Burthe, Sarah J.; Henrys, Peter A; Mackay, Eleanor B.; Spears, Bryan M.; Campbell, Ronald; Carvalho, Laurence; Dudley, Bernard; Gunn, Iain D.M.; Johns, David G.; Maberly, Stephen C.; May, Linda; Newell, Mark A.; Wanless, Sarah; Winfield, Ian J.; Thackeray, Stephen J.; Daunt, Francis. 2016. **Do early warning indicators consistently predict nonlinear change in long-term ecological data?** *Journal of Applied Ecology*, 53 (3). 666-676. 10.1111/1365-2664.12519

Do early warning indicators consistently predict non-linear change in long-term ecological data?

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Running title: Early warnings of change in long-term ecological data

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Summary

1. Anthropogenic pressures, including climate change, are causing non-linear changes in ecosystems globally. The development of reliable early warning indicators (EWIs) to predict these changes is vital for the adaptive management of ecosystems and the protection of biodiversity, natural capital and ecosystem services. Increased variance and autocorrelation are potential EWIs and can be readily estimated from ecological time series. Here, we undertook a comprehensive test of the consistency between EWIs and non-linear abundance change across species, trophic levels and ecosystem types.
2. We tested whether long term abundance time series of 55 taxa (126 data sets) across multiple trophic levels in marine and freshwater ecosystems showed: i) significant non-linear change in abundance ("turning points") and ii) significant increases in variance and autocorrelation ("EWIs"). For each data set we then quantified the prevalence of three cases: true positives (EWI and associated turning point), false negatives (turning point but no associated EWI) and false positives (EWI but no turning point).
3. True positives were rare, representing only 9% (16 of 170) of cases using variance, and 13% (19 of 152) of cases using autocorrelation. False positives were more prevalent than false negatives (53% vs. 38% for variance; 47% vs. 40% for autocorrelation). False results were found in every decade and across all trophic levels and ecosystems.
4. Time series that contained true positives were uncommon (8% for variance; 6% for autocorrelation), with all but one time series also containing false classifications. Coherence between the types of EWI was generally low with 43% of time series categorized differently based on variance compared to autocorrelation.
5. *Synthesis and applications.* Conservation management requires effective early warnings of ecosystem change using readily available data, and variance and autocorrelation in abundance data have been suggested as candidates. However, our study shows that they consistently fail to predict non-linear change. For early warning indicators to be effective tools for preventative management of ecosystem change, we recommend that multivariate approaches of a suite of potential indicators are adopted, incorporating analyses of anthropogenic drivers and process-based understanding.

Key-words: ecosystem resilience, food webs, non-linearity, preventative management, regime shifts, time series data, tipping points

Introduction

There is accumulating evidence that ecosystems are exhibiting profound changes in structure and function in response to climate change and other anthropogenic drivers (Walther *et al.* 2002; Parmesan 2006; Van der Putten, Macel & Visser 2010). Species abundance and ecosystem processes may show non-linear changes in response to environmental perturbations which can result in an irreversible shift to a different ecosystem state (a so-called “catastrophic shift”, Holling (1973); Scheffer *et al.* (2001)). Such a change involves a major reorganization of community structure that may lead to undesirable losses of natural capital and/or ecosystem services. These losses can also occur where changes are smooth and reversible (“non-catastrophic transitions”, Kefi *et al.* (2013)). Therefore, there is a strong focus amongst research ecologists, conservation managers and policy makers to develop early warning indicators (EWIs) so that undesirable ecosystem change can be prevented (Moss *et al.* 2013).

Extensive theoretical work has shown that prior to catastrophic shifts, ecosystems undergo a phenomenon known as “critical slowing down” (Scheffer *et al.* 2009). These models demonstrate that ecological time series show characteristic behaviours as a consequence of this process, notably an increase in variance and autocorrelation over time, and these behaviours have been suggested as potential EWIs (Wissel 1984; Carpenter & Brock 2006; van Nes & Scheffer 2007; Dakos *et al.* 2008; Scheffer *et al.* 2009). This theoretical work has received support from manipulative studies, some focused on artificial perturbations in laboratory experiments (Drake & Griffen 2010) and others on changes in predator abundance in whole lake experiments (Carpenter *et al.* 2011; Pace *et al.* 2013), which found that variance and autocorrelation in ecological time series increased prior to abrupt changes in these systems. Models have also demonstrated that similar patterns can occur in systems approaching non-catastrophic transitions, because they show increased sensitivity to environmental perturbations prior to the transition (Kefi *et al.* 2013). Thus, theory and experiments support the use of EWIs based on variance and autocorrelation as generic indicators of a wide array of non-linear ecosystem changes.

Despite this broad theoretical and experimental support, there is considerable uncertainty about the application of EWIs to real world ecological systems. Models suggest that ecosystems with complex dynamics may not exhibit EWIs prior to regime change (Hastings & Wysham 2010) and EWIs perform poorly when simulated data exhibit levels of noise similar to that seen in real world ecological data (Perretti & Munch 2012). Empirical studies that have explored the behaviour of real world ecological time series prior to non-linear change suggest that variance and autocorrelation have only limited application as EWIs (Hsieh *et al.* 2006; Litzow, Urban & Laurel 2008; Litzow, Mueter & Urban 2013; Krkosek & Drake 2014). However, these studies have typically been carried out on selected taxa and functional groups. The ecosystem-scale nature of potential non-linear change necessitates comprehensive, community-scale assessments utilizing existing long-term ecological time series to provide a catalogue of non-linear changes (hereafter, ‘turning points’) against which EWIs can be tested across contrasting ecosystems and multiple trophic levels. The ability to detect turning points and associated EWIs is predicted to differ among trophic levels because of differences in process variance and sampling protocols. For example, abundance time series of *K*-selected species, such as apex predators, show lower process variance and are typically sampled less frequently, often at annual intervals. Thus, they may be strong candidates for identification of turning points but weaker candidates for the detection of significant changes in variance or auto-correlation. In contrast, abundance time series of *r*-selected species, such as phytoplankton, generally show high process variance and sampling frequency, often at biweekly or monthly intervals. Thus, turning points may be more challenging to identify, but such time series may be stronger candidates for the detection of EWIs. These potential differences highlight the importance of assessing whether increases in variance and autocorrelation are consistent and reliable signals of impending non-linear change in multiple components of ecosystems.

