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Author(s): Vasseur, D. A., Fox, J. W., Gonzalez, A., Adrian, R., Beisner, B. E., Helmus, M. R., ... Steiner, C. F.

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Synchronous dynamics of zooplankton competitors prevail in temperate lake ecosystems.

David A. Vasseur\textsuperscript{1*}, Jeremy W. Fox\textsuperscript{2}, Andrew Gonzalez\textsuperscript{3}, Rita Adrian\textsuperscript{4}, Beatrix E. Beisner\textsuperscript{5}, Matthew R. Helmus\textsuperscript{6}, Catherine Johnson\textsuperscript{7}, Pavel Kratina\textsuperscript{8}, Colin Kremer\textsuperscript{9,10}, Claire de Mazancourt\textsuperscript{11}, Elizabeth Miller\textsuperscript{9,10}, William A. Nelson\textsuperscript{12}, Michael Paterson\textsuperscript{13}, James A. Rusak\textsuperscript{14}, Jonathan Shurin\textsuperscript{15}, and Christopher F. Steiner\textsuperscript{16}

\textsuperscript{1} Department of Ecology and Evolutionary Biology, Yale University, New Haven CT, 06520 USA
\textsuperscript{2} Department of Biological Sciences, University of Calgary, Calgary, AB, T2N 1N4 Canada
\textsuperscript{3} Department of Biology, McGill University, Montreal, Canada
\textsuperscript{4} Leibniz-Institute of Freshwater Ecology and Inland Fisheries, Berlin, Germany
\textsuperscript{5} Department of Biological Sciences, University of Quebec at Montreal, Montreal, QC, H3C 3P8 Canada
\textsuperscript{6} Amsterdam Global Change Institute, Department of Animal Ecology, Vrije Universiteit, 1081 HV Amsterdam, Netherlands
\textsuperscript{7} Fisheries and Oceans Canada, Bedford Institute of Oceanography, Dartmouth, NS, B2Y 4A2 Canada
\textsuperscript{8} School of Biological and Chemical Sciences, Queen Mary University of London, London E1 4NS, UK
\textsuperscript{9} W. K. Kellogg Biological Station and Department of Plant Biology, Michigan State University, Hickory Corners, Michigan 49060
\textsuperscript{10} Department of Plant Biology, Michigan State University, East Lansing, MI 48824
\textsuperscript{11} Centre for Biodiversity Theory and Modelling, Station d'Ecologie Expérimentale du Centre National de la Recherche Scientifique à Moulis, 09200 Moulis, France
\textsuperscript{12} Department of Biology, Queen’s University, Kingston ON, K7L 3N6 Canada.
\textsuperscript{13} Experimental Lakes Area, Fisheries and Oceans Canada, Winnipeg, MB R3T 2N6 Canada
\textsuperscript{14} Ontario Ministry of the Environment, Dorset Environmental Science Centre, Dorset, ON, P0A 1E0, Canada
\textsuperscript{15} Section of Ecology, Behavior and Evolution, University of California- San Diego, 9500 Gilman Dr., #0116, La Jolla, CA 92093
\textsuperscript{16} Department of Biological Sciences, Wayne State University, Detroit, MI 48202

*Author to whom all correspondence should be addressed
Abstract

Although competing species are expected to exhibit compensatory dynamics (negative temporal covariation), empirical work has demonstrated that competitive communities often exhibit synchronous dynamics (positive temporal covariation). This has led to the suggestion that environmental forcing dominates species dynamics; however synchronous and compensatory dynamics may appear at different length-scales and/or at different times, making it challenging to identify their relative importance. We compiled 58 long-term datasets of zooplankton abundance in north-temperate and sub-tropical lakes and used wavelet-analysis to quantify general patterns in the times and scales at which synchronous/compensatory dynamics dominated zooplankton communities in different regions and across the entire dataset. Synchronous dynamics were far more prevalent at all scales and times, and were ubiquitous at the annual scale. Although we found compensatory dynamics in approximately 14% of all combinations of time-period/scale/lake, there were no consistent scales or time-periods during which compensatory dynamics were apparent across different regions. Our results suggest that the processes driving compensatory dynamics may be local in their extent while those generating synchronous dynamics operate at much larger scales. This highlights an important gap in our understanding of the interaction between environmental and biotic forces that structure communities.

