve either no change (i.e. prevention of degradation) or change to a more desirable
47 ecological state (i.e. restoration of degraded systems). Despite the need to redress the pressures of
48 population growth and resource use (Carpenter *et al.* 2009), appropriate adaptation measures are
49 difficult to achieve (Beddington 2009). For example, although reductions in sulphur dioxide and
50 nitrous oxide emissions have been achieved, which has greatly reduced the input of "acid rain" to
51 freshwaters, ecological responses have been slow and region-specific due to stabilizing feedback
52 mechanisms (Battarbee *et al.* 2014).

53

54 The focus of policymakers is turning to enhancing the resilience of socio-ecological systems to
55 safeguard them from environmental change (i.e. future proofing Moss *et al.* 2013). This approach
56 relies upon our ability to detect, quantify and manipulate ecological resilience. A recent assessment
57 of resilience-enhancing measures, designed to address impacts of climate change across ecosystem
58 types, has revealed limited confidence in this approach (Kareiva *et al.* 2008). We discuss factors
59 limiting the manipulation of ecological resilience and draw on recent advances with the potential to
60 address them. We present these advances within an operational model designed to bridge theory and
61 practice.

62

63 **Barriers, successes and opportunities**

64 Ecological resilience was defined by Holling (1973) and adapted by Walker *et al.* (2004) as "the capacity
65 of a system to absorb disturbance and reorganize while undergoing change so as to retain essentially
66 the same function, structure, identity, and feedbacks". Evidence from a range of studies in terrestrial
67 and aquatic ecosystems has shown that ecological change often occurs suddenly in response to
68 pressures and management activities (Folke *et al.* 2004). As such, management must be conducted
69 with a comprehensive understanding of underlying processes (Seastedt *et al.* 2008). Shallow lakes
70 continue to be an important test-bed for practical resilience-based management (Batt *et al.* 2013) and
71 we inevitably draw on evidence from these systems. For example, practical demonstrations of
72 resilience-based management have been well documented in lakes where the disruption of stabilizing
73 feedback mechanisms (e.g. through catchment management or the manipulation of food webs) can
74 result in a rapid transfer of primary productivity from the plankton to the benthic macrophytes which
75 supports a fundamental shift in ecological structure and function associated with turbid and clear
76 water states, respectively (Scheffer 2009). However, in other ecosystems the key processes and
77 interactions responsible for resilience are, arguably, poorly understood leading to the consideration
78 of measures that target population- or individual-level responses. For example, a range of measures
79 have been proposed for climate change mitigation and adaptation in terrestrial ecosystems. 'Assisted
80 species migration' has been proposed to counteract climate change effects on key service provision
81 in forests where intolerant species are replaced with tolerant ones (Kareiva *et al.* 2008). The effects
82 of such 'species-swapping' are contentious (Minteer & Collins 2010) and resilience-based 'managed
83 evolution' has been proposed to consider intra- and inter-specific diversity, as opposed to single
84 species tolerances which builds on the need to consider ecological resilience across scales (Cavers &
85 Cottrell 2014). Lessons from large-scale environmental management successes, for example measures
86 to reduce the causes of 'acid rain' (Fowler *et al.* 1982), show that action at local and global scales must
87 complement each other if wide-scale environmental management efforts are to be successful.

88

89 Scheffer (2009) and Carpenter *et al.* (2009) demonstrate the value of understanding interactions
90 across scales and between socio-ecological systems as a basis for effective environmental

91 management and, collectively, lay out a blueprint for translating theory into practice. However, this
92 translation is limited by significant knowledge gaps including: (i) difficulties in detecting changes in
93 resilience (Batt *et al.* 2013); (ii) a lack of evidence and agreement to support successful preventative
94 management actions (Barrett *et al.* 2014) and (iii) the need to work across multiple geopolitical scales
95 to achieve effective management (Servos *et al.* 2013).

96
97 We argue that the evidence is available with which these limitations can be addressed and propose
98 an operational model with which resilience-based management can be used to develop a more
99 adaptive approach (Figure 1).

100 **An operational model for resilience-based management**

101 **Module 1. Detecting ecological sensitivity to pressures**

102
103 Our ability to detect the effects of environmental change on ecological processes is critical for effective
104 management of ecological resilience (Audzijonyte *et al.* 2013). Our understanding of ecological
105 process responses is generally underpinned by long-term case studies using simple chemical or
106 biological (often single species or simple community) indicators (Russel *et al.* 2012) impacted by single
107 pressures across limited scales (Allan *et al.* 2013). To address this, existing indicators are being
108 scrutinized for use in ‘resilience detection’ and where necessary, novel indicators are being developed
109 and validated towards use in routine monitoring programmes (Batt *et al.* 2013). Indicator
110 development has been conducted using three approaches discussed below.

111
112 First, time-series approaches have helped quantify variation in the nature of ecological systems (i.e.
113 demonstrating ecological resilience characteristics of an ecosystem (Angeler, Drakare & Johnson
114 2011)) including alternative ecosystem states (Angeler *et al.* 2013). In these studies, resilience has
115 been inferred by quantifying interactions between ecological processes across temporal and spatial
116 scales (Peterson, Allen & Holling 1998; Allen, Gunderson & Johnson 2005). Additionally, time-series
117 analysis has been used to detect change in ecosystem state indicators (e.g. increased variance and
118 autocorrelation) where, for example, slower and larger fluctuation in an indicator can precede a
119 sudden regime shift (e.g. Ives *et al.* 2003; Batt *et al.* 2013) allowing potential ‘early-warning’. These
120 studies demonstrate the use of existing indicators to detect changes in ecosystem resilience in
121 response to pressures across multiple scales. The detection of subtle changes in the structure of
122 ecological networks following perturbations shows promise as an early warning indicator of the loss
123 of ecological stability that considers the timing of structural and functional degradation and recovery
124 (Dakos & Bascompte 2014). These approaches can be applied to provide insight into scale-specific
125 structure in a system (Allen *et al.* 2014; Nash *et al.* 2014). Most delineation of scale is arbitrary and
126 subjective, and the development of objective methods to identify scale breaks and scale-specific
127 structure is a critical need in ecology.

128
129 Secondly, researchers have developed indicators capable of predicting ecological resilience across
130 multiple spatial scales without considering temporal dynamics. Specifically, the Discontinuity
131 Framework (Holling 1992) has been used to quantify resilience based on simple ecological metrics
132 (e.g. animal body mass or plankton biomass) (Allen & Holling 2008). This framework can detect a loss
133 of resilience across multiple scales (Allen *et al.* 2014) and may be useful when identifying
134 transboundary management approaches.

135
136 Finally, in microbial and higher organisms, changes in the genetic and epigenetic composition of
137 populations can be rapidly detected using next-generation sequencing methods (Stafford *et al.* 2013).
138 Such techniques may indicate systems undergoing ‘reorganization’ and show potential to rapidly
139 detect subtle but important ecological responses to pressures at intra-specific, population and
140 community scales (Shade *et al.* 2012).