In this paper, we focus on investigating coherence between changes in variance and autocorrelation and turning points in long-term abundance time series in six aquatic study systems that include shallow lake, deep lake and coastal marine ecosystems, across all trophic levels from primary producers to apex predators. Although there has been a documented regime shift in one of the systems examined (North Sea, Beaugrand 2004), we did not specifically test for associations between EWIs and regime shifts. Instead, we focused on non-linear change since theory suggests that increases in variance and autocorrelation are indicators or both catastrophic and non-catastrophic transitions. Study systems were selected because they comprised a broad range of ecosystems with structural differences, and with rich, long-term data on species abundance across all trophic levels from *r*-selected phytoplankton to *K*-selected apex predators. These data therefore enabled us to test the consistency between non-linear change and potential EWIs for a large sample of functionally-divergent species. Furthermore, the identification of reliable EWIs that would aid in averting undesirable change would align closely with relevant policy mechanisms tasked with identifying indicators of environmental change (EU Water Framework Directive and Marine Strategy Framework Directive). The study had four aims: i) to identify turning points in the abundance time series; ii) to identify significant increases in autocorrelation or variance in these time series; iii) to quantify the consistency with which turning points are preceded by significant increases in autocorrelation and/or variance; iv) to establish whether particular species, trophic levels or ecosystems consistently show coherence between non-linear change and EWIs.

Materials and methods

Data sets

We assessed the evidence for non-linear change, and associated EWIs, using 126 abundance time series representing 55 taxa (see Table S1 in Supporting Information for details on species and duration of time series). These study systems are all the subject of multi-decadal monitoring schemes which gather data on taxa from multiple trophic levels, from primary producers through to apex predators. The duration of the time series analysed ranged from 25 to 264 years (4926 cumulative years), with an average of 39 years. While all of our systems have exhibited long-term ecological change, they are not all the subject of documented regime shifts, providing an ideal opportunity to make a more generic assessment of the consistency between non-linear change and EWIs (*sensu* Kefi *et al*. 2013).

The Cumbrian lakes freshwater study system

Abundance data have been collected for over 65 years from lakes in the Windermere catchment, UK (54°21'N 2°56'W; Maberly and Elliott (2012)). The Cumbrian Lakes have been impacted by climatic change, nutrient enrichment and species introductions (George, Maberly & Hewitt 2004; Thackeray, Jones & Maberly 2008; Winfield, Fletcher & James 2010; Dong *et al.* 2012; McGowan *et al.* 2012). While significant changes in species abundance, community structure and seasonal dynamics have been observed in response to these drivers there is currently no quantitative evidence of regime shifts in these lakes. The abundance of dominant phytoplankton and zooplankton taxa or of annual catches of dominant fish species were analysed from the north and south basins of Windermere (all taxa), and from Esthwaite Water and Blelham Tarn (phytoplankton and zooplankton only). These lakes differ markedly in their morphology and trophic status (see Feuchtmayr *et al.* (2012)), with surface areas ranging from 0.1–8.1 km^2 and maximum depths from 15–64 m.

Raw phytoplankton data comprised counts at weekly to fortnightly intervals (Lund 1949). These taxonomically-resolved data were supplemented with data on chlorophyll-*a* concentrations (a widely used proxy for phytoplankton biomass; see Talling (1974) for details). Crustacean zooplankton data were derived from two sources (Thackeray *et al.* 2013): species-level data at weekly to fortnightly intervals (Windermere north basin), and aggregate total zooplankton filter paper counts for all lakes (Talling 2003). Plankton data were aggregated to genus level in order to minimize potential biases arising from differences in observers over the course of the monitoring scheme and analysis focused on a subset of easily identified commonly occurring genera. The study focused on data from 1978 onwards, when consistent counting methods were used. Fish data comprised Arctic charr *Salvelinus alpinus*, pike *Esox lucius* and perch *Perca fluviatilis* relative abundances from recreational catches, nets, and traps in the north and south basins of Windermere (see Paxton *et al.* (2004); Winfield, Fletcher and James (2008)).

The Loch Leven freshwater study system

Abundance data for plankton and birds were obtained from Loch Leven, a 13 km^2, shallow lake in lowland Scotland, UK (56°10'N 30°30'W). Over the study period, Loch Leven has been impacted by climate change, nutrient enrichment, changes in catchment management practices and industrial pollution (Spears & Jones 2010; Carvalho *et al.* 2012; May & Spears 2012). Although these drivers have been related to significant changes in ecosystem structure, there has been no formal quantification of regime shifts in this system. Long-term monitoring of phytoplankton has been undertaken since the late 1960s (May & Spears 2012). Raw plankton data comprised counts at weekly to monthly intervals (see Lund (1949); CEN (2004); Gunn *et al.* (2012)). Autumn and winter (September–March) waterfowl counts were collected by Scottish Natural Heritage (SNH) and the Royal Society for the Protection of Birds (RSPB) from land-based vantage points between 1968 and 2006 using Wetland Bird Survey (WeBS) methods (Austin, Collier & Rehfisch 2008). From 2006, fortnightly surveys were carried out. Here, we analysed winter peak counts.