Keywords: Synchrony, compensatory dynamics, zooplankton, wavelet
Introduction

The extent to which communities of interspecific competitors exhibit synchronized fluctuations over time is intrinsically linked to community stability and moreover may reflect important attributes of the functional diversity of communities [1,2] and of the processes structuring community composition [3–5]. Synchrony and its alternative pattern, compensation (or compensatory dynamics), are mutually exclusive phenomenological features of community dynamics that can arise from many underlying mechanisms [6,7]. Compensation may reflect a reciprocal negative interaction among competitors [4]; however, it also can arise when species respond oppositely to changes in an environmental factor [8], or when they respond to different environmental factors which are themselves negatively correlated through time. In contrast, species that exist in a temporally variable environment must also be qualitatively similar in their ability to tolerate the environment’s extremes (e.g. phosphorus is essential for plankton but some species better tolerate phosphorus depletion), suggesting that the environment may select species with similar traits, which in turn predisposes species to exhibit synchronized dynamics [1]. The extent of synchronous and compensatory dynamics in competitive communities may therefore reflect differences in the relative strength of environmental forcing and competition [1,3].

Synchronous and compensatory dynamics are also of fundamental interest in community ecology because they regulate the relationship between population and temporal community variability. At the scale of populations, temporal variability is an indicator of stability which is often linked to extinction probability [9,10]. Similarly, temporal variability at the aggregate or community level, ‘community variability’ [7,11], is of fundamental interest as an index of community stability [12,13], and is of applied interest as a potential leading indicator of nonlinear changes in ecosystem state [14,15]. When species contribute additively to a particular
community attribute (e.g. total biomass), the temporal variability of the attribute is given by the sum of all terms in the community variance-covariance matrix. All else being equal, communities with species dynamics that negatively covary over time (compensatory dynamics) will exhibit lower community variability than communities whose covariance terms are positive on average (synchronous dynamics) [7]; however, the same processes that generate negative covariation can also destabilize communities by increasing species fluctuations [16].

Many studies have measured the synchrony of competitors in experiments and nature [3,7,17–20] and some have attempted to infer the relative contributions of competition and environmental factors in these communities [1,3,20]. For example, using annual census of terrestrial plants and animals, ref. [3] found that species are on average synchronized, and suggested that environmental drivers were relatively more important than competition for shaping community dynamics. Although appealing, the argument that synchronous dynamics result when environmental drivers are relatively more important than density-dependent biotic feedbacks is challenging to verify, because the drivers leading to synchronous and compensatory dynamics need not necessarily be in conflict. Synchronous and compensatory dynamics may operate on different time-scales [20,21] or during different periods [21] in which case the frequency and temporal extent of sampling largely dictates which drivers are perceived to be the most critical. For example, if competing species are commonly and uniformly affected by environmental variation, it simply generates a temporally changing arena in which the outcomes of competition are enacted. If species are sampled once annually as in ref. [3], the signature of competition may be entirely obscured by the synchronizing effect of ‘good’ vs. ‘bad’ years (e.g. drought vs. wet), even if it is an important driver of species’ relative fitness and persistence [22]. Furthermore, it has been shown that embedding competitors in a food web context can cause
them to respond synchronously to environmental disturbance even when the underlying
dynamics are compensatory [23], highlighting the challenge of identifying the mechanisms
underlying dynamics. Measuring and interpreting synchrony and compensation thus requires, at
a minimum, refined estimators of synchrony and compensation across different timescales [17–
21].

Freshwater plankton communities have been a focus of recent work on the scale-
dependence of compensatory and synchronous dynamics. In phytoplankton and zooplankton
communities in Lake Constance (Bodensee), compensatory dynamics have been shown to occur
regularly at scales ranging from 6 months to 1 year while synchronous dynamics dominate at
most other scales [17,21]. Synchrony of zooplankton communities in Little Rock Lake
intensified at the annual scale during experimental acidification, with no apparent alteration of
covariation patterns at other scales [18,19]. Freshwater plankton are ideal for analyses of
community variability due to their short generation times and importance in long-term
monitoring programs worldwide. In temperate regions, lakes experience environmental
fluctuations on timescales ranging from short-term weather fluctuations (e.g. solar irradiance and
wind-driven mixing) to long-term trends in nutrient loading, pH, temperature and other factors.

