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Document type: Postprint

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Citation: Vasseur, D. A., Fox, J. W., Gonzalez, A., Adrian, R., Beisner, B. E., Helmus, M. R., ... Steiner, C. F. (2014). Synchronous dynamics of zooplankton competitors prevail in temperate lake ecosystems. *Proceedings of the Royal Society B: Biological Sciences*, 281(1788), 20140633. <https://doi.org/10.1098/rspb.2014.0633>

Synchronous dynamics of zooplankton competitors prevail in temperate lake ecosystems.

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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

1 **Introduction**

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

17 Synchronous and compensatory dynamics are also of fundamental interest in community
18 ecology because they regulate the relationship between population and temporal community
19 variability. At the scale of populations, temporal variability is an indicator of stability which is
20 often linked to extinction probability [9,10]. Similarly, temporal variability at the aggregate or
21 community level, 'community variability' [7,11], is of fundamental interest as an index of
22 community stability [12,13], and is of applied interest as a potential leading indicator of
23 nonlinear changes in ecosystem state [14,15]. When species contribute additively to a particular

24 community attribute (e.g. total biomass), the temporal variability of the attribute is given by the
25 sum of all terms in the community variance-covariance matrix. All else being equal,
26 communities with species dynamics that negatively covary over time (compensatory dynamics)
27 will exhibit lower community variability than communities whose covariance terms are positive
28 on average (synchronous dynamics) [7]; however, the same processes that generate negative
29 covariation can also destabilize communities by increasing species fluctuations [16].

30 Many studies have measured the synchrony of competitors in experiments and nature
31 [3,7,17–20] and some have attempted to infer the relative contributions of competition and
32 environmental factors in these communities [1,3,20]. For example, using annual census of
33 terrestrial plants and animals, ref. [3] found that species are on average synchronized, and
34 suggested that environmental drivers were relatively more important than competition for
35 shaping community dynamics. Although appealing, the argument that synchronous dynamics
36 result when environmental drivers are relatively more important than density-dependent biotic
37 feedbacks is challenging to verify, because the drivers leading to synchronous and compensatory
38 dynamics need not necessarily be in conflict. Synchronous and compensatory dynamics may
39 operate on different time-scales [20,21] or during different periods [21] in which case the
40 frequency and temporal extent of sampling largely dictates which drivers are perceived to be the
41 most critical. For example, if competing species are commonly and uniformly affected by
42 environmental variation, it simply generates a temporally changing arena in which the outcomes
43 of competition are enacted. If species are sampled once annually as in ref. [3], the signature of
44 competition may be entirely obscured by the synchronizing effect of ‘good’ vs. ‘bad’ years (e.g.
45 drought vs. wet), even if it is an important driver of species’ relative fitness and persistence [22].
46 Furthermore, it has been shown that embedding competitors in a food web context can cause

47 them to respond synchronously to environmental disturbance even when the underlying
48 dynamics are compensatory [23], highlighting the challenge of identifying the mechanisms
49 underlying dynamics. Measuring and interpreting synchrony and compensation thus requires, at
50 a minimum, refined estimators of synchrony and compensation across different timescales [17–
51 21].

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

63 In addition to time-scale, communities may transition between synchrony to
64 compensation over time at fixed scales. In Little Rock Lake, experimental acidification altered
65 the expression of synchronization at the annual-scale in a zooplankton community [18] and
66 elsewhere, natural and anthropogenic changes in long-term nutrient loads have been shown to
67 impact community composition [24,25]. Within the growing season the intensity of competition
68 among zooplankton can vary greatly as nutrients become depleted and well-edible algae are
69 replaced by colonial forms [26]. Transitions between synchrony and compensatory dynamics

70 may be common at a variety of scales and yield important insight into the mechanisms
71 structuring the distribution of temporal dynamics of species in competitive communities;
72 however, detecting such transitions requires advanced statistical machinery capable of resolving
73 patterns in both time and scale.

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

88

89 **Methods**

90 *Data*

91 Temporal data were compiled from a number of long-term monitoring programs of
92 temperate zone lakes in North America and Europe. Crustacean zooplankton data from the

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

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

116

117 *Wavelet analysis*

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

$$122 \quad W_{k,l}(n, s) = s^{-0.5} \sum_{i=1}^N x_{k,l}(\tau_i) \cdot \psi^* \left(\frac{n-t_i}{s} \right) \quad (1)$$

123 In expression (1), t_i represents the set of Julian dates on which $x_{k,l}$ was sampled and N is the total
124 number of samples of $x_{k,l}$. The parameters n and s represent the time and scale localization of the
125 Morlet wavelet, which is the product of a Gaussian distribution and a complex waveform,
126 $\psi(\tau) = \pi^{-1/4} e^{i\omega_0\tau} e^{-\tau^2/2}$. We set the wavenumber of the Morlet wavelet ω_0 , which controls the
127 number of oscillations within the effective width of the Gaussian distribution, equal to 6 as in
128 previous studies [18,27].