The North Sea marine study system

Count data were analysed across four trophic levels of a pelagic food web in the north-western North Sea. A major ecosystem regime shift occurred in the North Sea in the late 1980s, thought to be driven by hydro-climatic forcing (Beaugrand 2004). Fisheries are also considered important drivers of ecosystem change in this system (Kenny *et al.* 2009). Monthly abundance data on phytoplankton and zooplankton were obtained from the Sir Alister Hardy Foundation for Ocean Science (SAHFOS) Continuous Plankton Recorder (CPR) survey (data available from David Johns, SAHFOS, The laboratory, Citadel Hill, Plymouth, PL1 2PB, UK), an upper layer plankton monitoring programme (Richardson *et al*. 2006). Data were obtained from an area of the North Sea (55°–58°N 3°W–0°E; Johns (2009)) that provided a balance between sampling resolution and proximity to the Isle of May National Nature Reserve, Scotland (56° 11'N 2° 33'W), the focal point of the apex predator (seabird) data. We analysed counts of the ten most abundant phytoplankton (diatom) species, and zooplankton species that are known to be important in the diet of sandeels *Ammodytes marinus*, which occupy a key mid-trophic position in this system (see Burthe *et al.* (2012) for full details).

We analysed an index of sandeel biomass, modelled from the probability of sandeel larvae occurring in CPR samples and the summed mass of larvae in a sample (see Frederiksen *et al.* (2006)). Catch abundance data for sea-trout *Salmo trutta* were analysed from two netting stations in the River Tweed estuary, Berwick-Upon-Tweed, UK (55° 77'N 2° 01'W): Sandstell and Whitesands; and annual catch data based on average catches across 14 netting stations from this estuary (Waite (1831); Tweed Foundation; unpublished data extracted from the records of the Berwick Salmon Fishing company held in the Public Record Office, Berwick; data available from The Tweed Foundation, The Tweed Fish Conservancy Centre, Drygrange Steading, Melrose, Roxburghshire, TD6 9DJ, UK). We analysed abundance data for five seabird species that breed on the Isle of May National Nature Reserve, a major seabird colony adjacent to the western North Sea (Daunt *et al.* 2008). Abundance consisted of annual, whole-island counts of breeding pairs during the breeding season (see Walsh *et al.* (1995) for full details).

Data analysis

Data processing

Ecologically significant non-linear ecosystem changes are frequently long-term in nature, and so we analysed non-linear change in abundance data at an inter-annual scale. Twenty-six of the time series were originally recorded at an annual scale. The remaining data sets (all plankton species) were monthly average counts (15 data sets), or counts at finer than monthly resolution that had uneven gaps between sampling occasions (85 data sets). To standardize the temporal resolution of these plankton data sets, we calculated annual mean chlorophyll-*a* concentrations and population counts for further analysis. This approach also prevented outliers (anomalously high abundances on specific dates) from exerting strong leverage when estimating long-term change.

The biological basis for the interpretation of EWIs is implicitly grounded in shorter-term ecosystem behaviour (Scheffer *et al.* 2009). Therefore, in order to evaluate whether there were significant increases in autocorrelation or variance that could be used as EWIs, we focused on data at the original sampling resolution apart from the 85 data sets that had uneven gaps between sampling occasions. For these time series, data were interpolated to a biweekly resolution so that the sliding window used to calculate changes in the EWIs was consistent across the time series.

The first step in identifying changes in the abundance data was to ensure that, prior to investigating turning points, each time series was standardized. Models were fitted to the abundance data with day of year (*doy*) as a covariate in order to account for any seasonality. This model was fitted as a Generalized Additive Model (GAM, Hastie and Tibshirani (1990)) to allow for a non-linear, within-year relationship for the *doy* term and to allow for the non-normal error structure associated with the abundance data. The model formula used to standardize the abundance data y at time t was:

$$\log(y_t) = \beta_0 + f(doy_t) + \sum_{i=1}^{k} \gamma_i$$

where a log link was used (left hand side of equation), β_0 is the model intercept, which effectively corresponded to the overall mean abundance, doy is the day of year, which can run from 1 to 366; f is a smoothly varying function (derived using thin plate regression splines, Wood (2003)), with flexibility constrained according to the length of the time series (Fewster *et al.* 2000), and γ represents the k contrasting levels of any confounding factors (not fitted here). As the majority of abundance data was actually non-integer valued, a Gamma error distribution was assumed. Models were fitted using the mgcv package (version 1.8-3; Wood (2011)) in the R statistical environment (R Core Team, 2014). A standardized time series (one with within-year seasonality removed) was obtained by subtracting estimates of the fitted model from the observed abundance data. These residuals, representing long-term abundance change after partitioning out variation due to seasonality, were then used to assess evidence of any turning points in the time series.

Identifying turning points

To estimate changes in the long-term trend of each standardized abundance time series (i.e. turning points), and to characterize the pattern of the response, smoothly varying relationships were fitted to the data with respect to time. The smooth form is able to capture the general signal present in the standardized time series, while smoothing out random variation about the trend. This was fitted using a GAM with a smoothly varying function of time included as an explanatory covariate. In this case, the time covariate is a running day value continuously increasing from the first day of sampling until the last, fitted with a log link function and Gamma distribution.

From this fitted smoother, the nature of the trend was determined at all points along the whole time series. The trend was characterized according to three states: increasing trend, decreasing trend or stationary. To assign any point along the temporal axis to one of these three states, the first derivative of the fitted smoother with respect to time was calculated using finite differences. Standard errors of these derivatives were also estimated to provide 95% point-wise confidence intervals around the gradient and hence assess whether the gradient was significantly different from zero. If the gradient was non-significant the trend was classified as stationary, otherwise the trend was classified according to the sign of the gradient. This follows a similar approach to that taken by Large *et al.* (2013) and Monteith *et al.* (2013). A significant change in the time series was defined as the point at which the trend changed from one state to another. Similar approaches to estimating turning points have also investigated significant second derivatives (e.g. Fewster *et al.* (2000)). However, because of the requirement to classify the trend into the three states (stationary, positive, negative), the first derivative method was used – the second derivative method cannot inform on periods of stationarity.