In addition to time-scale, communities may transition between synchrony to
compensation over time at fixed scales. In Little Rock Lake, experimental acidification altered
the expression of synchronization at the annual-scale in a zooplankton community [18] and
elsewhere, natural and anthropogenic changes in long-term nutrient loads have been shown to
impact community composition [24,25]. Within the growing season the intensity of competition
among zooplankton can vary greatly as nutrients become depleted and well-edible algae are
replaced by colonial forms [26]. Transitions between synchrony and compensatory dynamics
may be common at a variety of scales and yield important insight into the mechanisms structuring the distribution of temporal dynamics of species in competitive communities; however, detecting such transitions requires advanced statistical machinery capable of resolving patterns in both time and scale.

Here we quantify patterns of dynamics within communities in long-term time-series (mean 17 years) of crustacean zooplankton species from 58 study sites originating from 52 North American and European temperate lakes and two sub-tropical lakes (Fig.1). We employ a wavelet analysis, which estimates the amount of variation in a time series attributable to a particular frequency (scale) at a particular point in time [27], to generate a scale and time resolved binary metric of synchronous/compensatory dynamics among zooplankton assemblages within each of our study sites. Our extensive dataset allows us to then overlay this information from various lakes to determine the relative prevalence of synchronous and compensatory dynamics over a wide range of temporal scales (monthly to decadally) and across a large span of time (1971-2008) in a large sample of 58 study sites (54 lakes). The objective of this work is to i) provide a critical assessment and frame of reference for the prevalence of synchronous and compensatory dynamics in competitive communities and ii) to highlight potentially important scales and times at which transitions in community dynamics occur and may help to identify the mechanisms structuring competitor dynamics.

Methods

Data

Temporal data were compiled from a number of long-term monitoring programs of temperate zone lakes in North America and Europe. Crustacean zooplankton data from the
following regions were included: 8 lakes WI, U.S.A. North Temperate Lakes Region LTER and
Mendota region (University of Wisconsin Center for Limnology); 8 lakes from the Dorset region
of Muskoka, ON Canada (Ontario Ministry of Environment Dorset Environmental Science
Centre); 10 lakes from the Sudbury region, ON Canada (Laurentian University Cooperative
Freshwater Ecology Unit); 12 lakes from the Experimental Lakes Area (Department of Fisheries
and Oceans Freshwater Institute) near Kenora, ON, Canada and 6 lakes from the Coldwater
Lakes Project in northwestern ON, Canada (Ontario Ministry of Natural Resources); 6 lakes
from the Northwest Ontario Lake Size Series project [28]; Lake Apopka, FL, USA (Mike
Coveney, St. Johns River Water Management District); Lake Okeechobee, FL, USA (5 basin
sites on this, the largest of our lakes; Karl Havens, Florida Sea Grant College Program;
Müggelsee in Berlin, Germany [29]; and Lake Zürich in the southwestern part of the canton of
Zürich, Switzerland [30]. This resulted in a total of 58 sample sites in 54 different lakes
distributed across North America and Europe (Fig. 1).

Surveys varied in their frequency of sampling and period of temporal coverage (Figure
S3); however, our methods (see below) select the scales and time-periods during which a
particular sampling site can reliably contribute information. Zooplankton were sampled,
depending on the survey, using nets, Schindler-Patalas traps or tube samplers, with identification
to species. 250 to >1000 individuals were counted in each sample. In this analysis we only
consider crustaceans (cladocerans and copepods) and exclude unidentifiable juvenile stages.
Species belonging to the genera *Bosmina*, *Chydorus* and *Alona/Alonella* were aggregated within
each of those genera due to variable taxonomic resolution among the surveys. A more detailed
description of the sampling methods is given in [31]. The average number of species present per
sampling site was 27 (range 11 to 40).
Wavelet analysis

To provide a scale and time resolved metric of synchronization, we began by calculating the continuous wavelet transformation \( W_{k,l} \) of the time series \( x_{k,l} \) for each zooplankton species \( k \) in each lake \( l \) as the convolution of \( x_{k,l} \) with the conjugate of the scaled and translated Morlet wavelet \([27,32]\):

\[
W_{k,l}(n,s) = s^{0.5} \sum_{i=1}^{N} x_{k,l}(\tau_i) \cdot \psi^* \left( \frac{n\tau_i}{s} \right)
\]

(1)

In expression (1), \( \tau_i \) represents the set of Julian dates on which \( x_{k,l} \) was sampled and \( N \) is the total number of samples of \( x_{k,l} \). The parameters \( n \) and \( s \) represent the time and scale localization of the Morlet wavelet, which is the product of a Gaussian distribution and a complex waveform, \( \psi(\tau) = \pi^{-1/4} e^{i\omega_0} e^{-\tau^2/2} \). We set the wavenumber of the Morlet wavelet \( \omega_0 \) which controls the number of oscillations within the effective width of the Gaussian distribution, equal to 6 as in previous studies \([18,27]\).