142

143 To support these developments, many research and regulatory bodies are providing open source data
144 including large spatial data sets and multiple biophysical and socio-economic indicators allowing the
145 assessment of interactions between resilience-based management and service delivery. For example,
146 Allan *et al.* (2013) mapped pressures impacting on ecosystem service delivery across the North
147 American Great Lakes and demonstrated the importance of considering landscape spatial
148 heterogeneity when planning restorative and preventative management. A range of national and
149 international research projects are underway in which linkages between pressures, ecological
150 structure and function and ecosystem service delivery will be examined across scales (aquatic
151 ecosystems: Herring *et al.* 2014; forests: Cavers & Cottrell 2014). These projects provide a platform
152 for scientific advances to consolidate our knowledge base of resilience that can then be translated
153 into practical guidance for policymakers and practitioners.

154

155 **Module 2. Developing more effective resilience-based management measures**

156 The balance of regulation and incentives to support management of ecological resilience may need to
157 be redrawn (Moss *et al.* 2013). For example, in the EU a number of policies call for restoration of
158 degraded ecosystems (e.g. EU Biodiversity Strategy). The cost estimates for habitat restoration to
159 achieve Target 2 of the EU Biodiversity Strategy (i.e. “maintain and restore 15% of degraded
160 ecosystems by 2020”) across all habitat types ranges between €506 million – €10.9 billion per year
161 (Tucker *et al.* 2013). Estimates of this kind are highly uncertain, partly due to a lack of confidence in
162 the efficacy of available management measures (Kareiva *et al.* 2008). Furthermore, cost estimates for
163 management of specific pressures in isolation (e.g. nutrient pollution) can be confounded by
164 unintended consequences of the measure on other pressures acting on the target system (e.g. the
165 potential effects of water quality management for climate change mitigation; Spears & Maberly 2014).
166 The global economic burden of natural catastrophes has increased from US \$528 billion in the 1980s
167 to US \$1213 billion in the 2000s (Michel-Kerjan 2012). As such, substantial economic savings may be
168 made by considering the potential effects of existing restorative management measures to reduce the
169 likelihood of future ecological degradation in the context of impending pressure changes. However,
170 field-based experimental manipulations of feedback mechanisms, necessary to support such
171 preventative action are rare. Instead, relevant field studies have commonly strived to achieve an
172 improvement of ecosystem state from a degraded state (Batt *et al.* 2013), but not an enhanced
173 capacity to resist degradation. To address this, researchers need to revise experimental manipulations
174 to demonstrate ‘no response’ treatment (i.e. enhanced resilience) in comparison to a ‘regime shift’
175 control (McGovern *et al.* 2013) allowing better understanding of adaptive capacity.

176

177 **Module 3 Achieving adaptive governance**

178 Implementation of ecological management measures at local scales is generally considered to be more
179 susceptible to ‘failure’ as a result of an inability to control larger scale processes (Lake *et al.* 2007).
180 However, our understanding of ecological processes that regulate restoration effectiveness across
181 scales is well established in theory and may be used to inform adaptation of governance systems. For
182 example, Allen *et al.* (2014) demonstrated the need to control processes operating across multiple
183 scales, simultaneously, to achieve a desirable and relatively stable ecological response. Such
184 developments offer a framework to integrate biophysical and socio-economic processes within
185 hierarchical conceptual models. Temporal scale is also critical to effective management. Sharpley *et al.*
186 (2014) demonstrated the importance of ‘legacy’ responses in restoration and recovery at eth
187 ecosystem and catchment scales where a combination of physical and ecological processes combine
188 to delay recovery in watersheds following catchment management for up to centuries. As a result of
189 these legacy effects, an apparent lack of response can be met with costly ‘knee-jerk’ management
190 interventions. Superimposed onto these ecological processes are a series of socio-economic ones. For
191 example, restoration objectives may be driven by socio-economic cycles including trade (Margolis *et al.*
192 *et al.* 2005) and longer term changes in the social construct of a community (Olsson & Folke 2004). These

193 issues of scale across socio-ecological systems must be considered more comprehensively to achieve
194 resilience-based management. Bryan *et al.* (2013) provide a useful demonstration of combining
195 hydrological modelling with socio-economic predictions to support decisions on the management of
196 the River Murray, Australia, based on a combination of ecohydrological and socio-economic benefits.

197
198 Issues of scale across socio-ecological systems must be considered within a common framework to
199 achieve resilience-based management. However, delineations exist within governance systems that
200 can restrict the effective management of ecological systems at appropriate temporal and spatial
201 scales. Garmestani & Benson (2013) propose expansive legal reform to allow for trials of new
202 legislative approaches to combine with adaptive or iterative management. To achieve this, they
203 propose: (i) delineating ecological and governance scales; (ii) identifying critical slow variables; (iii)
204 identifying scale-dependent ecological thresholds and (iv) linking ecological and legal thresholds.
205 These changes have the potential to address the limitations of existing environmental policies and
206 form the basis of Module 3 (Figure 1). However, such institutional level change will not happen quickly
207 and should be based on sound scientific evidence.

208

209 **Conclusions**

210 We argue that current knowledge supports the detection and prediction of 'ecological resilience'.
211 However, there is a need to consolidate the approaches and techniques described above to produce
212 an operational model capable of providing iterative resilience-based management of socio-ecological
213 systems. We believe that the model presented here fills this gap by providing a clear route through
214 identifying and using ecological indicators, identifying and applying appropriate management
215 measures at appropriate scales to enhance resilience through to scenario testing and adapting policy
216 in response to management outcomes. Following this, it is important that scales regulating
217 governance of ecological systems are clearly defined and should include identification of barriers (i.e.
218 policy, technical and social issues). Decision support tools with the potential to enhance resilience
219 should be made available to practitioners and planners as has been demonstrated for the effective
220 management of ecosystem services (US EPA 2009). Practical guidance documents for practitioners
221 underpinning the assessment and management of resilience in socio-economic systems have been
222 developed (Resilience Alliance 2010) and should be adapted as research progresses.