Identifying time periods with changing autocorrelation and variance (EWIs)

Lag-1 autocorrelation and variance components were extracted for all of the raw time series corresponding to those series which have been assessed for turning points. This was done across a rolling window that corresponded to 25% of the data using the R package "earlywarnings" following

Dakos *et al.* (2012a). The extracted autocorrelation and variance series were then subjected to the same routine as the abundance time series to determine when any significant changes in the state of the indicator had occurred. As theoretical models predict an increase in variance or a strengthening of autocorrelation prior to a turning point in the time series (Carpenter *et al.* 2008; Dakos *et al.* 2012a), we only considered changes from a positive state to a stationary state and changes from a stationary state to a positive state as being ecologically informative, these being, respectively, indicative of a change to a new state or an increase in EWI preceding change.

Coherence between EWIs and turning points

To be ecologically informative as EWIs, significant increases in the variance and autocorrelation of a time series must occur prior to turning points in the data. In the absence of *a priori* information on the timescale over which EWIs would precede abundance change, we considered ten years to be an appropriate period within which to assess coherence. A decade encompasses a broad range of potential lags between EWIs and turning points, and, based on existing knowledge of the population dynamics and generation times of the study organisms, we would expect demographic responses to occur within this time scale. Moreover, ten years is a practically-useful time horizon over which managers could respond. We undertook separate assessments of variance and autocorrelation. We first examined each case in which an EWI and/or a turning point was detected in a time series. Each case was categorized as either a turning point with an associated EWI, a turning point without an EWI or an EWI without a turning point; thus, there could be multiple cases per time series. When assessing cases, we did not differentiate between the direction of change in either the EWI (stationary to positive or positive to stationary) or the turning point (stationary to positive, positive to stationary, stationary to negative, negative to stationary). We followed the terminology used by Scheffer *et al.* (2009) to assign each case to one of three EWI detection classifications:

i) **False positive:** significant increase in the EWI but no associated turning point in the abundance time series.

ii) **False negative:** significant turning point in the abundance time series but no associated increase in the EWI.

iii) **True positive:** significant increase in the EWI in association with a significant turning point in the abundance time series.

Where a turning point in the abundance time series occurred within ten years of the start of the data set and with no EWI preceding it, we could not be confident that an EWI had not occurred previously. Similarly, where an EWI occurred within 10 years of the end of a data set but no turning point followed, we could not be certain of the absence of a turning point. We therefore did not consider these cases further.

We then classified each data set into the following categories according to the combination of EWI detection classifications that it contained: i) Null: no EWI detection classifications (no significant turning points in the time series and no EWIs); ii) False negative(s) only; iii) False positive(s) only; iv) True positive(s) only; v) False positive(s) and false negative(s); vi) True positive(s) and false negative(s); vii) True positive(s) and false positive(s); or viii) True positive(s), false positive(s) and false negative(s).

Finally, a bootstrap-based test was developed to see if there was a statistically significant association between EWIs and turning points. A test statistic was developed that: i) looped through all turning points in a given time series; ii) found the nearest preceding significant change in the EWI for each of these turning points; and iii) calculated the time lag between these events and the variance among lags (in days), as the test statistic. In a bootstrap procedure, this observed test statistic was then compared to 1000 other test statistics obtained by randomly generating the same number of pseudo turning points as had been found in the observed data according to a uniform distribution across the time period. The *p* value is given by the proportion of times the variance of the simulated data was more extreme than the variance of the observed data. This provided a clear test of whether the observed changes in the EWI were more consistently related to turning points than could be achieved by chance. Lag variance was used because our primary aim was to identify whether EWI variance or autocorrelation showed a consistent association with turning points in the time series, rather than estimating the proximity of the EWI to the turning point. If consistency was apparent, then the lag between the EWI and the turning point would be established. When only one turning point was identified in the time series data, the distance in days between that turning point and any significant change in the EWI was used as the test statistic. We quantified the number of significant relationships between EWIs and turning points according to species, ecosystem or trophic level in order to identify whether particular species groups showed high levels of coherence and hence had potential as effective species for management intervention.

Results

Turning points in annual scale time series data

Of the 126 time series tested, 91 (72%) did not show any significant turning points. Of the remaining thirty-five, 10 showed one turning point and 25 showed multiple turning points (range 2–8), giving a total of 81 turning points (see Figure 1, Figure 2, Figure S1 & Table S2). Expressed as the average turning point per unit time to standardize across time series of different lengths, this equated to 0.128 to 2.143 turning points per decade (mean 0.179). There was a broadly even distribution of turning points between the four different categorizations, with 24%, 27%, 21% and 28% of turns being negative to stationary, positive to stationary, stationary to negative and stationary to positive respectively. We did not detect any obvious temporal synchrony in the incidence of turning points among taxa within, or between, trophic levels or ecosystems (Figure 2 and Figure S1). A greater proportion of predator time series (91%; n=11) showed turning points than other trophic levels (primary producers 19% (n=83); primary consumers 28% (n=18); secondary consumers 29% (n=14)). Note, however, that 70% of the predator time series are from the North Sea (Figure 3). However, there was no difference among trophic levels in turning points per decade (Figure S2).

Early warning indicators: increases in variance and autocorrelation

A significant change in variance was detected in 74 (59%) of the 126 time series, whereas 56 (44%) showed a significant change in autocorrelation. For variance, 16 of 74 (22%) showed one change and 58 of 74 (78%) showed multiple changes (range 2–4), giving a total of 161 changes (76 positive to stationary and 85 stationary to positive). Equivalent values for autocorrelation were 13 of 56 (23%) with one change and 43 of 56 (77%) with multiple changes (range 2–7), totalling 137 (73 positive to stationary and 64 stationary to positive; see Table S3 and S4). The incidence of significant changes per unit time equated to 0.125 to 1.600 (mean 0.383) significant changes per decade for variance and 0.076 to 2.258 (mean 0.321) for autocorrelation.