In order to facilitate comparison across our study sites we chose standardized arrays of times \( n \) and scales \( s \) at which to sample the wavelet transformation and we subset these depending on the limitations of each time-series. In the temporal dimension we sampled the wavelet on every 10th Julian day provided that it fell within the ‘cone of influence’, which is defined as the range of points further than \( \sqrt{2} s \) from the start and end of the time-series \([27]\). In the scale dimension we generated an array of scales according to

\[
s = 365.25 \cdot 2^{i s}
\]

(2)
where $\delta_s = 0.1$ and $j$ is a sequence of integers. We set the minimum value of $j$ such that the smallest scale was not less than 3 times the average time between successive samples in the time-series. We set the maximum value of $j$ such that the largest scale did not exceed half the total period of sampling in the time-series; however, only scales smaller than this threshold included samples that were admissible based upon the ‘cone of influence’.

Most of our time-series were unevenly sampled through time, potentially producing combinations time and scale which were unreliable within the boundaries defined above. For example, if sampling was discontinued during winter (which is common in temperate lakes) there may be few or no data points in the neighborhood of the wavelet at shorter scales during winter. To deal with this, we further discarded any wavelet samples for which fewer than 10 observations occurred within $\pm \sqrt{2} s$ of the center of the Morlet wavelet.

Measuring synchrony

We first quantified the relative amplitude of zooplankton crustacean species dynamics within each of $l$ sites using the localized wavelet modulus ratio[18]:

$$\rho_j(n, s) = \frac{\Lambda_{n,s} \left( \sum_k |\mathcal{W}_j(n, s)|^2 \right)}{\Lambda_{n,s} \left( \sum_k |\mathcal{W}_j(n, s)| \right)}$$  \hspace{1cm} (3)

where $|\cdot|$ denotes the complex modulus and $\Lambda_{n,s}(\cdot) = \int e^{-\frac{(n-t)^2}{2s^2}} (\cdot) dt$ is a Gaussian localization function in time $n$. The localized wavelet modulus ratio computes the ratio of the actual amplitude of community fluctuations against the cumulative amplitude of population fluctuations at each time and scale. The numerator in equation (3) uses the modulus of the sum of the wavelet transform; by summing wavelet coefficients prior to computing the modulus, the
realized amplitude is discounted by species whose dynamics have opposite phases. The
denominator, the sum of species' moduli, is the maximum possible amplitude given a perfect
alignment of phases. Thus, the wavelet modulus ratio is bounded between values of zero and
one. A value of zero indicates that compensatory dynamics result in a community variance equal
to zero; whereas a value of one indicates perfect synchronization of population dynamics and a
maximum value of the community variance. The modulus ratio is akin to a family of
multivariate indices of synchronization [see ref. 7] that measure the sum or mean of pair-wise
species covariances (or here co-amplitudes) by comparing realized variances or amplitudes of
communities to the values that would be achieved under perfect synchronization, thus
superseding the need to compute pair-wise relationships directly using correlative or co-spectral
techniques. Although uneven sampling can generate bias in the estimates of wavelet power ($W^2$
), this bias is consistent within each sampling site because sampling occurred for all zooplankton
species at the same points in time, making our measure of synchronization (based on relative
amplitude) unbiased in the presence of uneven sampling.

