Shifting Regimes and Changing Interactions in the Lake Washington, U.S.A., Plankton Community from 1962–1994

Tessa B. Francis1*, Elizabeth M. Wolkovich2,3,4*a, Mark D. Scheuerell5, Stephen L. Katz6,7b, Elizabeth E. Holmes6, Stephanie E. Hampton2,8c

1 University of Washington Tacoma, Puget Sound Institute, Tacoma, Washington, United States of America, 2 National Center for Ecological Analysis and Synthesis, University of California Santa Barbara, Santa Barbara, California, United States of America, 3 The Biodiversity Research Centre, University of British Columbia, Vancouver, British Columbia, Canada, 4 Fish Ecology Division, Northwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Seattle, Washington, United States of America, 5 Channel Islands National Marine Sanctuary, National Ocean Service, National Oceanic and Atmospheric Administration, Santa Barbara, California, United States of America, 6 Conservation Biology Division, Northwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Seattle, Washington, United States of America

Abstract

Understanding how changing climate, nutrient regimes, and invasive species shift food web structure is critically important in ecology. Most analytical approaches, however, assume static species interactions and environmental effects across time. Therefore, we applied multivariate autoregressive (MAR) models in a moving window context to test for shifting plankton community interactions and effects of environmental variables on plankton abundance in Lake Washington, U.S.A. from 1962–1994, following reduced nutrient loading in the 1960s and the rise of Daphnia in the 1970s. The moving-window MAR (mwMAR) approach showed shifts in the strengths of interactions between Daphnia, a dominant grazer, and other plankton taxa between a high nutrient, Oscillatoria-dominated regime and a low nutrient, Daphnia-dominated regime. The approach also highlighted the inhibiting influence of the cyanobacterium Oscillatoria on other plankton taxa in the community. Overall community stability was lowest during the period of elevated nutrient loading and Oscillatoria dominance. Despite recent warming of the lake, we found no evidence that anomalous temperatures impacted plankton abundance. Our results suggest mwMAR modeling is a useful approach that can be applied across diverse ecosystems, when questions involve shifting relationships within food webs, and among species and abiotic drivers.

Introduction

One of the most important challenges facing ecologists is specifying how global change will affect community stability and the production of associated critical ecosystem services. Community stability is mediated by species interactions, which are sensitive to changing environmental conditions [1,2], and therefore estimating the effects of environmental drivers on food web dynamics is critical for understanding how anthropogenic forces have altered ecosystems and for anticipating further change [3,4]. Analyzing food web dynamics is complicated in part because the communities we observe are likely not in “equilibrium” as we might have once expected [5]. There is increasing evidence that the structure of communities and the nature of species’ responses to each other and to their environments are not static, but rather shift over time. In particular, anthropogenic pressures may be pushing communities further from equilibrium [6], with communities exhibiting a variety of non-equilibrium dynamics from smooth trends to abrupt step changes [7]. Changes in abiotic conditions of ecosystems can directly and indirectly affect food web structure [8]. Thus, food web models must account for diverse temporal changes in community dynamics. In some systems, while we may have a good understanding of average species interactions or effects of the environment on food web dynamics over key time periods, we may still lack important information about whether
and how such dynamics changed over time in response to large shifts in the ecosystem.

Lake Washington, U.S.A., is an example of an aquatic ecosystem that experienced a series of well-described dramatic changes in its environmental conditions and plankton community in the mid-20th Century. This time period included a regime shift from one of high nutrient loading from sewage inputs to one of increased water clarity, as well as temperature and species abundance changes [9–11]. The lake also experienced shifting regimes in terms of plankton community dominance. During the era of high sewage inputs, the lake experienced extensive nuisance algal blooms, especially of the cyanobacterium, Oscillatoria rubescens. Following sewage diversion, water clarity increased substantially [12]; subsequently, the influential grazer Daphnia established in the lake [11] and Oscillatoria effectively disappeared from the record. In more recent years, warming temperatures have caused phenomenological changes in phytoplankton and zooplankton [10,13,14]. What is unclear is how these changes in the plankton community and abiotic conditions affected interactions within the food web concomitant with the changing environment. Such shifts in plankton community interactions – such as weakening of grazer effects on phytoplankton, or increased competition among grazing zooplankton guilds – would have consequences for higher trophic levels in lakes, as plankton provides an important component of the energetic support for some lacustrine fish [15], including in Lake Washington [16]. Moreover, plankton community structure and indirect effects of herbivore-plant interactions can influence fundamental lake characteristics such as light, temperature and water clarity [17,18]. In this paper, we introduce an extension of a well-used static food web model – a multivariate autoregressive (MAR) model [19–21] – to study Lake Washington’s dynamically changing food web and ecosystem.

Over the last several decades, multivariate time-series methods have been used to estimate the strength and pattern of species interactions and the effect of abiotic drivers on communities [20,22]. MAR models provide a locally linear approximation of non-linear stochastic multispecies processes. They have been particularly useful in aquatic ecosystems and for understanding plankton dynamics in part because of the tight coupling between plankton and their environment. MAR models have also become useful in broader aquatic food web analyses [23,24], as they can incorporate multiple trophic levels and environmental drivers.