Coherence between EWIs and turning points: EWI detection classifications per case

A total of 88 time series for variance and 78 for autocorrelation contained cases that could be assigned an EWI detection classification (contained a turning point and/or an EWI). There were a total of 239 cases based on variance. Sixty nine cases occurred within 10 years of the start or end of the time series and were not considered further (see methods), leaving a total of 170 cases to test for coherence. Of these, 16 (9%) were true positives where the variance change preceded a significant turning point within a 10 year period. For autocorrelation, there were a total of 209 cases, of which 57 were excluded due to proximity to the start or end of the time series, leaving 152 cases that could be assigned an EWI detection classification. Of these 152 cases, 19 (13%) were true positives. False results were more common in the time series than true positives (91% of cases for variance and 87% for autocorrelation), of which false positives were more common than false negatives (53% vs. 38% for variance; 47% vs. 40% for autocorrelation; see Table 1). Moreover, false results were found in every decade across all trophic levels and ecosystem types.

Coherence between EWIs and turning points: EWI detection classifications per time series

When considering associations between increased variance and turning points, 55 time series contained cases with uncertain classification due to proximity to the start or end of the time series. Of the 71 remaining data sets, 6 (8%) contained true positives (five with one true positive, one with two), but all of them also contained false cases. For autocorrelation, 43 time series were unclassified, leaving 83 data sets of which 5 (6%) contained true positives (two with one true positive, one with two and two with three), with all but one of these also containing false cases. Therefore, only one time series contained a true positive without any false results and this had a single true positive case. No time series contained multiple true positive cases without any false cases being present, either for variance or autocorrelation. In total, 38 (30%) data sets tested for change in variance and 48 (38%) for autocorrelation were classed as null because there was no significant change in the EWI or turning points in the time series (Figure 4 and Table S5). There was generally poor concordance between the classifications for variance and those for autocorrelation. Of the 54 time series that did not contain cases with uncertain classification for both variance and autocorrelation, 25 (43%) were assigned a different classification (see Table S6 for a full breakdown).

Formal testing of the significance of associations between the EWI and turning points was undertaken on the 35 data sets showing significant turning points. Two time series, both from the south basin of Windermere, showed a significant relationship between the timing of an EWI and a turning point in the time series: *Staurastrum* sp. showed an increase in autocorrelation in 1993 and a turning point in 1994; pike showed an increase in variance in 1979 and a turning point in 1990 (see Table S7). Note that for pike this coherence between variance and turning points was not included in previous assessments at the case level, due to the gap between EWI and turning point being greater than 10 years. As only two species showed significant coherence between EWIs and turning points, we were not able to address our aim of identifying whether particular species, trophic levels or ecosystems were more sensitive to showing effective EWIs.

Discussion

Variance and autocorrelation as EWIs of non-linear change

This paper presents an analysis of temporal coherence between turning points and significant increases in variance and autocorrelation in abundance time series. Based on 126 long-term data sets from a suite of species across four trophic levels in shallow lake, deep lake and coastal marine ecosystems, we believe it represents one of the most comprehensive tests of EWIs in real world data yet undertaken. Although our analysis identified both significant increases in variance and autocorrelation, and turning points in abundance, there was scant evidence that turning points were consistently preceded by significant increases in variance and autocorrelation. False results were found to be prevalent in all decades, trophic levels and ecosystems. False positives (significant increases in variance or autocorrelation but no associated turning point) and false negatives (the converse) were both more commonly found than true positives. Furthermore, the majority of data sets containing true positives also contained false results. Based upon our bootstrapping procedure, only two true positive cases were unlikely to have occurred by chance. Our results therefore support modelling and empirical studies that have quantified changes in variance and autocorrelation in selected taxa or functional groups and found inconsistent or little evidence that they precede non-linear change (Hsieh *et al.* 2006; Litzow, Urban & Laurel 2008; Dakos *et al.* 2012b; Batt *et al.* 2013; Dakos, van Nes & Scheffer 2013; Litzow, Mueter & Urban 2013; Krkosek & Drake 2014).

We adopted a flexible approach by considering turning points as generic indicators of non-linear change, which may have included both catastrophic and non-catastrophic transitions. Abundance data were used because they are readily analysed using freely available statistical packages and long time series were available. The analysis identified turning points in 38% of the amassed time series. In general, there was little evidence of temporal synchrony among turning points detected for different taxa or trophic levels within ecosystems (Figure S1, Table S2), which is unsurprising since generation times and life-history strategies of different species and trophic levels differ. Although we are unable to establish whether turning points represented species and systems undergoing non-catastrophic or catastrophic shifts, our time series encompassed a well documented regime shift in the North Sea in the 1980s (Beaugrand 2004) and turning points of key species, notably zooplankton, accorded with the shift.

Variance and autocorrelation were selected as candidate EWIs because they have an established theoretical basis, empirical verification from experimental work, and can be calculated readily (Scheffer *et al.* 2009; Carpenter *et al.* 2011). In addition, models have demonstrated that they offer different advantages: variance can be calculated for shorter time series, whilst autocorrelation is generally more effective because it is less influenced by environmental noise (Dakos *et al.* 2012b). We successfully identified significant increase in variance and autocorrelation in 41% and 44% of time series respectively. Overall, we were therefore confident that we had sufficient cases of turning points and increases in candidate EWIs to test the association between them. However, we found poor temporal coherence between variance, autocorrelation and turning points both among and within data sets, with false results predominating and present in data sets exhibiting cases of positive coherence. This finding supports our assertion that we would be constrained by the particular characteristics of different trophic levels. Thus, our data suggest that *K*-selected species are strong candidates for the detection of turning points but do not show sufficient process variance or sampling frequency to detect EWIs that precede them. In contrast, *r*-selected species have higher process variance, even when integrated to the same sampling intervals as *K*-selected species, making the detection of turning points more challenging. Alternatively, EWIs may be more effective prior to catastrophic change, in association with the phenomenon of critical slowing down, and the predominance of false associations could have occurred if the majority of turning points were linked to non-catastrophic change. However, theoretical work has shown that EWIs also occur prior to non- catastrophic transitions, because ecosystems show increased sensitivity at this time (Kefi *et al.* 2013). Had we found a greater degree of coherence between EWIs and abundance change across our time series, the next step would have been to identify which species, species groups or trophic levels had the greatest potential as sensitive indicator species for management. Secondly, we would have identified critical indicator levels of change in variance or autocorrelation occurring prior to a non-linear change that could be used to trigger a management response (as advocated by Biggs, Carpenter and Brock (2009)). However, the high prevalence and broad distribution of false results across ecosystems precluded us from fulfilling these aims.