To measure synchronization we generated 1000 null-model outcomes in each site ($l$), at
each scale ($s$) and time ($n$) by attributing a random phase-shift on the interval ($0, 2\pi$) to each of
the $k$ species and recalculating the modulus ratio (3) (see ref [18]). Because this procedure
retains the distribution of amplitudes of variation expressed by different species, it generates an
accurate distribution for the value of the local wavelet modulus ratio under the assumption that
species' dynamics are unrelated. Although it is possible to use this distribution of outcomes to
statistically differentiate synchronous and compensatory dynamics from independent fluctuations
(see [18]), the $p$-value adjustment required by the combined number of scales, times and lakes to
which we would apply this test would require on the order of $10^6$ randomizations at each of the
ca. 1.1 million combinations of time, scale and sample site, an operation which is computationally infeasible. Instead, we generate a binary response metric at each combination of scale, time and lake by assigning a value of one to cases where $p_i(n,s)$ exceeded the median value of the 1000 bootstrapped realizations and a zero otherwise. We then summarized this metric across our study regions and across the entire dataset to determine the fraction of all lakes demonstrating synchronized dynamics at any particular time and scale.

For the entire dataset we determined whether the set of lakes contributing information to a particular time and scale were more or less synchronized than expected by chance using a binomial test. Given the large number of tests performed (all combinations of time and scale) we applied a Benjamini–Hochberg–Yekutieli correction to control the false discovery rate [33]. Similar analyses were not possible at the regional scale due to small sample sizes (number of lakes). The wavelet analysis was performed using custom code in R version 2.6.0 (R development core team) and summary statistics and plots were generated using Mathematica ver. 9.0. A summary schematic of our analysis is available (Supplementary Figure S1).

Results

Synchronous dynamics are common in freshwater zooplankton communities. Considering all temporal scales (approximately monthly to decadal scales of variation), times (sampling dates ranging from 1971 to 2008) and study sites (58 sites in 54 lakes), we found that zooplankton communities where more synchronized than the median of our null-model in 85.8% of these combinations (14.2% showed compensatory dynamics) (figure 2). The vast majority of incidences (79%) were associated with a $q$-value equal to 1, meaning that the observed dynamics were more synchronized than all 1000 of our null-model realizations (result not shown). Values
of the wavelet modulus ratio less than approximately 0.4 were predominantly compensatory whereas those greater than approximately 0.4 were predominantly synchronous. This implies that communities that were more synchronized than the median of null-model realizations still expressed substantial variation in their extent of synchronization. Strong synchrony (wavelet modulus ratios close to 1) mainly occurred at scales near 1 year; shorter and longer scales tended to exhibit weaker synchronization (cf figure 2b-d).

We searched for the consistency of dynamics (synchrony or compensation) across study sites by region (using 6 different study regions) and across the entire 58-site dataset (Fig 3). With the entire dataset we applied a binomial test to determine if lakes exhibited similar dynamics at each combination of time and scale. At the regional scale, smaller sample sizes precluded the use of statistical tests. Synchronous dynamics are pervasive at the annual scale in all regions and across the entire dataset ($p < 0.0066$); however, there are no combinations of time and scale at which a significant fraction of sites exhibit compensatory dynamics across the entire dataset ($p > 0.05$). Rather, times and scales at which compensatory dynamics are predominant tend to differ across regions; while both the Experimental Lakes Area (ELA) and Sudbury area lakes (Fig 3a,e) show periods of compensatory zooplankton dynamics at scales greater than 1 year, these are expressed at different times in the two areas and thus are not visible in the aggregate plot (Fig 3m). Similar mismatches among regions are also evident at scales smaller than 1 year.

At longer timescales (2-10 years) the entire dataset exhibits a larger fraction of lakes with synchronized dynamics after ca. 1984, but not prior ($p < 0.0066$; Fig. 3m). This temporal transition is echoed at the regional scale in the Sudbury and Dorset areas (Fig 3e,g) suggesting
that important and widespread changes that yielded greater long-term synchronization of zooplankton dynamics within lakes occurred at this time.

Discussion

Characterizing patterns across all combinations of time scale, sampling date and study site, we found that synchronous dynamics were far more prevalent in lake zooplankton communities than compensatory dynamics. Although we found a range of scales over which a significant fraction of our study lakes demonstrated synchronized dynamics, we found no scales at which a significant fraction demonstrated compensatory dynamics. Furthermore, we detected a significant change over time in the fraction of study sites demonstrating synchronized dynamics at long time scales, an effect that may be caused by recovery from anthropogenic disturbance in a subset of our study lakes.