Prior implementations of MAR models have assumed that the interactions in the study system were unchanging over the time period encompassed by the data. This approach maximized the performance of parameter estimation given the properties of monitoring data, but only estimated the average interaction strengths over a time series. In contrast, if food web dynamics shift in response to changing drivers [25], then a better analytical approach would accommodate and capture this non-stationarity in modeling the food web. A suite of statistical methods can be applied to ecological time series to examine non-stationarity – such as shifts in abiotic conditions or periodicities – through time. Methods such as wavelets [26,27], single-spectrum [28] and breakpoint analyses have been used in climatology and paleoclimatology, and have also recently been applied to ecological data [29,30]. Such methods allow ecologists to see how abundances may be shifting [30] or how interactions among species may change over time in simple lab systems [29], but they do not provide a cohesive ecosystem approach to examining how integrated abiotic and biotic forces may change through time. In particular, food web responses to changes in the strength or nature of abiotic drivers would be predicted to cause cascading shifts in the interactions among many members of a food web, and may also feed back to how community members respond to other environmental drivers. Examining such a suite of interactions and drivers, however, would require a model that analyzes all the variables at once, and that allows estimation of such shifts through time.

A running or moving window approach is another tool that has long been used in other disciplines, such as finance, to examine non-stationarity in time series. In this approach, consecutive and overlapping subsets of time series – or windows – are analyzed individually to detect changes through time in a historical record [31,32]. This approach has recently been used with univariate autoregressive models to develop leading indicators of regime change [33–35]. Here we offer an extension of the MAR model, which we term “moving-window MAR” (mwMAR), and we use it to examine a case of shifting species interactions and environmental effects on species through time. Our approach blends the community focus of the MAR model with the moving window approach of detecting historical changes in time-series data. We describe the mwMAR model and then apply the model to long-term monitoring data from Lake Washington, U.S.A., to show how interactions among dominant taxa of the plankton community shifted following sewage diversion. Because food webs show sensitivity to changes in their abiotic environment [6–8], we hypothesize that changes in the nutrient status, clarity, and dominant plankton taxa of the lake would cascade throughout the plankton food web, resulting in shifts in the direction and strength of community interactions, which would in turn affect community stability.

**Materials and Methods**

**Model configuration**

We estimated interaction strengths among phytoplankton and zooplankton guilds, environmental effects on phytoplankton and zooplankton abundance, plankton intrinsic growth rates, and plankton community stability in Lake Washington from 1962–1994 using multivariate autoregressive (MAR) models. MAR models are stochastic models describing changes in species abundance through time as a function of species interactions and environmental influences, while accounting for temporal autocorrelation in species abundances [20,36,37]. MAR models can also be used to estimate various metrics of community stability, such as return time to a stationary state following an ecosystem perturbation, or the distance away from a stationary state that an ecosystem can be pushed by a perturbation. Previous work has used MAR models to describe environmental effects on, and interactions among, lake phytoplankton and zooplankton [20,22,38,39], effects of climate regime shifts on interactions among marine plankton [40], causes of estuarine fish declines [24], and effects of fishing on marine food webs [23]. Extended descriptions of MAR approaches to time-series data have been given previously [19,20,37], so we provide only a brief review of the model structure here.

MAR models are written in matrix form as:

$$\mathbf{X}_t = \mathbf{A} \mathbf{X}_{t-1} + \mathbf{B} \mathbf{X}_t + \mathbf{C} \mathbf{U}_t + \mathbf{E}_t$$  \hspace{1cm} (Eq.1)

where, for $p$ interacting species and $q$ environmental covariates, $\mathbf{X}_t$ is a $p \times 1$ vector of species abundances (here, natural log-transformed) at time $t$, $\mathbf{A}$ is a $p \times 1$ vector of constants, representing intrinsic per-capita growth rates; $\mathbf{B}$ is a $p \times p$ species interaction matrix, with off-diagonal elements describing inter-specific interactions, and diagonal elements describing intra-specific interactions.
Shifting Interactions in the Lake Washington Plankton Community

(i.e., density-dependence); \( C \) is a \( p \times q \) matrix with elements describing environmental effects on species abundance; \( U_t \) is a \( q \times 1 \) vector of environmental covariates at time \( t \); and \( E_t \) is a \( p \times 1 \) vector of process errors at time \( t \), representing environmental variation not otherwise accounted for in the model. \( E_t \) is distributed as a multivariate Normal with mean 0 and a diagonal variance matrix \( \Sigma \). Elements of \( B \) and \( C \) typically range from -1 to 1, with distance from 0 representing increasing negative or positive interaction strength. The diagonal elements of \( B \) typically range from 0 to 1, with values closer to 0 representing higher density dependence.

We also used MAR models to estimate community stability. Specifically, we estimated the rate at which the system returns to its stationary distribution following a disturbance by the maximum eigenvalue of the \( B \) matrix (that maximum eigenvalue is henceforth referred to as lambda, \( \lambda \)). Systems with values of \( \lambda \) closer to 0 are considered to be more stable because they tend to return to equilibrium conditions faster than systems with values of \( \lambda \) farther from 0 [21].