223

224 **Data accessibility**

225 Data have not been archived because this article does not contain data.

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Detecting ecological resilience to environmental pressures

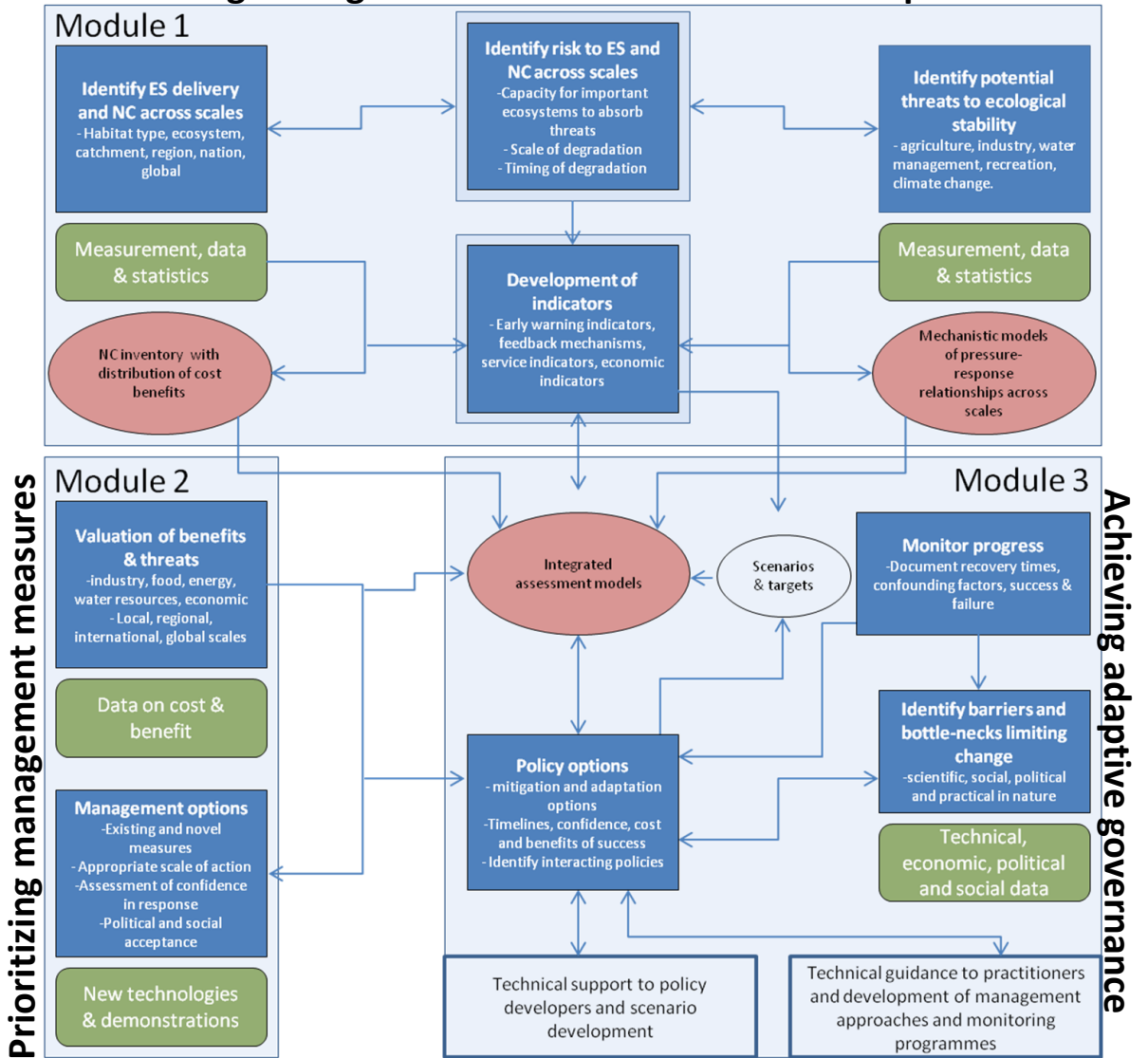


Figure 1. Operational model showing potential for linkages between research areas that stand to improve the evidence base with which policy and practical management can be developed towards more effective management of ecological resilience. ES – ecosystem services; NC – natural capital. Blue boxes represent the major resilience-based research fields; green boxes represent the production of data and tools; pink boxes represent the development and use of models.

Appendix C

Ecological Resilience: a Probability Check using Lakes as a Model System

For submission as a Perspective Article in *Nature Ecology and Evolution*

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Author Contributions

All authors contributed to the original concept of this paper and to the development of the text. B.M.S., M.F., E.J., T.A.D., B.J.H. and S.J.T. led the preparation of the text and paper structure. S.I., B.H., E.J., M.F., and S.J.T. prepared the figures with data provided by E.B.M., H.W., S.I., L.M., B.H., R.A., M.S., M.F. and A.G. B.M.S. led the final draft preparation and submission stages with comments from all authors being received prior to submission.

1 Abstract

2 There is a pressing need to apply stability and resilience theory to environmental management in such
3 a way as to restore degraded ecosystems effectively and to mitigate the effects of impending
4 environmental change. Lakes represent excellent model case studies in this respect and have been
5 used widely to demonstrate theories of ecological stability and resilience that are needed to underpin
6 preventative management approaches. However, we argue that this approach is not yet fully developed
7 because the pursuit of empirical evidence to underpin such theoretically-grounded management
8 continues in the absence of an objective probability framework. This has blurred the lines between
9 intuitive logic (based on the elementary principles of probability) and extensional logic (based on
10 assumption and belief) in this field.

11

12 Introduction

13 Boettiger and Hastings (2012)¹ proposed that there was a systemic bias in reasoning within ecological
14 resilience research resulting from the conditional selection of ecosystems for study that exhibit desirable
15 responses. This issue extends to the application of resilience approaches in general and must be
16 addressed to avoid the separation of theoretical application from mechanistic understanding of the
17 system of interest. Here we explore this issue using lakes as a model system. The issue can be
18 conceptualised generally using a probability framework that is commonly applied in social psychology:
19 *the conjunction rule*². This rule states that the probability of two events occurring together cannot exceed
20 the probability of either of the respective single events. A *conjunction fallacy* occurs when it is stated
21 that the co-occurrence of two events is more likely than either event alone. This can happen when basic
22 laws of probability have been ignored, with conclusions being reached via simple heuristics that are
23 derived from beliefs rather than robust probabilistic assessment. For example, in lake ecology, observed
24 changes in monitoring data have often been interpreted as evidence of a sudden ecological
25 reorganisation and, as such, have been used to underpin assessments of changes in ecological stability
26 indicators (e.g. Carpenter et al., 2011)³. However, such interpretations are often based on assumptions
27 about the nature of profound ecological change (i.e. an underlying “model”) and faith in this underlying
28 model may be misplaced². In the context of ecological resilience, a fallacy occurs when an assumption
29 is made that sudden ecosystem-scale change has occurred in response to changes in an environmental
30 stressor. Such an assumption is commonly presented to support reports that statistical signatures of
31 reduced stability have been detected prior to a profound ecological change. In the context of applying
32 the conjunction rule to these systems, the probability of each of these responses occurring individually,
33 and the overall probability of the conjunction of those responses occurring together can be calculated
34 to provide a level of statistical certainty with which preventative management approaches⁴ could be
35 underpinned. In reality, there is a degree of uncertainty about whether either of these phenomena can
36 be detected and this has led to contentious methodological debates (e.g., Wang et al., 2015)⁵. We argue
37 that overconfidence in the reporting of these phenomena limits our ability to perform preventative,
38 ‘resilience-based’ management. We draw on the experiences of the research community working in
39 this field to demonstrate these underlying issues and propose an alternative approach to evaluating
40 available evidence. We propose that the next phase of research in this potentially transformative field
41 should be grounded in robust assessments of probability coupled with an *a priori* understanding of
42 ecological processes.