It is no surprise that we find a predominance of strong synchronization of zooplankton species at and around the scale of 1 year in our analysis (figures 2 and 3) and that this predominance is unchanged through time. Seasonal variation drives strong patterns in both the abiotic (e.g. temperature, nutrients) and biotic (e.g. resources, predators) factors that determine zooplankton abundance [26,34] and the extent to which the prevailing factors seasonally vary in temperate systems leads to synchronous variation among a large fraction of zooplankton species [26]. More interesting, is the rarity of compensatory dynamics at scales below and above 1 year. Below the 1 year scale, we expect resource competition to be ongoing and species may exhibit compensatory dynamics via their temporal partitioning of the growing season [26]; above 1 year and competitive exclusion and species replacement may be important processes driving compensatory dynamics [7].
Given the wealth of theory suggesting that compensatory dynamics should be a common facet of coexisting competitors \([4,6–8,35,36]\), the rarity of compensatory dynamics in our analysis is surprising. A possible explanation is that freshwater zooplankton species are highly differentiated and therefore only weak interspecific competitors. However, this is unlikely given that co-occurring species of zooplankton are known to demonstrate little variation in life-history traits suggesting use of common resources \([37]\) and negative reciprocal interactions among zooplankton taxa common to our study lakes have been previously demonstrated \([38,39]\). A more likely hypothesis explaining the rarity of compensatory dynamics is that the period during which intense competition occurs may be confined to a rather short portion of the seasonal cycle \([21,26]\); detecting compensatory dynamics would therefore then require sampling frequencies greater than those employed in most of our study lakes. In addition, our analysis of the complete assemblage of zooplankton species includes interactions other than competition. Larger bodied crustacean zooplankton are known to prey on smaller cladocerans and copepods and although these species make-up a relatively small fraction of the zooplankton biomass in most lakes they may have important impacts on the expression of patterns in the dynamics.

Although our analysis revealed compensatory dynamics in 14.2% of all scales and times in our 58 zooplankton communities, we detected no times or scales at which compensatory dynamics co-occurred in the majority of these lakes and very few instances where compensatory dynamics dominated any particular region. This suggests that the mechanisms driving compensatory dynamics may be local in their extent and/or vary substantially in their strength across lakes. Because compensatory dynamics are more likely to occur during periods where resources are limiting for a subset of species \([4,7,21]\), and such periods occur only during certain parts of the seasonal succession \([26]\), differences in the physical and biological characteristics of
nearby lakes, and differences in the seasonal forcing regime of spatially distant lakes, may ensure that compensatory dynamics lack coherence across study sites and/or regions. In addition metacommunity models have shown that locally-driven compensatory dynamics can be quickly overcome by environmental- and dispersal-driven synchronization [40] suggesting that compensatory dynamics may be unstable in the presence of other regional factors.

In addition to these broader patterns, our method also revealed scale-specific temporal changes in synchrony and compensation. Although we find no consistent temporal changes at short scales (< 1 year), we find that zooplankton communities in the Sudbury and Dorset regions became more synchronized at longer scales (> 1 year) from ca. 1984 onwards. This shift towards long-term synchronization of the zooplankton communities in these lakes is potentially a result of biological restructuring and recovery from anthropogenic disturbances such as lake acidification and eutrophication. In the Sudbury region, it has been well-established that the growth of acid-sensitive species was substantially impaired prior to 1980, but as pH increased over the mid-1980s the biomass of acid-sensitive species increased [41]. The shift toward synchronized dynamics at long time-scales suggests that there was no compensating decline in the biomass of acid-tolerant species in this system, but rather that both acid-tolerant and acid-intolerant species exhibited slowly increasing biomass (albeit at different rates), during the recovery period. In the Dorset area lakes, larger zooplankton body sizes have increased biomass due to a variety of factors stemming from acidification recovery [42]. Similar results have been witnessed in response to eutrophication in Lake Constance from 1920-1980 (Southern Germany); during eutrophication, crustacean species that did not go extinct all increased in biomass but at relatively different rates [25]. Previous work has shown that whole-lake acidification induced synchronized dynamics at the annual scale in the zooplankton community.
in Little Rock Lake because cold-tolerant species were more greatly affected, thereby selecting
differentially for warm-season growers [18]. In contrast we find that synchronous dynamics are
prevalent at the annual scale and across most other scales even in the absence of anthropogenic
disturbances.