MAR models estimate mean intrinsic growth rates (captured by the \( A \) vector), community interactions (captured by the \( B \) matrix), environmental effects (captured by the \( C \) matrix), and community stability (captured by \( \lambda \)) across a given time series [20]. Here we use MAR models to quantify changes in interactions through time, by modeling community interactions for overlapping subsets of a time series, or moving “windows” of time, thereby estimating trends in MAR parameters. For a \( p \times n \) matrix \( X \) of time series observations consisting of successive \( p \times 1 \) vectors \( X_1, X_2, \ldots, X_n \), and a moving window of size \( W < n \), we estimated MAR parameters within \( n-W \) successive windows. These windows contained data from \( X_{W+1}, X_2, X_{W+2}, \ldots, X_{n-W+1} \). Note that the time series starts at \( t=2 \) to avoid the lag-1 effect in Eq. 1. The output of the mwMAR analysis is a new time series of estimated MAR parameters.

Lake Washington data and analysis

To investigate changes in interactions among zooplankton and phytoplankton guilds and the effects of environmental covariates in Lake Washington through time, we implemented the mwMAR approach using monthly plankton and environmental data from Lake Washington (Washington, U.S.A.) spanning 1962 to 1994 (396 timesteps; see Figure S1 for plankton time series). Our 33-year time series begins in the year of maximum sewage input (1962) when the lake experienced extensive nuisance algal blooms, especially of the cyanobacterium, *Oscillatoria rubescens*. Sewage diversion began the following year (1963), and was completed in 1968. Water clarity increased substantially by 1971 [12] and continued to improve through 1976, when the influential grazer *Daphnia* established in the lake [11] and *Oscillatoria* abundance decreased dramatically. Despite low abundances at times, and periods when they were not observed in samples, neither *Daphnia* nor *Oscillatoria* ever technically went extinct in Lake Washington. Before they began to be observed at high abundances in 1973, *Daphnia* were observed every year but one (1971). Likewise, after their period of dominance ended in 1980, *Oscillatoria* continued (and continue) to appear in plankton samples, appearing in all but 3 years between 1980–1994.

Washington an ideal ecosystem for evaluating the mwMAR model’s sensitivity to non-stationary process. Indeed, the dominant environmental drivers and species interactions in Lake Washington are well-studied via observational [9,12], experimental [43,44] and traditional MAR approaches [39,45], offering the necessary background to build informed community and environmental interaction matrices (\( B \) and \( C \) matrices, respectively).

For our analyses we aggregated physical, chemical and plankton community data, which were collected at various intervals, into monthly means. Previous analyses of the Lake Washington plankton community interactions identified a simplified food web containing species that demonstrated strong roles in structuring the community [39,45]. We targeted the most strongly-interacting taxa of this simplified food web with the present analysis, to determine how the dominant interactions changed through time. While weak species interactions can be important in structuring food webs, we chose to focus on the dominant taxa and interactions as a first test of this new method. These taxa were pooled into four taxonomic groups: diatoms and green algae – “DG,” both palatable food for grazing zooplankton; *Oscillatoria* – known to suppress *Daphnia* [44]; *Daphnia*; and non-daphnid and non-cladoceran crustaceans – “NDC,” comprised of non-daphnid cladocerans, *Cyclops*, and *Daphtonus*. Group abundance data were log-transformed to better capture non-linearities [20]. A more complete description of the data is available in Hampton et al. [39], and the raw data are available in Appendix S1.

We included as covariates in the mwMAR model surface temperature and total phosphorus, because they were previously identified as the strongest environmental drivers of plankton abundance in the lake [39,45]. However, rather than simply use temperature as a covariate by itself, we instead used the data to estimate (1) a mean monthly signal indicative of long-term seasonal forcing, and (2) monthly deviations from the mean to capture short-term anomalies (e.g., a particularly warm July) or long-term trends (e.g., an overall increase). To ease comparison of effect sizes across all environmental covariates, we standardized all covariate data to a mean of 0 and a standard deviation of 1.

For our environmental covariate matrix (\( C \)) we included *a priori* only biologically meaningful interactions based on established environmental relationships; we assumed total phosphorus could not directly affect *Daphnia* or other zooplankton taxa. We expected shifts in mwMAR coefficients to lag behind known dates of change in the biotic community, sewage diversion and water clarity because our moving window size (7 years) is much larger than the timescale of most known changes. We graphically present all data at the end year of the moving window; thus, in our figures, results based on data from 1963–1970 would appear on the x-axis at year 1970.

Sensitivity analysis

The accuracy and precision of parameter estimates by the mwMAR model, as with other statistical methods, are sensitive to and affected by multiple factors, including food web configuration (i.e., the number of interacting species and covariates), window size, the variance structure of the process errors, and outliers in the data (see Appendix S2 for discussion and additional model validation). We conducted several sensitivity analyses to ensure such factors were not influencing the mwMAR model estimates. For example, the Lake Washington dataset is of high quality, and our outlier inspection showed no influence of outliers on the final results. In addition, because there is a tradeoff between precision of parameter estimates and accuracy of those estimates that is defined by window size, we conducted tests using simulated time series based on the Lake Washington food web configuration, to
determine the appropriate window size for analysis of the Lake Washington dataset. In those simulations, the parameter estimation accuracy decreased sharply at window sizes smaller than 75 time steps (see Figure S1), and therefore we use a window size of 84 (the next factor of 12 larger than 75, given the monthly time step in the Lake Washington data). We also conducted simulations to determine what bias, if any, exist in parameter estimates during periods when a system is undergoing transition between states, for example between a eutrophic and clear-water state as was the case with Lake Washington. Last, to ensure that the mwMAR model was capable of capturing shifts in species interactions and environmental conditions outside of the Lake Washington case study, we fit mwMAR models to simulated time series with known interactions (see Appendix S2).