43 Ecological stability and resilience in lakes

44 *Ecological stability theory* is a major contemporary theme in ecology and environmental management,
45 and has stimulated much debate. Two key aspects of the theory, referred to by Grimm et al. (1992)⁶ as
46 resistance and resilience, describe the tendency of species, communities, meta-communities or
47 ecosystems to depart from established relationships with their biological and physical environments,
48 and their capacity to return to pre-defined baseline conditions in response to perturbations. These
49 departures can be profound, resulting in the reorganisation of communities in response to the
50 breakdown of internal feedback mechanisms at the ecosystem scale. Within *ecological resilience*
51 theory, this latter phenomenon is described as a *regime shift*. Regime shifts can be either smooth
52 (linear), non-linear (threshold) or discontinuous (hysteresis, critical) transitions^{7,8}. Lees et al. (2007)⁸
53 proposed that, to confirm the occurrence of a regime shift, a reorganisation that produces a novel and
54 stable ecosystem must be detectable across multiple physical and biological components. Quantifiable
55 terms relating to regime shifts include the *critical threshold*: the point on the pressure axis at which the
56 system shifts, and the *transition*: the period over which the switch between stable states occurs⁹.

57 Ecological resilience theory suggests that discontinuous regime shifts may be preceded by subtle
58 changes in ecological behaviour that can be detected using quantifiable indicators, thus providing useful
59 early warning of impending transitions. For example, an increase in the variance or autocorrelation of
60 phytoplankton biomass, due to phenomena known as *critical slowing down (CSD)* or *flickering*, may be
61 expected to precede the well documented transition between phytoplankton dominated conditions and
62 macrophyte dominated conditions in shallow lakes. Put simply, CSD is characterised by a reduction in
63 the speed of ecological recovery after a disturbance as an ecosystem approaches a critical threshold,
64 and flickering results from the alternation between stable ecological states following perturbations^{5,10,11}.
65 Frameworks for detecting changes in ecological stability⁵ and for the use of statistically derived early
66 warning indicators¹²⁻¹⁴ (EWIs) have been developed for predicting regime shifts. Currently, the
67 performance of these frameworks has been evaluated, mainly using simulated or experimental data^{14,15}.

68 Lakes are particularly important model ecosystems with which to examine the aforementioned
69 phenomena given that they represent 'aquatic islands' that are relatively contained, easily quantified
70 and manipulated, and exhibit a vast array of ecological responses to well-defined gradients of multiple
71 and interacting pressures. These pressures include eutrophication, acidification, and climate change.
72 Recent tests using long-term lake monitoring data have indicated low levels of agreement between
73 EWIs and statistically defined sudden ecological change. Burthe et al. 2015¹⁶ highlight that this lack of
74 coherence may arise due to insufficient knowledge of the causes of sudden changes in ecological
75 indicators that occur in long-term monitoring data and their relation to regime shifts. One significant
76 weakness in this approach is that the form and rate of regime shifts are very difficult to quantify, even
77 though they may dictate whether or not CSD or flickering may be expected to occur. Using the
78 terminology of the conjunction rule, this underlying model is flawed. Capon et al. (2015)¹⁷ reviewed the
79 evidence available for regime shifts in freshwater ecosystems and concluded that many of the studies
80 purporting to demonstrate this phenomenon fail to do so. Of the 135 studies analysed, few met all of
81 the criteria proposed by Lees et al. (2006)⁸ to confirm a regime shift. This suggests that regime shifts
82 are less common in nature than the abundant literature would suggest. Ultimately, these reports of
83 regime shifts based on unwarranted extensional reasoning about the consequences of observed EWIs
84 support the widespread occurrence of conjunction fallacies in this field, with the occurrence of regime
85 shifts having been widely reported despite a lack of robust probabilistic evidence.

86 **Predicting regime shifts in real world systems**

87 If we are to improve our capacity to estimate the probability of regime shifts and changes in ecosystem
88 stability preceding them, we must first examine our underlying model and our capacity to quantify its
89 individual components. We can demonstrate this approach by considering lake ecosystems, which have
90 been widely used as model systems for the development and application of ecological resilience
91 theory^{16,19} and EWIs^{20,21}.

92 [FIGURE 1]

93 While EWIs have been applied with apparent success in small-scale and whole-lake experimental
94 settings, significant caveats have been identified regarding their use in real-world systems. Authors
95 have stated that EWIs may occur before specific types of regime shifts only^{22,23}, potentially including
96 both critical and non-critical transition types²⁴, and they may not be exclusive signals of critical
97 transitions²⁵. So, failure to observe an EWI may arise if the drivers of a regime shift are, themselves,
98 inherently unpredictable (e.g. noise-induced transitions¹¹), or as a result of methodological issues such
99 as the resolution of monitoring data and/or the selection of (rolling) time windows within which EWIs are
100 calculated (Fig 1). When applied to monitoring data from lakes with reported regime shifts, the predictive
101 success of EWIs has been reported to be only at best about 50%²⁶. To achieve acceptable levels of
102 confidence in their application, any reliable use of EWIs needs to be embedded within *a priori*
103 knowledge of system-specific ecological mechanisms that underlie change²⁶; this limits wide scale
104 practical applications considerably¹⁶.

105 By considering the underlying processes that drive change in EWIs more generally, we can begin to
106 understand important limitations in their current application. All EWIs are likely to be inherently variable
107 within a given ecosystem state, even one that is a long way from an impending transition, due to
108 transient ecological dynamics. For example, the widely ranging variance in phytoplankton biomass and
109 submerged macrophytes²⁷ exhibited over the long-term by apparently stable lakes makes it difficult to
110 identify changes that are indicative of a regime shift (Fig 1). Changes in EWIs can only be judged to be
111 "significant" if they vary outside of the range that is found under typical baseline conditions or in a
112 parallel and statistically well-defined control system¹². Such assessments require time series data of

113 sufficient frequency and duration with which any departure from baseline conditions can be adequately
114 quantified.

115 Decisions must be made regarding ecologically relevant timescales over which loss of stability can be
116 assessed²⁸. Our definition of “sudden” change, which underlies the definition of discontinuous regime
117 shifts, is perhaps better judged on a scale of organismal and community turnover times, rather than
118 calendar dates or funding timelines. For example, Pace et al. (2016)⁴ consider the onset of a
119 phytoplankton bloom to be a short-term (i.e. days to months) ecological event that was preceded by a
120 change in EWIs from baseline. In shallow lakes, palaeolimnological records²⁹ and long-term monitoring
121 data³⁰ show that a regime shift, characterised by the complete loss of submerged plants, can be
122 preceded by decades to centuries of change in community composition that culminates in the
123 dominance of a few nutrient tolerant species (i.e. *Potamogeton crispus*, *P. pusillus*, *P. pectinatus* and
124 *Zanichellia palustris*) before they disappear completely. In contrast to the duration of a typical
125 experiment (months to years), the plant loss regime shift described above demonstrates a mean
126 transition time from a non-eutrophic macrophyte flora to the penultimate community state of about 100
127 years, and from the penultimate state to plant loss of about 20 years. Similarly, studies of contemporary
128 monitoring data that quantify the responses in fish and macrophyte communities to catchment
129 phosphorus loading abatement in shallow lakes often report gradual time scales of response of the
130 order of decades^{31,32}. In this context, it is difficult to distinguish between categories of regime shifts or
131 to establish clear timelines across which EWIs would be expected to respond. To address this, there is
132 a need to develop more systematic definitions of regime shifts that occur in nature and to use these as
133 a framework within which changes in indicators of ecological stability can be assessed.