Synthesis and applications

While abundance time series and associated variance and autocorrelation have great appeal in being widely available and readily analysed, we believe that additional approaches are required to identify EWIs that managers of real world ecosystems can use. It is clear from our analyses that despite variance and autocorrelation showing promise as EWIs using simulated data, these approaches are currently inadequate for widespread application to real world data. To increase their utility for real ecosystems, further development of EWIs is therefore a high priority.

We focused our analysis on temporal coherence between EWIs and generic turning points, which may have included both catastrophic and non-catastrophic changes. We recommend further exploration of systems exhibiting well characterized regime shifts to establish whether EWIs are more effective indicators of catastrophic change. We also recommend the application of these approaches beyond abundance data to other ecologically-relevant state variables such as phenology, productivity, physiology and behaviour. Such parameters may be more sensitive and responsive to environmental change than abundance, which typically integrates multiple processes affecting fitness traits. Incorporating spatial information into time series analyses may help increase statistical power and inference (Dakos *et al.* 2011). However, models must include spatial as well as temporal variance and autocorrelation, and factoring in a spatial component considerably reduces the number of available data sets.

The efficacy of EWIs may also be a matter of ecological scale. Herein we assessed change at the population scale and sought coherence among these population-level results. However, EWIs may in fact be more strongly manifest in measures of community or ecosystem structure. Multivariate modelling techniques that analyse community-level data could therefore enhance our ability to identify transitions (Dakos *et al.* 2012a; Lindegren *et al.* 2012). Community-level turning points may be more indicative of ecosystem-level catastrophic change than single time series (Angeler *et al.* 2013; Eason, Garmestani & Cabezas 2014; Spanbauer *et al.* 2014), and testing could be focussed on systems with well documented regime shifts (Wouters *et al.* 2015).

Furthermore, we also recommend exploring a larger suite of candidate EWIs (Lindegren *et al.* 2012). Changes in skewness, flickering and conditional heteroscedasticity show promise as effective EWIs in theoretical studies and warrant investigation in real world data sets (Scheffer *et al.* 2009; Seekell *et al.* 2012; Dakos, van Nes & Scheffer 2013). Finally, establishment of EWIs for ecosystem change using state variables such as abundance time series might be challenging without incorporating drivers of change and process based understanding into models. However, more sophisticated approaches are challenging to communicate and of more limited management potential which would introduce constraints on building capacity among the research and conservation communities.

There is accumulating evidence that species and communities are exhibiting non-linear changes in response to environmental change. These transitions have resulted in considerable concerns among conservation managers and policy makers that ecosystem change may become more frequent, with associated losses in natural capital and ecosystem services. Preventing such change is more desirable and practical than reversing it, hence there is widespread interest in developing reliable EWIs for real world situations. Long-term monitoring plays a vital role in ensuring that the development, testing and refinement of such indicators can continue into the future. While studies should focus on the most promising time series in terms of quality and length, our study supports the assertion that there is unlikely to be a "silver bullet" that meets this challenge (Dakos *et al.* 2012a; Lindegren *et al.* 2012) and that early detection of non-linear change using variance and autocorrelation as early warnings may be wishful thinking (Ditlevsen & Johnsen 2010). Thus, it is recommended that further studies could adopt some of the alternative approaches suggested here. Ultimately, there is likely to be a limit to what can be achieved with time series analysis in isolation. Therefore, such studies should be undertaken in tandem with empirical analyses and modelling that enhance process understanding.

Acknowledgements

The present study was funded by the Centre for Ecology & Hydrology Ecological Resilience project, supported by the Natural Environmental Research Council. We thank NERC for supporting the Lake studies. We thank staff at the Freshwater Biological Association for initiating the ongoing long-term monitoring scheme in the Cumbrian Lakes. Waterfowl count data were provided by Scottish Natural Heritage, and collected by SNH and the Royal Society for the Protection of Birds. The Kinross Estates provided access to Loch Leven. We are grateful to all past/present members and supporters of the Sir Alister Hardy Foundation for Ocean Science for establishment and maintenance of the CPR data set and the owners and crews of ships towing the CPRs. We thank Mike Harris and many others who collected seabird data. We thank NERC and the Joint Nature Conservation Committee for supporting the long-term seabird studies, and Scottish Natural Heritage for allowing work on the Isle of May and for providing seabird count data. We thank two anonymous referees for helpful comments on the manuscript.

Data Accessibility

Species descriptions are included in the online supporting information (Table S1). All data sets are available online from the NERC data centre (Carvalho et al. 2015: http://doi.org/10/6c2; Gunn et al. 2015: http://doi.org/10/5xc; Mitchell et al. 2015: http://doi.org/10/6gx; Thackeray et al. 2015: http://doi.org/10/5q8) apart from North Sea plankton data (available on request from David Johns, SAHFOS, The laboratory, Citadel Hill, Plymouth, PL1 2PB, UK), sea-trout data (available on request from Ronald Campbell, The Tweed Foundation, The Tweed Fish Conservancy Centre, Drygrange Steading, Melrose, Roxburghshire, TD6 9DJ, UK) and seabird data (available online from the Seabird Monitoring Programme; http://jncc.defra.gov.uk/smp/sitesBrowser.aspx?siteID=84986).