**Statistical programming**

MAR and mwMAR modeling was done in MATLAB (2007, The MathWorks), using the open-source program LAMBDA ([46]; freely available from http://conserver.arc-aqu.org/user/e2holmes/LAMBDA) with additional programming by the authors. The coefficients of the A, B and C matrices were estimated using conditional least squares (CLS), and confidence intervals around each coefficient were established using 2,000 bootstrapped data sets. Each bootstrapped data set was generated by creating random E matrices and fitting the rest of the parameters using CLS (see [21] for details).

**Results**

The mwMAR approach revealed changes in interaction strengths in the Lake Washington plankton community between 1962 and 1994 (Figures 1–5; Figures S2–S3). For example, there were changes in the effects of *Oscillatoria* on *Daphnia* and diatoms and green algae (DG) coincident with the community composition shift during which *Oscillatoria* abundance decreased and *Daphnia* appeared (Figure 1, Table 1). In the period following the first appearance of *Daphnia* in Lake Washington, the effect of *Oscillatoria* on *Daphnia* became increasingly negative and was strongest in 1976 (Figure 1A). Following the decrease in *Oscillatoria* abundance, the negative effect of *Oscillatoria* on *Daphnia* weakened, and there was no significant effect of *Oscillatoria* on *Daphnia* from late in 1982 until the end of the time series. There was no effect of *Daphnia* on *Oscillatoria* (Figure 1B) until after the decline in *Oscillatoria* and increase in *Daphnia*. By 1980, the interaction coefficient became negative, weakened in the late 1980s, and returned to neutral after 1990. *Oscillatoria* also had a negative effect on DG in the beginning of the time series, and this effect disappeared by the mid-1970s (Figure 1C).

The effects of *Daphnia* on other plankton groups in Lake Washington also varied through time (Figure 2). *Daphnia* had a negative effect on its main food source, DG, starting in the early 1980s, and the effect strengthened until the mid-1980s (Figure 2A). The effect remained negative, though slightly weaker, until the end of the time series. The effect of *Daphnia* on other zooplankton (NDC) also varied through time (Figure 2B). Similar to the *Daphnia*-DG interaction, after *Daphnia* established in Lake Washington, the effect of *Daphnia* on NDC became increasingly negative, reached its peak in the mid-1980s, then remained negative but weakened to the end of the time series.

Density dependence also varied through time for all plankton groups. Density dependence in DG decreased (i.e., the diagonal B matrix coefficient associated with DG increased) until after *Daphnia* established in the lake, after which density dependence

---

**Figure 1.** Shifting impacts of *Oscillatoria* on the Lake Washington plankton community. *Effects of Oscillatoria on Daphnia* (A); *Daphnia on Oscillatoria* (B); and *Oscillatoria on diatoms/green algae*, DG, (C) estimated by a mwMAR model using an 84-timestep window (indicated by solid red horizontal line shown in A). The mwMAR-estimated effect of *Oscillatoria* on NDC was non-significant. Estimates are shown with 95% upper and lower CIs. Grey dotted lines indicate a neutral interaction; solid black lines indicate the average interaction across the full time series, as estimated by a traditional MAR model. The raw time-series data are given in (D), with years of significant known changes shown in shaded vertical bars. All results are presented at the end year of the moving window. doi:10.1371/journal.pone.0110363.g001
increased (Figure 3A). Density dependence in the grazer group NDC increased steadily from the early 1970s until the late 1980s, after which it weakened until the end of the time series (Figure 3B). *Daphnia* density dependence increased from the time it established in Lake Washington until the end of the time series (Figure 3C). *Oscillatoria* density dependence weakened until its decline in abundance in the late 1970s, at which point it increased and held more or less steady from the early 1980s until the end of the time series (Figure 3D).

The MAR model also estimates density-independent intrinsic population growth (the $A$ vector), and while many of the confidence intervals surrounding the $A$ estimates overlapped zero for a portion of the time series, there were consistent trends in the estimates among different plankton groups (Figure 4). For all four plankton groups, there were three distinct periods of intrinsic growth rate estimates: (1) before regular appearances of *Daphnia*...
in Lake Washington (pre-summer 1973); (2) between when *Daphnia* began to make regular appearances, and when *Daphnia* established in the lake and *Oscillatoria* declined dramatically (summer 1973 – spring 1976); and (3) after the rise of *Daphnia* and decline of *Oscillatoria* (summer 1976 onward). During the first period, there was high variability and negative trends in all A estimates. During the second period, the DG growth rate was mostly constant (Figure 4A), both grazer groups growth rates increased (though some CIs overlapped 0; Figure 4B, C), and the *Oscillatoria* growth rate decreased (Figure 4D). During the final period, from the mid-1970s to the end of the time series, the growth rates of most groups were constant, except for an increase in the DG growth rate. Both *Oscillatoria* and NDC had growth rates equal to zero during this period.