134 Despite the fact that regime shifts are ecosystem-scale phenomena, ecological indicators used for
135 calculating EWIs are often simple state variables that may not reflect ecosystem scale processes³³. The
136 selection of suitable indicators is not trivial, considering that complex ecosystem dynamics can amplify
137 or dampen EWIs in specific variables³⁴. The components of an ecosystem that are most likely to exhibit
138 the behaviours that underpin EWIs will depend upon the type of regime shift and on the underpinning
139 ecological mechanisms. Retrospective analyses of long-term monitoring data from lakes in which
140 regime shifts have been observed and defined can be used to test the sensitivity of EWIs²⁶. For the
141 development of monitoring programmes designed to predict unforeseen regime shifts, however, the
142 identification of suitable EWIs from the suite available is challenging. This selection must be combined
143 with *a priori* mechanistic understanding of the relevant ecological processes, feedback mechanisms
144 and regime shifts that occur across a wide range of pressure scenarios, lake types and timescales. That
145 is, we must develop more detailed underlying models, based on comprehensive understanding of the
146 ecosystem and its responses to defined environmental stressors. These models can then be used to
147 support diagnosis of time-varying ecosystem-scale changes in indicators of stability needed to quantify
148 the probability of regime shifts based on departure from baseline conditions using EWIs^{35,36}.

149 **Learning from Experiments**

150 The probabilities of observing both detectable changes in EWIs and subsequent regime shifts can best
151 be estimated by the statistical analysis of data from controlled experiments. Such estimates or
152 probabilities could be used to infer the likelihood of observing these phenomena in real world monitoring
153 data. Most experimental studies focusing on resilience and EWI development have assessed relatively
154 short-term responses to perturbations (i.e. weekly to monthly resolution) using high frequency data. The
155 advent of high-frequency monitoring systems (at hourly to daily level resolution) in lakes provides lake
156 ecologists with an impressive capacity to detect subtle and rapid changes in ecological indicators in
157 response to perturbations. As next generation monitoring systems are developed and/or improved (e.g.
158 remote sensing approaches including multi-parameter monitoring buoys), our detection power will also
159 improve. In contrast to this, we draw attention to the vast legacy of experimental studies that have
160 collected lower frequency monitoring data. These low-frequency experiments represent an untapped
161 resource with which non-stationary behaviour in ecosystems can be examined using the statistical tools
162 developed as EWIs in response to a controlled perturbation or otherwise.

163 One criticism of short-term experiments is that it is difficult to conclude that a persistent regime shift has
164 occurred, although they do provide important evidence of short-term dynamics in ecological responses
165 at high temporal frequency. With a few exceptions, mesocosm experiments span periods of only 3-12
166 months³⁷ (Fig 2). So, longer term changes including potential regime shifts, and changes in ecological
167 behaviour preceding (and following) them, are often difficult to assess. Nevertheless, they offer
168 invaluable insights into short-term effect, return, and recovery rates following perturbations. Tightly

169 controlled experiments in which regime shifts are achieved maintain a powerful approach to examining
170 and quantifying the performance of EWIs and responses in ecological stability, more generally.
171 Unfortunately, although an impressive legacy dataset exists documenting ecological responses
172 following manipulation of nutrient cycling or food-web structure, this evidence has been poorly utilised
173 in the context of ecological resilience in lakes.

174 [FIGURE 2]

175 Here we provide an example of the use of a short-term mesocosm experiment³⁸ to examine ecological
176 resilience in lakes and some misgivings in the context of the conjunction rule. Mesocosms were
177 subjected to contrasting nitrogen (N) loading during a 9 month shallow lake experiment that led to the
178 complete loss of submerged macrophytes at high N loading (Fig 2), a well-established regime shift
179 known to occur in shallow lakes. There were no apparent EWI signals or trends when the macrophytes
180 started to decline in the high N loaded mesocosms. EWI values from the treatment mesocosms were
181 found to be both higher and lower than the control mesocosms. When one considers the general
182 treatment effects, it is apparent that EWIs were significantly different across the treatments and that an
183 interaction between treatment and time was reported. However, the results provide no conclusive
184 evidence of an increase in EWIs prior to the regime shift in the high nutrient loading treatment. In
185 general, we observed more stable conditions under the highest N loading treatment, which appears to
186 contradict the increase in variance expected when CSD occurs prior to a regime shift. In this example
187 it is impossible to determine the form of the regime shift and so our underlying model, which
188 hypothesises the occurrence of CSD preceding the demise of the macrophytes, may be unfounded, as
189 in other similar experimental studies.

190 Few ecosystem scale experiments have been conducted to test the hypothesis that CSD can be
191 detected before a regime shift. The most comprehensive study to date involved the detection of
192 responses across a range of indicators in a treatment lake relative to a control lake, following
193 manipulation of the fish community from planktivore- to piscivore dominance^{3,13,34,29,40}. Thresholds in
194 some of these indicator variables were reported more than a year before the transition to piscivore
195 dominance was complete, providing evidence to support CSD. However, evidence also existed for
196 similar fluctuations in EWIs following the regime shift, suggesting on-going longer-term processes that
197 are not easily explained. While this experiment provided a rich and detailed dataset with at least daily
198 sampling resolution for a range of variables, there are three potentially important caveats that are
199 relevant to interpretation of the data. Firstly, the results indicated that ecosystem 'state variables' (e.g.
200 dissolved oxygen) were more sensitive indicators of the reported transition than estimates of rates (e.g.
201 gross primary production³³). This potentially indicates insufficiencies in available methods for
202 quantifying key system changes. Secondly, even in this very comprehensive study, response patterns
203 of different indicators and EWIs varied quite substantially. Thirdly, the methods used in whole lake
204 experiments require that the manipulated and reference lake(s) are in synchrony over the sampling
205 period and frequency of interest, which may be unlikely at such high monitoring frequency.