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Supporting Information

Additional supporting information may be found in the online version of this article:

Table S1: Species information

Table S2: Timing of turning points and direction of change per species

Table S3: EWI detection classifications (classes) per species for variance

Table S4: EWI detection classifications (classes) per species for autocorrelation

Table S5: Overall classification of time series based on EWI detection classes

Table S6: Agreement between classifications of time series according to the two EWI methods

Table S7: Results of formal testing by bootstrapping of association between EWI and turning points

Figure S1: Turning points in time series across ecosystems.

Figure S2: Significant turning points per decade per trophic level.

Table 1: Number of cases in each early warning indicator (EWI) detection classification

EWI detection classification	No. of cases based on variance	No. cases based on autocorrelation
True positive	16	19
False positive	90	72
False negative	64	61

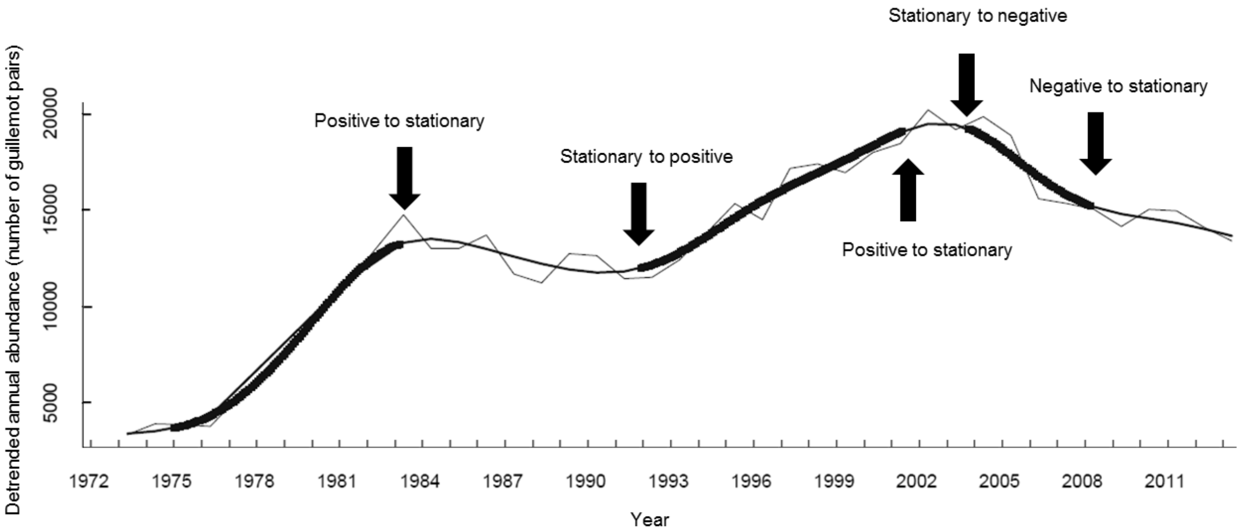

Figure 1: Example plot showing abundance of common guillemots *Uria aalge* in the North Sea ecosystem. Turning points occur where the fitted line changes thickness. All four directions of change were observed in this data set.

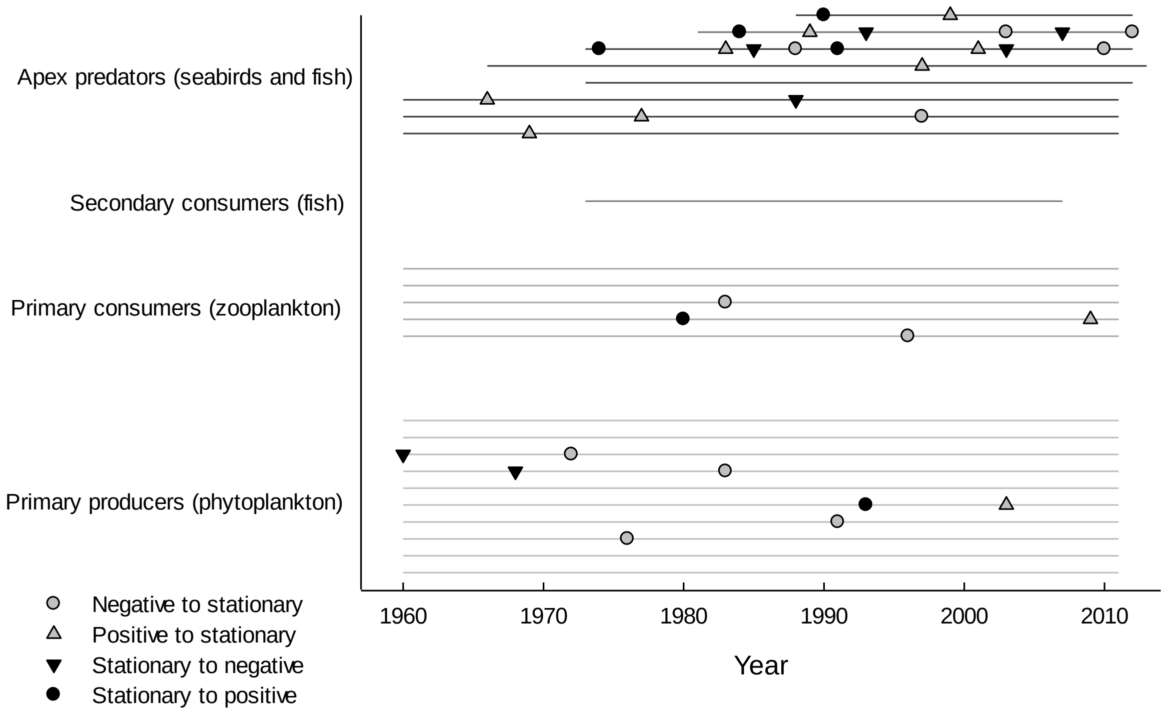

Figure 2: Timing and direction of change of turning points in time series across different trophic levels for the North Sea (see Figure S1 for plots of other study ecosystems). The direction of change is indicated by the filled symbols. The lengths of the lines represent the duration of the time series (truncated to 1960 for ease of viewing).