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

$$135 \quad s = 365.25 \cdot 2^{j\delta_s} \quad (2)$$

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

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

147

148 *Measuring synchrony*

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

$$151 \quad \rho_l(n, \mathbf{s}) = \frac{\Lambda_{n,s} \left(\left| \sum_k \mathbf{W}_{k,j}(n, \mathbf{s}) \right| \right)}{\Lambda_{n,s} \left(\sum_k \left| \mathbf{W}_{k,j}(n, \mathbf{s}) \right| \right)} \quad (3)$$

152 where $|\cdot|$ denotes the complex modulus and $\Lambda_{n,s}(\cdot) = \int e^{-\frac{1}{2}\left(\frac{n-t}{s}\right)^2} (\cdot) d\mathbf{n}$ is a Gaussian localization

153 function in time n . The localized wavelet modulus ratio computes the ratio of the actual
 154 amplitude of community fluctuations against the cumulative amplitude of population fluctuations
 155 at each time and scale. The numerator in equation (3) uses the modulus of the sum of the
 156 wavelet transform; by summing wavelet coefficients prior to computing the modulus, the

157 realized amplitude is discounted by species whose dynamics have opposite phases. The
158 denominator, the sum of species' moduli, is the maximum possible amplitude given a perfect
159 alignment of phases. Thus, the wavelet modulus ratio is bounded between values of zero and
160 one. A value of zero indicates that compensatory dynamics result in a community variance equal
161 to zero; whereas a value of one indicates perfect synchronization of population dynamics and a
162 maximum value of the community variance. The modulus ratio is akin to a family of
163 multivariate indices of synchronization [see ref. 7] that measure the sum or mean of pair-wise
164 species covariances (or here co-amplitudes) by comparing realized variances or amplitudes of
165 communities to the values that would be achieved under perfect synchronization, thus
166 superseding the need to compute pair-wise relationships directly using correlative or co-spectral
167 techniques. Although uneven sampling can generate bias in the estimates of wavelet power (W^2
168), this bias is consistent within each sampling site because sampling occurred for all zooplankton
169 species at the same points in time, making our measure of synchronization (based on relative
170 amplitude) unbiased in the presence of uneven sampling.

171 To measure synchronization we generated 1000 null-model outcomes in each site (l), at
172 each scale (s) and time (n) by attributing a random phase-shift on the interval $(0, 2\pi)$ to each of
173 the k species and recalculating the modulus ratio (3) (see ref [18]). Because this procedure
174 retains the distribution of amplitudes of variation expressed by different species, it generates an
175 accurate distribution for the value of the local wavelet modulus ratio under the assumption that
176 species' dynamics are unrelated. Although it is possible to use this distribution of outcomes to
177 statistically differentiate synchronous and compensatory dynamics from independent fluctuations
178 (see [18]), the p -value adjustment required by the combined number of scales, times and lakes to
179 which we would apply this test would require on the order of 10^6 randomizations at each of the

180 ca. 1.1 million combinations of time, scale and sample site, an operation which is
181 computationally infeasible. Instead, we generate a binary response metric at each combination
182 of scale, time and lake by assigning a value of one to cases where $p_i(n, s)$ exceeded the median
183 value of the 1000 bootstrapped realizations and a zero otherwise. We then summarized this
184 metric across our study regions and across the entire dataset to determine the fraction of all lakes
185 demonstrating synchronized dynamics at any particular time and scale.

186 For the entire dataset we determined whether the set of lakes contributing information to
187 a particular time and scale were more or less synchronized than expected by chance using a
188 binomial test. Given the large number of tests performed (all combinations of time and scale) we
189 applied a Benjamini–Hochberg–Yekutieli correction to control the false discovery rate [33].
190 Similar analyses were not possible at the regional scale due to small sample sizes (number of
191 lakes). The wavelet analysis was performed using custom code in R version 2.6.0 (R
192 development core team) and summary statistics and plots were generated using *Mathematica* ver.
193 9.0. A summary schematic of our analysis is available (Supplementary Figure S1).