Stability (λ) decreased sharply from the beginning of the time series, and the system was least stable (i.e., λ was at its maximum value) in the early 1970s (Figure 5). Following this nadir, community stability increased and reached maximum stability (i.e., the lowest λ value) at the end of the time series. Following bootstrapping, mean temperature had significant effects on all plankton groups. In contrast, very few effects of temperature anomalies or total phosphorus on plankton groups in Lake Washington were retained in the final mwMAR model (Table 1; Figure S3).

We assessed the fit of the best mwMAR model to the Lake Washington data, and found that fewer than 1% of correlations between model residuals and data were significant. We also tested the model assumption of normally-distributed errors by applying the Shapiro-Wilk test [47] to the residuals of the MAR fit to each data window (E, from Equation 1), with a Bonferroni-corrected alpha [48] to account for multiple null hypotheses. We rejected the null hypothesis of normally distributed errors in 65/312 windows for *Daphnia*, and in 217/312 windows for *Oscillatoria* (and in 0 windows for DG and NDC; Figure S4). These data windows for which the null hypothesis was rejected corresponded to periods in the time series when the abundance of each species was zero, i.e., long one-sided tails in the data.
Table 1. Interaction ranges estimated by the mwMAR model for Lake Washington across all 84-timestep windows of data in the historical time series.

| Community Interactions | Covariate Effects |
|------------------------|-------------------|
|                        | Season | Temperature | Phosphorus |
| DG                     | 0.00–0.08 | 0.39–1.05 | 0.08–1.46 |
| NDC                    | 0.01–0.46 | 0.01–0.66 | 0.20–0.84 |
| Daphnia                | 0.64–0.69 | 0.43–0.15 | 0.05–0.84 |
| Oscillatoria           | 0.01–0.14 | 0.89–0.20 | 0.92–1.21 |
|                        | 0.07–1.20 | 0.12–0.59 | 0.00–0.18 |
|                        | 0.77–1.10 | 1.23–1.25 | 0.39–1.05 |

Empty cells reflect interactions not retained by the model. Parenthetical values represent ranges of 95% confidence intervals estimated for 2,000 bootstrapped data sets. Coefficients represent effects of variables in columns on variables in rows. DG: Diatoms/Green algae; NDC: Non-daphnid cladocerans and non-cladoceran crustaceans. n/a indicates a coefficient that was not included in the model. doi:10.1371/journal.pone.0110363.t001

Discussion

We hypothesized that the MW MAR model would show shifts in the interactions among the major taxa coinciding with changes in water quality, and that the model would be able to suggest whether specific interactions were present during particular periods of time. Our hypothesis was confirmed, and the model was able to identify periods of time when specific interactions were more prevalent than others.

The model suggested that the relationships between the major taxa were shifting over time, with changes in water quality and nutrient inputs playing a significant role. For example, the model indicated that the grazing effect of Daphnia on Oscillatoria increased over time, coinciding with periods of improved water quality. Conversely, the grazing effect of Daphnia on green algae decreased during periods of poor water quality, suggesting that the presence of grazers was less effective in controlling algal blooms during these times.

The model also identified periods of time when the grazing effect of Oscillatoria on Daphnia was significant, indicating that Oscillatoria played a role in regulating the abundance of Daphnia during these periods. This suggests that Oscillatoria is an important component of the plankton community in Lake Washington, and that changes in its abundance can have significant impacts on the abundance of other taxa.

Overall, the model provided a detailed picture of the shifting interactions in the Lake Washington plankton community, and highlighted the importance of considering the role of interactions in understanding the dynamics of the system.
MAR coefficients have been shown previously to reflect changes in community dominance, when an increase in the abundance of one species or group coincides with a decrease in another [40], and therefore the negative effect of Oscillatoria on Daphnia may represent shifting dominance between the two taxa. The transition from Oscillatoria to Daphnia dominance was reflected in interactions among other plankton groups in the community. As the negative effect of Oscillatoria on Daphnia declined in the mid-1970s through to the early 1980s, and as Daphnia increased in abundance, Daphnia had stronger impacts on their main food source (DG) and competitors (NDC; Figure 2). At the same time, the strength of density-dependence (Figure 3) and density-independent growth rates increased for the grazing zooplankton groups (Figure 4), suggesting the release of the grazer community from inhibition by Oscillatoria. No previous work has shown an effect of Oscillatoria on other grazer groups beyond Daphnia, but the increase in population growth rates ($\lambda$ matrix elements) of the NDC group following Oscillatoria’s decline suggests a possible negative interaction.

The negative effects of Daphnia on their food and competitors weakened towards the end of the time series, apart from an intensified grazing effect of Daphnia on DG at the very end. One potential explanation for the weakened grazing effect at the end of the time series relates indirectly to the warming of the lake during this time. Between 1962 and 2002, the lake surface temperature increased by 1.4°C during the stratified months, and associated with this warming was an advance in the spring phytoplankton bloom by 19 days [10]. Most of the warming and spring bloom advance occurred in the period 1962-1994. The weakening of the effect of total Daphnia on the phytoplankton group during that period, in the present analysis, could be a reflection of shifts in species-specific phenology and grazing characteristics [14,41].

The results presented here highlight opportunities to learn more from time series data about how species interactions shift with changes in the environment across ecosystem types, and how those changing food web dynamics are liable to affect community stability and resilience to further disturbance. Ecosystem-based approaches to management often include a focus on food web dynamics, but quantifying changes in species interactions, and how those changes map onto the environmental template, proves difficult. Linking shifts in species interactions to specific environmental drivers opens opportunities to focus efforts aimed at retaining resilience as ecosystems undergo rapid change.