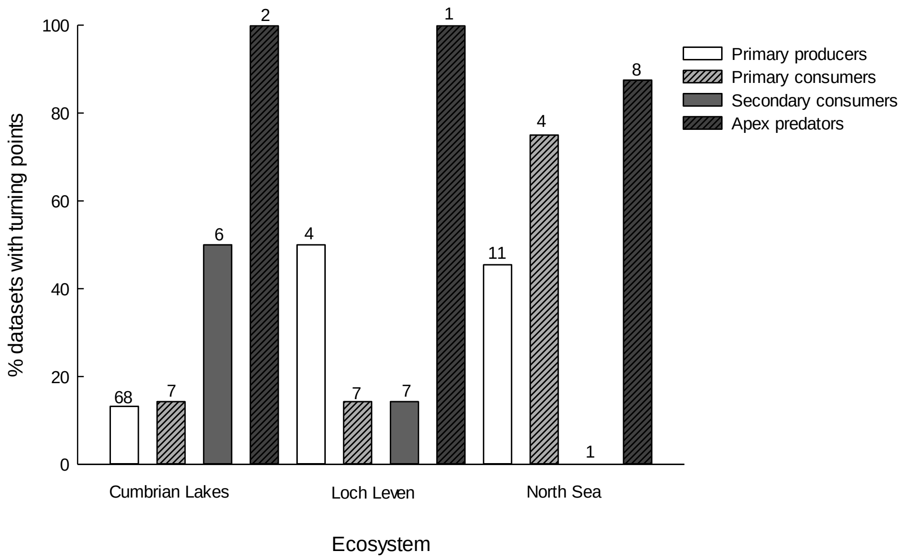

Figure 3: The percentage of data sets with at least one turning point, by trophic level, across ecosystems (four Cumbrian Lakes grouped for ease of viewing). The numbers above the bars indicate the number of time series in each category. Secondary consumers in the North Sea showed no turning points.

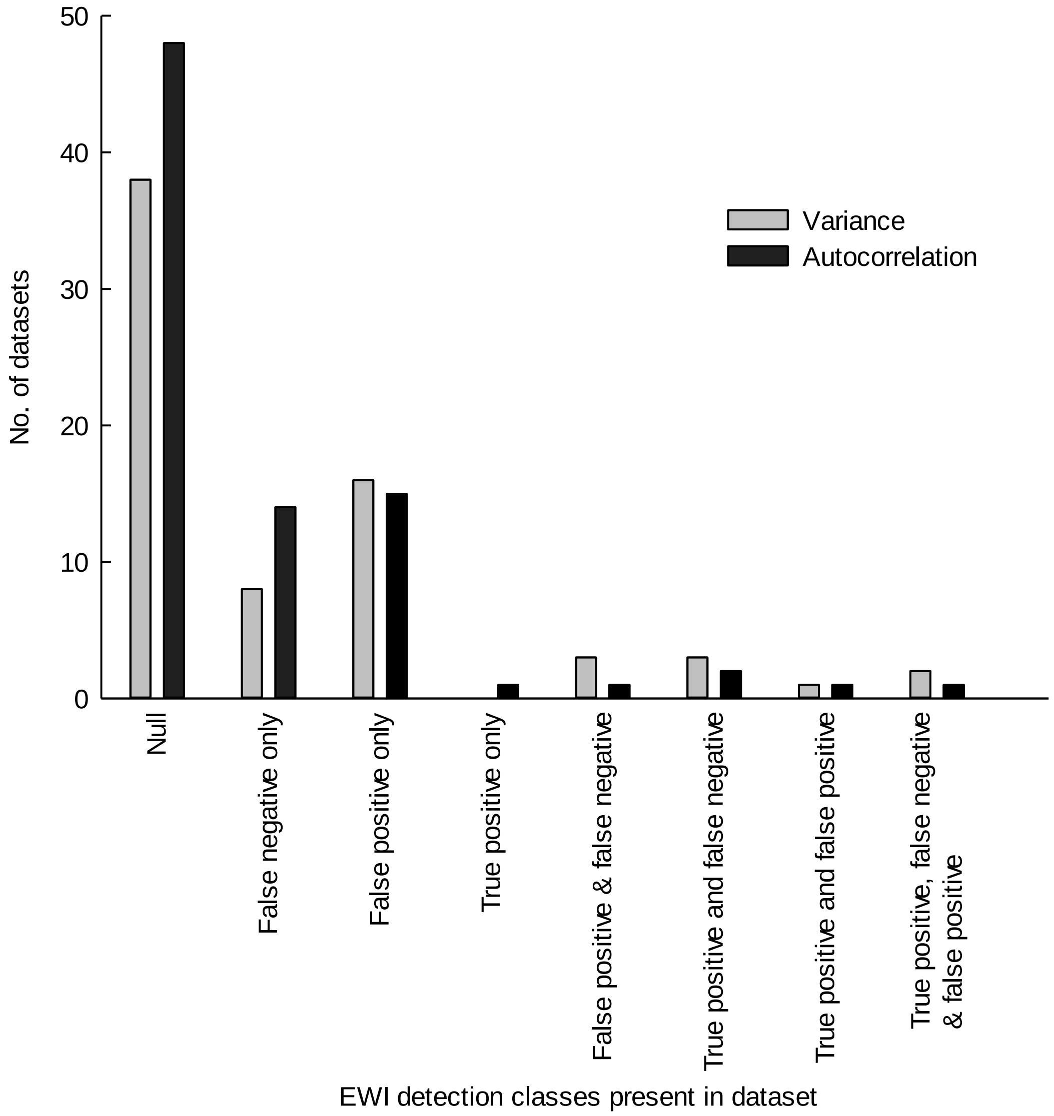

Figure 4: Classification of time series with respect to early warning indicator (EWI) detection classifications. Null classification occurs when data sets have no significant change in EWIs (variance or autocorrelation) or turning points. Bars show the number of data sets in each category, with classifications based on variance shown in grey and autocorrelation shown in black.