194

195 **Results**

196 Synchronous dynamics are common in freshwater zooplankton communities.
197 Considering all temporal scales (approximately monthly to decadal scales of variation), times
198 (sampling dates ranging from 1971 to 2008) and study sites (58 sites in 54 lakes), we found that
199 zooplankton communities were more synchronized than the median of our null-model in 85.8%
200 of these combinations (14.2% showed compensatory dynamics) (figure 2). The vast majority of
201 incidences (79%) were associated with a q -value equal to 1, meaning that the observed dynamics
202 were more synchronized than all 1000 of our null-model realizations (result not shown). Values

203 of the wavelet modulus ratio less than approximately 0.4 were predominantly compensatory
204 whereas those greater than approximately 0.4 were predominantly synchronous. This implies
205 that communities that were more synchronized than the median of null-model realizations still
206 expressed substantial variation in their extent of synchronization. Strong synchrony (wavelet
207 modulus ratios close to 1) mainly occurred at scales near 1 year; shorter and longer scales tended
208 to exhibit weaker synchronization (*cf* figure 2b-d).

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

222 At longer timescales (2-10 years) the entire dataset exhibits a larger fraction of lakes with
223 synchronized dynamics after ca. 1984, but not prior ($p < 0.0066$; Fig. 3m). This temporal
224 transition is echoed at the regional scale in the Sudbury and Dorset areas (Fig 3e,g) suggesting

225 that important and widespread changes that yielded greater long-term synchronization of
226 zooplankton dynamics within lakes occurred at this time.

227

228 **Discussion**

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

237 It is no surprise that we find a predominance of strong synchronization of zooplankton
238 species at and around the scale of 1 year in our analysis (figures 2 and 3) and that this
239 predominance is unchanged through time. Seasonal variation drives strong patterns in both the
240 abiotic (e.g. temperature, nutrients) and biotic (e.g. resources, predators) factors that determine
241 zooplankton abundance [26,34] and the extent to which the prevailing factors seasonally vary in
242 temperate systems leads to synchronous variation among a large fraction of zooplankton species
243 [26]. More interesting, is the rarity of compensatory dynamics at scales below and above 1 year.
244 Below the 1 year scale, we expect resource competition to be ongoing and species may exhibit
245 compensatory dynamics via their temporal partitioning of the growing season [26]; above 1 year
246 and competitive exclusion and species replacement may be important processes driving
247 compensatory dynamics [7].

248 Given the wealth of theory suggesting that compensatory dynamics should be a common
249 facet of coexisting competitors [4,6–8,35,36], the rarity of compensatory dynamics in our
250 analysis is surprising. A possible explanation is that freshwater zooplankton species are highly
251 differentiated and therefore only weak interspecific competitors. However, this is unlikely given
252 that co-occurring species of zooplankton are known to demonstrate little variation in life-history
253 traits suggesting use of common resources [37] and negative reciprocal interactions among
254 zooplankton taxa common to our study lakes have been previously demonstrated [38,39]. A
255 more likely hypothesis explaining the rarity of compensatory dynamics is that the period during
256 which intense competition occurs may be confined to a rather short portion of the seasonal cycle
257 [21,26]; detecting compensatory dynamics would therefore then require sampling frequencies
258 greater than those employed in most of our study lakes. In addition, our analysis of the complete
259 assemblage of zooplankton species includes interactions other than competition. Larger bodied
260 crustacean zooplankton are known to prey on smaller cladocerans and copepods and although
261 these species make-up a relatively small fraction of the zooplankton biomass in most lakes they
262 may have important impacts on the expression of patterns in the dynamics.

263 Although our analysis revealed compensatory dynamics in 14.2% of all scales and times
264 in our 58 zooplankton communities, we detected no times or scales at which compensatory
265 dynamics co-occurred in the majority of these lakes and very few instances where compensatory
266 dynamics dominated any particular region. This suggests that the mechanisms driving
267 compensatory dynamics may be local in their extent and/or vary substantially in their strength
268 across lakes. Because compensatory dynamics are more likely to occur during periods where
269 resources are limiting for a subset of species [4,7,21], and such periods occur only during certain
270 parts of the seasonal succession [26], differences in the physical and biological characteristics of

271 nearby lakes, and differences in the seasonal forcing regime of spatially distant lakes, may ensure
272 that compensatory dynamics lack coherence across study sites and/or regions. In addition
273 metacommunity models have shown that locally-driven compensatory dynamics can be quickly
274 overcome by environmental- and dispersal-driven synchronization [40] suggesting that
275 compensatory dynamics may be unstable in the presence of other regional factors.