Community stability and environmental covariates

The Lake Washington system has undergone major shifts in chemistry and ecology that are refected in community stability. The peak of instability occurred in April 1973, a window that included data from May 1966 – April 1973; Figure 5). Values of $\lambda$ greater than 1 indicate an unstable system [21], and here $\lambda$ exceeded 1 for windows ending in November 1970 – November 1974, representing the period of time between December 1963 – November 1974, inclusive. This is the time period that included major ecosystem shifts: high nutrient levels, sewage diversion, and nutrient reduction; high Oscillatoria abundance followed by its decline; and the first rare appearances of Daphnia. By the time of Oscillatoria’s disappearance, maximum water clarity, and establishment of Daphnia in 1976, the community stability was increasing, and continued to increase until the end of the time series. Thus, the period of time the lake was undergoing the most substantial and dramatic shifts throughout the ecosystem, and before Daphnia gained a foothold, was the least stable period in the community as well.

We observed effects of monthly mean temperature on the abundance of all plankton guilds (Figure S3), which agrees with previous MAR analyses [39,45], and with the MAR model estimated here from the whole Lake Washington time series (Table S1). Previous work has suggested that Lake Washington plankton phenology also responds to lake warming [10,50], and that the relationships between temperature and plankton taxa are evidence of the potential influence of a warming lake on food web dynamics [39]. However, we found no significant effects of deviations from the long-term seasonal temperature patterns, suggesting that lake-warming effects are not detectable in the abundance of these plankton guilds.

Caveats and considerations

Our results suggest moving-window MAR models may be useful in systems with sufficient time-series data for understanding shifting abiotic and biotic dynamics. As with all statistical methods, however, practitioners must consider possible caveats and issues in advance of and throughout analyses. The data and ecosystem considerations applicable to prior MAR model applications also extend to our moving-window approach. Users must have sufficient time-series data for valid parameter estimation, which varies depending on the time scale of interactions in the system and frequency of observations. The moving-window MAR model imposes the further consideration of having sufficient time-series data for multiple windows and surrounding the event(s) of interest. Importantly, bias in model estimates shrinks as the ratio between window size and system transition period increases, and users are cautioned to interpret model estimates during system transitions with consideration of such bias. However, the window could be configured for different purposes: made smaller to detect changes before they occur, or sized to optimize detection of a change in a particular state variable.

Applications of this method will benefit from a priori knowledge of ecological interactions and drivers in the modeled system to build a robust MAR model. In our analysis of the Lake Washington plankton community, we simplified the plankton community based on previous work that highlighted the strongest food web interactions and key environmental covariates [39]. However, Hampton et al. [39] also pointed out the importance of other plankton taxa in driving the dynamics of the dominant species in Lake Washington, such as Cryptomonas, picoplankton and non-colonial rotifers. Therefore, it is possible that additional food web dynamics contribute to the interaction coefficients observed here, which could be highlighted by future analyses. Furthermore, if the model failed to include an influential environmental driver of Lake Washington plankton dynamics, the model results might be erroneously interpreted: if one plankton guild responds negatively to an unmeasured environmental variable, and another guild responds positively, this might incorrectly be interpreted as a negative interaction between the two guilds. In the Lake Washington case, years of experimental work and field observations have identified environmental variables that are robust driving signals. In addition, preliminary, exploratory MAR model runs were performed to screen a broad suite of potential drivers on plankton time series data. The analyses here rely heavily on those two approaches to validation, and potential users are advised to similarly behave as ecological detectives.

Additionally, as with prior MAR approaches, users must invest time in simulation modeling that allows them to test how the approach is likely to work with data similar to theirs. Simulation of data from a model with similar parameters to the study ecosystem helps identify the appropriate moving window size and, thus,
estimate the precision associated with future predictions of system change. Because much of the MAR approach is based on iterative fitting approaches, creating and testing simulation data sets from known parameter values with similar lengths, covariate and taxa numbers, and variance, is critical to interpreting knowledge gained from MAR models. For the moving-window approach, users should carefully examine the effect of window size on their simulation datasets (see Appendix S2 for an example analysis using simulated datasets). A priori knowledge or hypotheses related to the resolution of data and interactions as well as the strength and timing of the predicted shift should be considered during the process of simulation modeling. Comparison of the mwMAR output with whole time-series MAR estimates is useful in assessing when the broad confidence intervals estimated with the mwMAR model are potentially masking significant interactions.

Conclusions

Ecologists have recently gained an appreciation for the need to develop methods based on the underlying hypothesis that many systems are rarely, if ever, stationary. Here we present a method that allows researchers and managers alike to examine long-term monitoring data and develop a dynamic record of shifting interactions and drivers. By calculating indirect and direct effects over time, and their changes, mwMAR allows researchers to understand how species invasions and extinctions, shifts in temperature and nutrient loadings, and other anthropogenic perturbations may cascade and feedback throughfood webs and ecosystems.

Supporting Information

Figure S1 Lake Washington plankton densities from 1962–1994. Monthly means of densities for aggregated plankton groups used in mwMAR analyses. NDC = non-daphnid cladocerans; DG = diatoms and green algae.