206 Lower temporal frequency data from many other whole lake experiments are available for the
207 determination of longer term effects of environmental change on ecological stability indicators. Such
208 studies are important because they have been conducted in systems for which there is adequate causal
209 understanding of the relevant ecological mechanisms driving change. Although few of these studies
210 have been framed using ecological resilience or stability terminology, we demonstrate the potential to
211 retrospectively explore the effects of perturbations on ecological stability more generally, irrespective of
212 whether a regime shift was reported or planned in the original design (Fig. 3). There are many whole
213 lake experiments lasting from years to decades, the longest of which are those aiming to restore lakes
214 from external pressures⁴¹. While some of these have focused solely on reducing external pressures,
215 others have been conducted to control some of the intrinsic processes, or feedback mechanisms,
216 known to determine ecological conditions after changes in external pressures have occurred. These
217 include measures to reduce internal phosphorus cycling in lakes⁴², or to alter food-web structure and
218 macrophyte community by manipulating fish stocks and/or transplanting submerged macrophytes⁴³.
219 Whilst the data frequency may not be appropriate for assessing EWIs of regime shifts when potentially
220 expected, these experiments can be used to characterise the timelines of changes in the stability of
221 lake variables, for example, following commonly used management approaches (Fig. 3). In addition,
222 they may be used to explore non-stationary behaviour with and without management interventions.
223 When considered in the context of simple indicators of ecological stability, it becomes apparent that
224 responses to management can take decades to manifest and do not necessarily result in a more stable
225 ecosystem.

226 [FIGURE 3]

227 To maximise their applicability, we recommend these novel insights from single site experimental
228 studies be used to inform the re-analysis of the vast quantities of data from other experimental studies
229 so as to develop testable hypotheses of whole system responses to specific and controlled pressure
230 scenarios. The results of this work should inform the development of novel management approaches
231 designed to manipulate ecological stability at the ecosystem scale, which could, in turn, facilitate a more
232 valid conjunction of EWIs and subsequent regime shifts.

233 **Capitalising on Natural Events**

234 Given the recent focus on developing EWIs, we stress the need to continue to build and refine our best
235 conceptual models of ecosystem scale responses to pressures, in general. Multi-decadal to century-
236 long lake monitoring data⁴⁴⁻⁵² are becoming increasingly available for use in this endeavour. Although
237 such data are useful for the identification of regime shifts, their relatively coarse temporal resolution,
238 may provide only limited opportunities to assess EWIs¹¹. Long time series provide more context to
239 ecosystem change than can be achieved by short term experiments however, and are more realistic in
240 terms of noise and stochasticity. We advocate the use of these long-term data which have, at their core,
241 the sound *a priori* knowledge of the mechanisms underlying ecosystem scale responses to past or
242 current environmental change needed to provide credible alternative approaches to early warning of
243 regime shifts across large populations of lakes.

244 Most studies purporting to show discontinuous regime shifts report that shallow lakes may switch from
245 a turbid to clear water state¹⁸. The most commonly reported regime shift is the response of shallow
246 lakes to increasing and decreasing phosphorus loading, which can cause a critical transition between
247 clear water, macrophyte dominated and turbid water phytoplankton dominated states, respectively⁵².
248 While such shifts have been observed, numerous studies of shallow lakes in recovery after external
249 nutrient loading reduction have not exhibited this response, even when theory suggests they should
250 have³¹. These results suggest that either pressure reductions may have been insufficient to reach a
251 critical threshold, thresholds were not reached because of the impacts of other interacting processes
252 (warming, food web structure changes), not all shallow lakes exhibit regime shifts, or that reorganisation
253 at the ecosystem scale takes much longer than expected and follows the path of gradual adjustment of
254 the system as the pressures change. Process based modelling (i.e. PCLake) has been used in this
255 context to construct testable hypotheses with which the effects of lake typology (e.g. fetch, depth, fishery
256 practices, etc.) and pressure intensity interact to shape a continuum of ecosystem responses⁵³.
257 Additionally, evidence of multiple and varied ecosystem responses to alternative pressure scenarios
258 have been confirmed using multi-lake observations. For example, Bayley et al. (2007)⁵⁴ showed that
259 the 'clear water' to 'turbid water' regime shifts occurred across Canadian Prairie shallow lakes in
260 response to extreme weather.

261 [Figure 4]

262 The pursuit of evidence to support the classical shallow lake regime shift described above in single site
263 studies has dominated efforts in recent years. We call on the community to further develop ecological
264 understanding and encapsulate this within conceptual and process based models to help predict the
265 likelihood of novel regime shifts that threaten many lakes globally. For example, based on evidence
266 from long-term lake monitoring data and remote sensing archives coupled with process-based
267 modelling, we hypothesise that the widespread increase in dissolved organic carbon (DOC)
268 concentrations in temperate lakes associated with recovery from acidification⁵⁵ and a changing climate
269 will result in an increased occurrence of regime shifts across many lakes in the⁵⁶ coming decades. The
270 form of the regime shift is apparent from a critical transition observed in Lake Hårsvatten (Fig. 4) and
271 confirmed by other studies that have reported an increase in surface water DOC concentrations
272 resulting in a decrease in transparency, an increase in warming of epilimnetic waters, and longer and
273 stronger thermal stratification⁴⁷, potentially inducing a regime shift as lakes switch from di- to mono-
274 mixis. This, in turn, has the potential to cause more intense periods of anoxia in hypolimnetic waters⁵⁷,
275 resulting in increased internal loading of phosphorus (Fig. 4), stabilising the novel state. Couture et al.
276 (2015)⁵⁸ present a process based model for this form of regime shift that could be used to simulate the
277 effects of lake type on the probability of occurrence in response to changes in DOC concentrations.
278 Thus, while the principle response variable in this context (DOC) displays a linear response over time,
279 it can induce thresholds and a regime shift in secondary response variables. This DOC-response regime
280 shift represents a hitherto unforeseen effect of post-acidification recovery.

281 While the shifts in hypolimnetic water chemistry for Lake Hjärsvatten would not, necessarily, have been
282 detected using statistical EWIs, they could have been predicted based on a *priori* mechanistic
283 knowledge of lake function combined with process-based modelling. This well-established approach
284 should be developed to provide estimates of the probability of occurrence of regime shifts at the lake-
285 district scale to provide a test bed on which to address the current uncertainty associated with EWIs.
286 We propose that existing theory frameworks (e.g. alternative stable-state theory) be combined with the
287 requirements of EWI analysis to support future monitoring of lakes for which there is a high probability
288 of an impending regime shift, for example, following wide spread reduction in catchment phosphorus
289 loading or recovery from acidification, in response to increasing frequency of extreme weather events
290 or in line with the DOC example provided above.

291 **Quantifying Ecological Resilience: A New Perspective**

292 One primary focus of the discipline of ecology is the quantification of patterns of change in organism
293 productivity and biomass accumulation in response to changes in their biological and physical
294 environment. Clearly, the early detection of deviations from desirable, stable conditions promises
295 practical benefits in terms of motivating rapid management responses to mitigate potential, undesirable
296 regime shifts. However, recent assessments of regime shift EWIs using commonly collected monitoring
297 data have confirmed that confidence in their application to support management decisions is too low
298 for wide-scale practical application. This is due, at least in part, to a lack of consideration of temporal,
299 spatial and ecological scales, a failure to embed EWIs in an *a priori* mechanistic understanding of
300 ecosystem function and the lack of a clear probabilistic framework with which the co-occurrence of
301 regime shifts and loss of ecological stability preceding them have been confirmed.