276 In addition to these broader patterns, our method also revealed scale-specific temporal
277 changes in synchrony and compensation. Although we find no consistent temporal changes at
278 short scales (< 1 year), we find that zooplankton communities in the Sudbury and Dorset regions
279 became more synchronized at longer scales (> 1 year) from ca. 1984 onwards. This shift towards
280 long-term synchronization of the zooplankton communities in these lakes is potentially a result
281 of biological restructuring and recovery from anthropogenic disturbances such as lake
282 acidification and eutrophication. In the Sudbury region, it has been well-established that the
283 growth of acid-sensitive species was substantially impaired prior to 1980, but as pH increased
284 over the mid-1980s the biomass of acid-sensitive species increased [41]. The shift toward
285 synchronized dynamics at long time-scales suggests that there was no compensating decline in
286 the biomass of acid-tolerant species in this system, but rather that both acid-tolerant and acid-
287 intolerant species exhibited slowly increasing biomass (albeit at different rates), during the
288 recovery period. In the Dorset area lakes, larger zooplankton body sizes have increased biomass
289 due to a variety of factors stemming from acidification recovery [42]. Similar results have been
290 witnessed in response to eutrophication in Lake Constance from 1920-1980 (Southern
291 Germany); during eutrophication, crustacean species that did not go extinct all increased in
292 biomass but at relatively different rates [25]. Previous work has shown that whole-lake
293 acidification induced synchronized dynamics at the annual scale in the zooplankton community

294 in Little Rock Lake because cold-tolerant species were more greatly affected, thereby selecting
295 differentially for warm-season growers [18]. In contrast we find that synchronous dynamics are
296 prevalent at the annual scale and across most other scales even in the absence of anthropogenic
297 disturbances.

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

309 Although we find a predominance of synchronized dynamics, our results also
310 demonstrate that synchronized communities can have an aggregate (e.g. total biomass) variance
311 that is relatively low. For example, synchrony was more prevalent than compensatory dynamics
312 when the modulus ratio varied between 0.35 and 1.0 (figure 2) but at the lower end of this range
313 the community variance is more than four times smaller than that of a perfectly synchronized
314 community. Thus, the widespread synchronization we detect in our analysis still represents a
315 significant reduction in community variability and therefore may not be as detrimental to
316 ecosystem stability and population persistence as is commonly thought [6,17,43].

317 Unlike previous work that used methods sensitive to only the dominant mode of variation
318 and produced a measure of variability averaged across time, our analysis parses out the effect of
319 variation occurring at different time scales and during different time periods. Although scale and
320 time resolving methods have become commonplace in understanding patterns of species
321 covariation [17,18,20,44], ours is the first analysis to seek patterns across broad spatial and
322 temporal scales. We found evidence for widespread synchronous dynamics at a broad range of
323 times and scales, while compensatory dynamics were relatively rare and incoherently distributed
324 among different times and scales in our study lakes. Although, we found only few regionally
325 consistent changes in zooplankton synchronization over time, this result is itself important –
326 indicating that local drivers of zooplankton dynamics and heterogeneity among lakes are strong
327 enough to obscure larger-scale patterns. The rarity of compensatory dynamics, which are
328 assumed to be an essential feature of competitive coexistence, brings into question our
329 understanding of the mechanisms maintaining coexistence of competitors. Future theoretical and
330 experimental work should aim to address how diverse species assemblages persist despite their
331 tendency to display synchronous dynamics across long reaches of time and scale.

332

333 **Acknowledgements**

334 This paper emerged as part of the *Predicting Ecological Change: Multi-Scale Analysis of*
335 *Plankton Diversity and Dynamics* working group funded by the Canadian Institute for Ecology
336 and Evolution (CIEE/ICEE). Toni Klausiches assisted in the development and execution of
337 programs in R. This is Kellogg Biological Station contribution no. 1718. RA was funded by
338 Limnotip (O1LC1207A; Biodiversa) founded under the FP7 ERA-Net Scheme and the DFG-
339 LakeRisk Project; WAN and BEB acknowledge support of NSERC discovery grants; AG is

340 supported by the Canada Research Chair program; DAV acknowledges support of NSF DEB
341 grant 1050803. Data can be made available upon request.

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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 Okechobee 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 $\frac{1}{2}$ 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.