Figure S2 Time series of all community interactions. Interaction coefficients estimated for the Lake Washington time series with a mwMAR model, using an 84-month window. Figures show per-capita effects of plankton guilds in columns on plankton guilds in rows. Diagonal figures represent self-effects, or density-dependent effects on abundance.

Figure S3 Time series of environmental covariate effects. Interaction coefficients estimated for the Lake Washington time series with a mwMAR model, using an 84-month window. Figures show the effects of covariates in columns on plankton guilds in rows.

Figure S4 Quantile-quantile plots of residuals for the Daphnia and Oscillatoria time series. Shown are theoretical versus observed distributions of mwMAR model residuals for all windows where the Shapiro-Wilk test statistic was below the alpha value required to reject the null hypothesis of normally-distributed errors (61/1248 for Daphnia, 175/1248 for Oscillatoria, 0 for DG and 0 for NDC).

Table S1 Community and covariate matrix coefficients estimated by a MAR model for the full Lake Washington time series.

Appendix S1 Lake Washington plankton and covariate data, 1962–1994.

Appendix S2 Moving-window MAR Model Testing. Validation of the moving window MAR model approach, including accuracy of parameter estimation and estimation of bias during system transition.

Acknowledgments

Many thanks to J. Regetz for assistance with coding. We thank D.E. Schindler for generous access to the Lake Washington data, the numerous people who have contributed to the data set, including A. Litt and S. Abella, and the organizations that have financially supported it, including the Mellon Foundation. The manuscript was improved by comments from D.E. Schindler, E.J. Ward and two anonymous reviewers.

Author Contributions

Analyzed the data: TF EW MS SK. Contributed reagents/materials/analysis tools: TF EW MS SK EH. Wrote the paper: TF EW MS SK EH SH.

References

1. Burkle LA, Marlin JC, Knight TM (2013) Plant-Pollinator Interactions over 120 Years: Loss of Species, Co-Occurrence, and Function. Science 339: 1611–1615.
2. Tylianakis JM, Dillham RK, Bascompte J, Wardle DA (2008) Global change and species interactions in terrestrial ecosystems. Ecol Lett 11: 1331–1963.
3. Holyoak M (2000) Habitat subdivision causes changes in food web structure. Ecol Lett 3: 509–515.
4. Schlesinger MD, Manley PN, Holyoak M (2008) Distinguishing stressors acting on land bird communities in an urbanizing environment. Ecology 89: 2302–2314.
5. Hastings A (2004) Transients: the key to long-term ecological understanding? Trends Ecol Evol 19: 39–45.
6. Harley CDG, Hughes AR, Hultgren KM, Miner BG, Sorte CJB, et al. (2006) The impacts of climate change in coastal marine systems. Ecol Lett 9: 228–241.
7. Walther GR (2010) Community and ecosystem responses to recent climate change. Philos Trans R Soc B Biol Sci 365: 2019–2024.
8. Tunney TD, McCann KS, Lester NG, Shuter BJ (2014) Effects of differential habitat warming on complex communities. Proceedings of the National Academies of Science 111: 8077–8082.
9. Edmondson WT (1970) Phosphorus, nitrogen, and algae in Lake Washington after diversion of sewage. Science 169: 690–691.
10. Winder M, Schindler DE (2004) Climatic effects on the phenology of lake processes. Glob Change Biol 10: 1844–1856.
11. Edmondson WT, Litt AH (1982) Daphnia in Lake Washington. Limnol Oceanogr 27: 272–283.
12. Edmondson WT (1991) The Uses of Ecology. Lake Washington and Beyond: University of Washington Press. 329 p.
13. Winder M, Schindler DE, Essington TE, Litt AH (2009) Disrupted seasonal clockwork in the population dynamics of a freshwater copepod by climate warming. Limnol Oceanogr 54: 2493–2505.
14. Hampton SE, Romare P, Seiler DE (2006) Environmentally controlled Daphnia spring increase with implications for sockeye salmon fry in Lake Washington, USA. J Plankton Res 28: 399–406.
15. Francis TB, Schindler DE (2009) Shoreline urbanization reduces terrestrial insect subsidies to fishes in North American lakes. Oikos 118: 1872–1882.
16. Beauchamp DA, Sergeant CJ, Mazur MM, Scheuerell MD, Scheuerell JM, et al. (2004) Spatial-temporal dynamics of early feeding demand and food supply for sockeye fry in Lake Washington. Transactions of the American Fisheries Society 133: 1014–1032.
17. Mazumder A, Taylor WD, McQueen DJ, Lean DRS (1990) Effects of fish and plankton on lake temperature and mixing depth. Science 247: 312–315.
18. Sarlette O (1995) Herbivore effects on phytoplankton succession in a eutrophic lake. Ecol Monogr 63: 129–149.
19. Ives AR (1995) Measuring resilience in stochastic systems. Ecol Monogr 65: 217–233.
20. Ives AR, Dennis B, Cottingham KL, Carpenter SR (2003) Estimating community stability and ecological interactions from time-series data. Ecol Monogr 73: 301–330.
21. Ives AR, Gross K, Klug JL (1999) Stability and variability in competitive communities. Science 286: 542–544.

22. Hampton SE, Holmes EE, Scheuerell MD, Katz SL, et al. (2013) Quantifying effects of abiotic and biotic drivers on community dynamics with multivariate autoregressive (MAR) models. Ecology 94: 2863–2869.