302 Given the need for evidence based management underpinned by robust estimates of uncertainty, we
303 return to the framework of the conjunction rule. We have demonstrated that the research field is at an
304 early stage of development. Specifically, statistical tools are needed to credibly evaluate the probability
305 that regime shifts will occur in combination with responses in EWIs. To address this, we urge the
306 community to use the well-established statistical tools that are available to examine ecological resilience
307 theory by using objective criteria⁸ within a robust probabilistic framework. To address issues of detection
308 of EWIs and regime shifts outlined herein, we argue for future studies to adopt a formal probabilistic
309 framework, based on the conjunction rule. Specifically, quantification of the probability of detecting both
310 EWIs and a regime shift ($P(EWI_{t,s} \& RS_{t,s})$) in monitoring data given the probability of detecting EWIs
311 ($P(EWI_{t,s})$) and the conditional probability that we will then observe a subsequent regime shift (RS),
312 given the previously-identified EWIs ($P(RS_{t,s} | EWI_{t,s})$):

$$313 \quad P(EWI_{t,s} \& RS_{t,s}) = P(EWI_{t,s}) \times P(RS_{t,s} | EWI_{t,s})$$

314 This statement applies across statistical “populations” of lakes. The subscripts *t* and *s* acknowledge that
315 we would expect the probabilities of observing EWIs and regime shifts to differ among lakes belonging
316 to different ecological typologies (*t*, e.g. shallow versus deep, or nutrient-rich versus nutrient-poor lakes)
317 and with respect to the specific stressor (*s*, e.g. increased phosphorus loading, rising water
318 temperature) acting on lakes of any given typology. In order to properly evaluate the widespread
319 applicability and efficacy of any specific EWI, to inform lake management, we need to correctly quantify
320 the conditional probability $P(RS_{t,s} | EWI_{t,s})$ using experimental and observational data; the probability
321 that we will actually observe a regime shift following the detection of an EWI, for a lake of type *t*
322 responding to stressor *s*. Of specific interest is the “false discovery rate”, $1 - P(RS_{t,s} | EWI_{t,s})$, which is
323 the probability that a regime shift will not follow detectable EWIs^{1,39,59}, a scenario that could result in
324 unnecessary and costly management interventions.

325 As a first step toward providing robust estimates of probability to support the prediction of ecological
326 responses to multiple pressures, co-ordinated analyses of empirical case studies and scenario-based
327 modelling should be used to estimate the likely numeric values of the probabilities of the terms above.
328 In this respect, ensemble-modelling would be a particularly powerful approach, allowing systematic
329 assessment of multiple ecological scenarios using a series of structurally-different process-based
330 models. This approach allows more objective assessment of uncertainties in mechanistic knowledge,
331 ecological responses and current and future stressor scenarios⁶⁰.

332 We propose that, alongside efforts to evaluate the real-world generic applicability of statistical EWIs of
333 “sudden change”, we should also strive to improve our capacity to predict, observe and manipulate
334 ecosystem stability, more generally. Ecosystems respond to a multitude of perturbations operating over
335 a wide range of temporal and ecological scales. The wide range of EWIs developed offer a suite of

336 indicators designed to provide insight into a short, but nevertheless critical, window of change preceding
337 regime shifts. However, these indicators can also be used to examine general ecological responses to
338 environmental change or management, as demonstrated here. The relative merits of these indicators
339 for such applications should be founded on advanced *a priori* mechanistic knowledge of lake ecology,
340 encapsulated within conceptual, empirical and theoretical ecological models.

341 There is a need to confront our current “best” projections of ecological responses to environmental
342 change scenarios with newly collected monitoring data and identify where models need to be developed
343 or improved to increase predictive power. The move from single experimental studies to integration of
344 data and *a priori* mechanistic understanding over broad scales will allow an iterative process of model
345 development and revised projections. This evidence base is essential to underpin effective preventative
346 management grounded with intuitive logic.

347

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Figure Legends

Figure 1. Standard deviation (SD) as an early warning indicator (EWI) for three lake ecosystems, over different time scales. Left panel: 30-year time series of phytoplankton biomass (measured directly, or using chlorophyll *a* as a proxy). Right panel: corresponding long-term changes in SD after seasonally-detrending these data. For each lake, the SD is calculated using all 30 years of data, and when truncating the time series to 20- and 10-year periods. Also, the SD is calculated within sliding windows encapsulating 10, 25 and 50% of the available data (visualised using bars at the top right of each panel), for each whole and truncated time series. The range of variation in the EWI increases when sliding time windows are shorter (compare rows). Variable data availability (time series length) can have similar effects; holding the percentage sliding window size constant, SD is more variable when calculated from shorter time series than when calculated from longer ones (compare columns). This demonstrates the impact 'catch-all' solutions can have on findings and the importance of 'informed' analytical decisions.

Figure 2. An assessment of early warning indicators during a regime shift from macrophyte to phytoplankton dominance in a 9 month mesocosm experiment³⁸, 24th September 2012 to 2nd August 2013. The experiment was conducted in the Wuhan Botanical Gardens Pond, China (upper left photograph). Eleven mesocosms (1.2 m internal diameter and depth; upper right photograph) were placed in the pond covering natural stands of the macrophytes *Potamogeton lucens* and *Cabomba caroliniana*. The figure shows three replicated treatments of increasing nitrogen (N) loading via the addition of ammonium nitrate (NH₄NO₃) granules dissolved into pond water on every tenth day for the duration of the experiment. Mesocosms were inoculated with *c.* 10 cm bighead carp (*Aristichthys nobilis*; fish stocking density of 100g m⁻² per mesocosm). Samples for chlorophyll *a* analysis and observations of macrophyte PVI were collected every ten days, during the day, and analysed as outlined by Olsen et al. (2015)³⁸. This experiment achieved a regime shift from macrophyte to phytoplankton dominated state, only under the highest N loading treatment. In the low N loading treatment, macrophytes declined initially but recovered towards the end of the experiment. To demonstrate variation in ecological stability throughout the experimental period, standard deviation, kurtosis and autocorrelation values were calculated across a rolling window covering 25% of each time series using phytoplankton chlorophyll *a* concentrations for each treatment mesocosm during the experiment. The display is relative to the mean and +/- 1 standard deviation of the control mesocosms for each sample date and as ranges for each treatment for the duration of the experiment. The effects of treatment and time, and interactions between them were quantified using 2-way repeated measures analysis of variance with adjusted p-values using the statistical programme R, using a data set constrained to May 2012 allowing examination of changes preceding and during the transition period. These tests show significantly higher standard deviation in the control treatment ($f = 12.73$, $p = 4.10e-05$) compared to the low and high treatments and a significant treatment:time interaction ($f = 12.95$, $p = 3.41e-05$). Significantly higher skewness and kurtosis was also seen in the high addition treatments compared to low and control (skewness: $f = 8.062$, $p = 0.002415$, kurtosis: $f = 9.333$, $p = 0.00078$). All other tests were not significant.