Our results provide a new and detailed baseline against which the study of zooplankton
community dynamics, and the dynamics of competitive communities in general, can be
compared and contrasted. For example, the compensatory dynamics described in the acidified
basin of Little Rock Lake [18] are an anomaly relative to not only the reference basin of the same
lake, but to our entire set of study lakes, suggesting that anthropogenic disturbances may be
possible to detect by identifying anomalies against (or within) our reference data. Additionally,
contrasting our results to zooplankton communities from lakes without fish, with introduced top
predators such as rainbow trout, or where fish are anadromous, could provide important insight
into the top-down structuring forces of predators. Furthermore, coupling our results with lake
hydrology, water chemistry and climate data may provide insight into the mechanisms linking
the environment to the dynamics of competitors.

Although we find a predominance of synchronized dynamics, our results also
demonstrate that synchronized communities can have an aggregate (e.g. total biomass) variance
that is relatively low. For example, synchrony was more prevalent than compensatory dynamics
when the modulus ratio varied between 0.35 and 1.0 (figure 2) but at the lower end of this range
the community variance is more than four times smaller than that of a perfectly synchronized
community. Thus, the widespread synchronization we detect in our analysis still represents a
significant reduction in community variability and therefore may not be as detrimental to
ecosystem stability and population persistence as is commonly thought [6,17,43].
Unlike previous work that used methods sensitive to only the dominant mode of variation and produced a measure of variability averaged across time, our analysis parses out the effect of variation occurring at different time scales and during different time periods. Although scale and time resolving methods have become commonplace in understanding patterns of species covariation [17,18,20,44], ours is the first analysis to seek patterns across broad spatial and temporal scales. We found evidence for widespread synchronous dynamics at a broad range of times and scales, while compensatory dynamics were relatively rare and incoherently distributed among different times and scales in our study lakes. Although, we found only few regionally consistent changes in zooplankton synchronization over time, this result is itself important – indicating that local drivers of zooplankton dynamics and heterogeneity among lakes are strong enough to obscure larger-scale patterns. The rarity of compensatory dynamics, which are assumed to be an essential feature of competitive coexistence, brings into question our understanding of the mechanisms maintaining coexistence of competitors. Future theoretical and experimental work should aim to address how diverse species assemblages persist despite their tendency to display synchronous dynamics across long reaches of time and scale.

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References


Figure Captions

Figure 1. Geographical locations of study sites grouped by region. The inset map shows an enlargement of the region in the black box. Numbers in parentheses indicate the number of study sites in each region. Study sites represent individual lakes in all regions except Florida, where Lake Okeechobee was sampled in five basins within the lake. In addition to North American lakes our study included two European sites: Muggelsee, Germany, (52.43N, 13.65E) and Lake Zurich, Switzerland (47.37N, 8.55E).

Figure 2. a) The frequency of values of the wavelet modulus ratios observed across all combinations of time, scale and site in the analysis; a value of 0.3 indicates that the amplitude of biomass variability in the community is 30% the amount it would express if species’ dynamics were perfectly synchronized. Colors demarcate how common synchronous and compensatory dynamics are at each value of the wavelet modulus ratio – as determined by comparison against the null model that assumed no correlation among species dynamics. In total, the relative incidence of synchronous dynamics was 85.8% (compensatory dynamics 14.2%). Panels b through d further partition this result by different scales of variation (axes are the same as panel a); relatively more contributions come from intermediate scales (between ½ and 2 years) since many sites were sampled at frequencies commensurate with this range.

Figure 3. The fraction of study sites demonstrating synchronized zooplankton dynamics (left-side panels) and the number of lakes contributing information (right-side panels) at each time and scale, broken down by region. Panels a,b show aggregated information for the ELA, NOLSS and Coldwater lakes; panels c,d show NTL and Mendota lakes; panels e,f show Sudbury lakes; panels g,h show Dorset lakes; panels i,j show Florida lakes; panels k,l show Lake Zurich and Muggelsee, and panels m,n show aggregated information from all study lakes. In panel m, the black etching encloses a domain in which synchronized dynamics are more common across sites than expected by chance ($\alpha = 0.025; p < 0.0066$). There are no domains on this plot in which compensatory dynamics are more common across sites than expected by chance. Typically, between 10 and 25 study sites contributed information at each combination of time and scale; however, as many as 44 sites contributed at certain combinations. The conical shape of these figures arises because longer scales require longer time-series to generate reliable Wavelet transformations.