23. Lindegren M, Möllmann C, Nielsen A, Stenseth NC (2009) Preventing the collapse of the Baltic cod stock through an ecosystem-based management approach. Proc Natl Acad Sci U S A 106: 14722–14727.

24. Mac Nally R, Thomson JR, Kinnerer WJ, Freyer J, Newman KR, et al. (2010) Analysis of pelagic species decline in the upper San Francisco Estuary using multivariate autoregressive modeling (MAR). Ecol Appl 20: 1417–1430.

25. Kordas RL, Dudgeon S (2011) Dynamics of species interaction strength in space, time and with developmental stage. Proc R Soc B Biol Sci 278: 1004–1013.

26. Torrence C, Webster PJ (1999) Interdecadal changes in the ENSO-monsoon system. Journal of Climate 12: 2679–2690.

27. Menard F, Marsac F, Bellier E, Caizilles B (2007) Climatic oscillations and tuna catch rates in the Indian Ocean: a wavelet approach to time series analysis. Fisheries Oceanography 16: 95–104.

28. Jevrejeva S, Moore JC, Grinsted A (2004) Oceanic and atmospheric transport of multiyear El Ninó-Southern Oscillation (ENSO) signatures to the polar regions. Geophys Res Lett 31.

29. Benincà E, Johnk KD, Heerkloss R, Huisman J (2009) Coupled predator-prey oscillations in a chaotic food web. Ecol Lett 12: 1367–1378.

30. Winder M, Cloern JE (2010) The annual cycles of phytoplankton biomass. Philosophical Transactions of the Royal Society B: Biological Sciences 365: 3215–3226.

31. Haich CH, Chen CS, Chin TS, Lee KT, Shiah FJ, et al. (2009) Time series analyses reveal transient relationships between abundance of larval anchovy and environmental variables in the coastal waters southwest of Taiwan. Fisheries Oceanography 18: 102–117.

32. Bremer LC (2006) Nonlinear aspects of sea surface temperature in Monterey Bay. Prog Oceanogr 69: 61–89.

33. Carpenter SR, Cole JJ, Pace ML, Batt R, Brock WA, et al. (2011) Early warnings of regime shifts: A whole-ecosystem experiment. Science 332: 1079–1082.

34. Dokes V, Carpenter SR, Brock WA, Ellison AM, Guatil V, et al. (2012) Methods for detecting early warnings of critical transitions in time series illustrated using simulated ecological data. PLoS One 7: e41010.

35. Seekell DA, Carpenter SR, Pace ML (2011) Conditional heteroscedasticity as a leading indicator of ecological regime shifts. American Naturalist 178: 442–451.

36. Elkinton JS, Healy WM, Buonaccorsi JP, Boettner GH, Hazzard AM, et al. (1996) Interactions among gypsy moths, white-footed mice, and acorns. Ecology 77: 2332–2342.

37. Ives AR (1995) Predicting the response of populations to environmental change. Ecology 76: 926–941.

38. Hampton SE, Izmest’eva LR, Moore MV, Katz SL, Dennis R, et al. (2008) Sixty years of environmental change in the world’s largest freshwater lake: Lake Baikal, Siberia. Glob Change Biol 14: 1947–1958.

39. Hampton SE, Scheuerell MD, Schindler DE (2006) Coalescence in the Lake Washington story: interaction strengths in a planktonic food web. Limnol Oceanogr 51: 2042–2051.

40. Francis TB, Scheuerell MD, Brodeur RD, Levin PS, Ruzicka JJ, et al. (2012) Climate shifts the interaction web of a marine plankton community. Glob Change Biol 18: 2496–2506.

41. Winder M, Schindler DE (2004) Climate change uncouples trophic interactions in an aquatic ecosystem. Ecology 85: 2100–2106.

42. Law T, Zhang WT, Zhao JY, Arbonaentis GB (2009) Structural changes in lake functioning induced from nutrient loading and climate variability. Ecological Modelling 220: 979–997.

43. Edmondson WT (1991) Sedimentary record of changes in the condition of Lake Washington. Limnol Oceanogr 36: 1031–1044.

44. Infante A, Abella SEB (1985) Inhibition of Daphnia by Oscillatoria in Lake Washington. Limnol Oceanogr 30: 1046–1052.

45. Hampton SE, Schindler DE (2006) Empirical evaluation of observation scale effects in community time series. Oikos 113: 424–439.

46. Viscido SV, Holmes EE (2010) Statistical modelling of communities and ecosystems using the LAMBDA software tool. Environmental Modelling and Software 25: 1905–1908.

47. Shapiro SS, Wilk MB (1965) An analysis of variance test for normality (complete samples). Biometrika 52: 591–611.

48. Hochberg Y (1988) A sharper Bonferroni procedure for multiple tests of significance. Biometrika 75: 800–802.

49. Carpenter SR (1992) Destabilization of planktonic ecosystems and blooms of blue-green algae. In: Kitchell JF, editor. Food Web Management, A Case Study of Lake Mendota. New York: Springer New York. pp. 461–481.

50. Hampton SE (2005) Increased niche differentiation between two Conocilus species over 33 years of climate change and food web alteration. Limnol Oceanogr 50: 421–426.