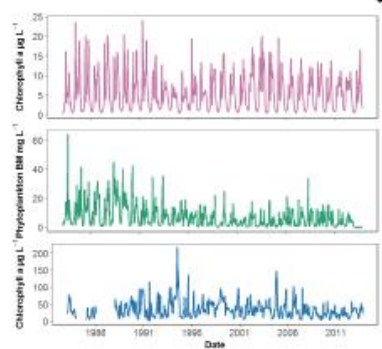
Figure 3. Examples of changes in variability following management intervention. Variability in chlorophyll *a* concentrations (Standard Deviation, SD, calculated on log (X+1) data across a rolling window covering 10% of the time series length). The arrows represent the timing of the disturbances, as described. Lake Engelsholm was biomanipulated in 1992-1993 to support its recovery after nutrient loading reduction^{43,44}. Nineteen tonnes of cyprinids were removed, decreasing the estimated biomass from 675 to 150-300 kg ha⁻¹. This led to a substantial decrease in chlorophyll *a* concentrations, total phosphorus (TP) and total nitrogen (TN) as well as an increase in Secchi depth, and marked changes in SD; initially SD increased substantially, but then it declined markedly reaching the pre-manipulation level in 2000 before increasing to a relatively consistent level 10 years after the manipulation; by then SD was 30-50% higher than before manipulation. Aluminium (Al) was added to Lake Calhoun in 2001 (42 g m⁻²; see arrow) to reduce the release of excess, legacy P accumulated in the sediment (internal loading). The Al inactivated 10.9 metric tonnes of mobile sediment P (by converting

it the more stable Al-bound P), thereby reducing sediment release by 953 kg P/y (>90%)^{45,46}. This decrease in internal P release led to a substantial reduction of epilimnetic chlorophyll *a* concentration (70%) and TP (58%) and an increase in Secchi depth (74%) compared to pre-treatment (1991-2000). After Al treatment, SD decreased substantially until 2005, stabilized over the following 5 years (2006-2010), and then returned to near pre-manipulation levels from 2011 onwards. The data for Lake Calhoun features late spring/ summer data only due to ice cover, therefore EWIs were calculated for each year individually. This resulted in less data being contained within the rolling window but a consistent amount for each year across the dataset.

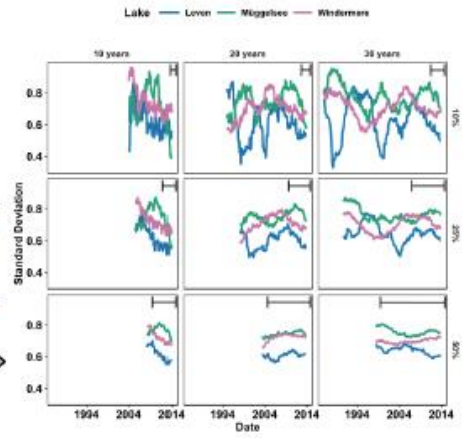
Figure 4. Long term water quality measurements from Härsvatten, a lake experiencing a regime shift in hypolimnetic dissolved oxygen levels (DO) associated with increasing epilimnetic total organic carbon (TOC) concentrations (upper panel) and cumulative distribution of long-term (1988-2012) TOC trends for lakes in the Swedish national monitoring programme. Water chemistry measurements (dots), long term means (lines) and standard deviations (shaded boxes) before and after the 2004 DO regime shift are shown in the upper panel. At Härsvatten, there has been a continuous increase in epilimnetic TOC concentrations (blue dots), which is likely to have lengthened the duration and intensity of thermal stratification, leading to declining summer hypolimnetic DO concentrations (red dots). Repeated measurements of DO concentrations below 2 mg L⁻¹ are a potential early warning indicator for a regime shift where internal P loading associated with suboxic and anoxic hypolimnetic waters induces a positive feedback in which greater P availability facilitates higher rates of DO consumption, thereby maintaining suboxic hypolimnetic conditions and ongoing internal P release. There was a step change in the mean and standard deviation of annual average hypolimnetic DO concentrations at the end of 2004 (Pettit's test; $p < 0.001$ for mean and $p < 0.02$ for variance) followed by an approximately 250% increase in hypolimnetic total phosphorus (TP) concentrations, most likely due to a sharp increase in internal P loading. The lower panel puts the observations at Härsvatten into context by showing the cumulative distribution of TOC trends for 233 Swedish lakes where long-term monitoring data are available. Concentrations increased in 88% of monitored lakes (orange lines) and Härsvatten is at the 42nd percentile of the cumulative distribution of trends (purple lines). While there is limited long term monitoring of hypolimnetic water chemistry in Swedish lakes ($n=14$), the trends in TOC ($n=233$) are suggestive of widespread regime shifts for dissolved oxygen in northern lakes. The 50th and 75th percentiles of the trend distribution (grey lines) are at 0.13 and 0.23 mg TOC L⁻¹ yr⁻¹, respectively.



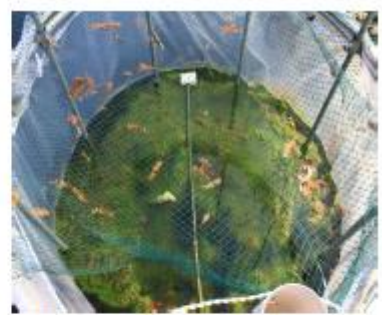
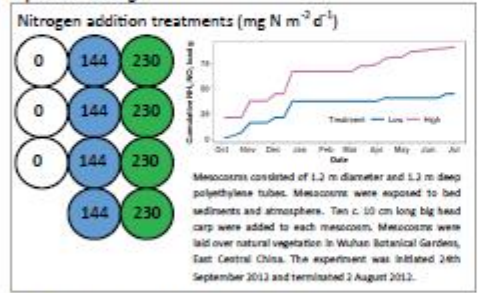
Long term environmental monitoring of phytoplankton biomass over 30 years



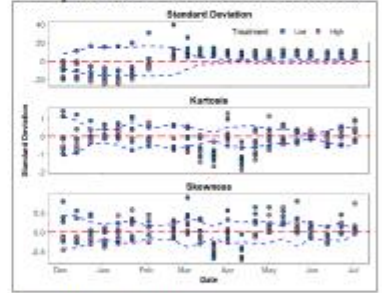
Changes in antecedent variance of phytoplankton biomass and the effects of window size and observation period



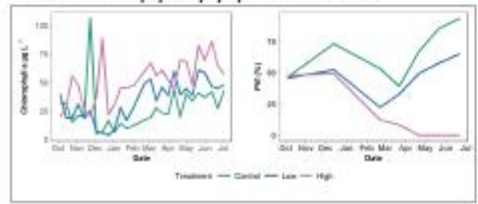
Experimental design



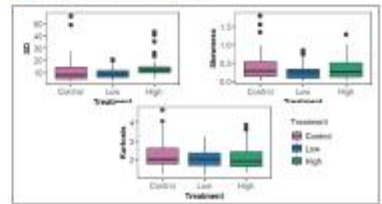
EWI responses relative to control for each mesocosm



Switch from macrophyte to phytoplankton dominance



Effects of treatment on EWIs





Lake Engelshom, Denmark



Calhoun Lake, USA

