

# Resilience of phytoplankton dynamics to trophic cascades and nutrient enrichment

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## Abstract

Resilience was compared for alternate states of phytoplankton pigment concentration in two multiyear whole-lake experiments designed to shift the manipulated ecosystem between alternate states. Mean exit time, the average time between threshold crossings, was calculated from automated measurements every 5 min during summer stratification. Alternate states were clearly identified, and equilibria showed narrow variation in bootstrap analysis of uncertainty. Mean exit times ranged from 13 to 290 h. In the reference ecosystem, Paul Lake, mean exit time of the low-pigment state was about 100 h longer than mean exit time of the high-pigment state. In the manipulated ecosystem, Peter Lake, mean exit time of the high-pigment state exceeded that of the low-pigment state by 30 h in the cascade experiment. In the enrichment experiment mean exit time of the low-pigment state was longer than that of the high-pigment state by about 100 h. Mean exit time is a useful measure of resilience for stochastic ecosystems where high-frequency measurements are made by consistent methods over the full range of ecosystem states.

Lake ecosystems provide diverse examples of complex dynamics, including multiple stable states and critical transitions among them (Scheffer 1998, 2009). These include alternate states of phytoplankton biomass resulting from either trophic cascades or nutrient enrichment (Carpenter 2003).

Holling (Holling 1973) recognized that ecosystems exhibit multiple states and occasionally shift among them. Holling introduced *resilience* as “the persistence of relationships within a system” and “a measure of the ability of these systems to absorb changes of state variables, driving variables, and parameters, and still persist.” He distinguished resilience from *stability*, “the ability of a system to return to an equilibrium state after a temporary disturbance.” Unlike stability which is a local measure that treats perturbations as isolated events, resilience accounts for perturbations of large amplitudes and the ongoing tempo of sequential disturbances. A section titled “The Random World” (pp. 13–15 of Holling 1973) discusses the role of random fluctuations in resilience, including

examples from lake eutrophication, food webs, and fisheries. Holling’s ideas of resilience imply probabilities of persistence of an ecosystem state or identity in a stochastic environment. However, most research has focused on deterministic aspects of resilience and few quantitative studies have addressed resilience in a stochastic framework.

Arani et al. (2021) proposed “exit time” as a stochastic measure of resilience. Exit time, a stochastic variable, is the average time until a shift between states of a stochastic system is first observed. The mean exit time, or the median, can serve as a resilience measure. A familiar example is half-life of a radioisotope. Decay from the radioactive state to the daughter state is a stochastic process of single atoms. Its half-life is the median exit time, or time until half of the radioactive atoms have decayed. In global change science, Kleinen et al. (2003) mentioned exit time from Atlantic Meridional Overturning Circulation (AMOC, the state of the ocean that brings a mild climate to Western Europe) as a measure of the expected time available for policy action to maintain resilience of Europe’s climate. Arani et al. (2021) present empirical methods for measuring exit time from ecosystem states using time series data. We apply that method here to assess resilience of experimental lakes to trophic cascades and nutrient enrichment.

In 2008, we began a series of experiments designed to gradually shift lake ecosystems between alternate states. Our goal was to evaluate dynamic indicators of resilience based on

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statistical changes in time series as the lake shifted from one state to another (Carpenter et al. 2011; Scheffer et al. 2015; Pace et al. 2017; Wilkinson et al. 2018). Because these studies measured lake ecosystem variables frequently during both states of the ecosystem and the transition, the data are suitable for estimating exit time. Here, we determine mean exit times for two different manipulations that induced alternate states and provided high-frequency time series needed to assess exit time as a quantitative measure of resilience as described by Holling (1973).

## Methods

### Peter and Paul Lakes

Paul and Peter lakes are paired lakes in Gogebic County, Michigan, USA (46°250 N, 89°500 W). Since 1951 the lakes have been used for whole-lake experiments with Paul as the reference lake and Peter as the manipulated lake (Elser et al. 1986). Since 1984 the lakes have been used for a series of experiments on trophic cascades, allochthony measured by  $^{13}\text{C}$  addition, and eutrophication by nutrient enrichment (Carpenter and Pace 2018).

### Trophic cascade experiment

At the start of the trophic cascade experiment, Peter Lake's food web was dominated by planktivorous minnows. In 2008 and 2009, small numbers of adult largemouth bass (*Micropterus salmoides* L.) were gradually added to Peter Lake (Carpenter et al. 2011). A large year class of bass resulted in 2010. Increasingly with bass additions, minnows sought refuge in shallow water and the surrounding bog (Cline et al. 2014). The decline of minnow numbers in offshore waters was followed by expansion of large-bodied grazing zooplankton (Pace et al. 2013) and decline in chlorophyll concentration (Carpenter et al. 2011). Paul Lake's food web was dominated by largemouth bass throughout the experiment (Carpenter et al. 2011).

### Nutrient enrichment experiment

Nutrients in the form of inorganic phosphorus and nitrogen were added to enrich Peter Lake in 2013, 2014, and 2015. Nutrients were added daily over the summer season for the first 2 yrs and only until early warning signals were obtained in the third year (Pace et al. 2017; Wilkinson et al. 2018). Phytoplankton responded to the additions of nutrients but bloom timing and magnitude varied considerably among years (Wilkinson et al. 2018). Paul Lake, which drains into Peter Lake, did not receive added nutrients and served as an unmanipulated reference ecosystem.

### High-frequency pigment measurements

We used automated pigment measurements during summer stratification to estimate mean exit times. Data were recorded every 5 min.

During the cascade experiment, each lake was monitored with two Yellow Springs Instruments multiparameter sondes

(model 6600-V2-4) equipped with optical chlorophyll *a* (Chl *a*) sensors (model 6025) deployed at a depth of 0.7 m at a central station (Batt et al. 2013). Chl *a* is reported in  $\mu\text{g/L}$ . We did not use phycocyanin sensors in this study because cyanobacteria were at low concentrations throughout and did not reflect the dynamics of the phytoplankton community.

During the enrichment experiment each lake was monitored with a Hydrolab DS5X sonde including a sensor for phycocyanin fluorescence (model 007291) deployed at a depth of 0.75 m (Pace et al. 2017). Chlorophyll sensors in this study were not responsive to phytoplankton blooms unlike direct manual measurements of extracted chlorophyll (S.I.). Unknown processes likely related to the presence of large cyanobacterial filaments resulted in low detection of chlorophyll—a phenomena observed by others (Gregor and Maršálek 2004). Phycocyanin fluorescence and extracted chlorophyll had similar dynamics consistent with limited microscopic counts indicating blooms were dominated by cyanobacteria (Wilkinson et al. 2018). Phycocyanin is reported in relative fluorescence units (RFU). Direct laboratory measurements of phycocyanin concentration ( $\mu\text{g/L}$ ) were linearly related to RFU (Pace et al. 2017).

### Estimation of mean exit time

Mean exit time was estimated by the following steps: (1) Standardize the pigment time series (Arani et al. 2021) (S.I. *Dynamic Linear Models*); (2) Test the Markov hypothesis for standardized time series by the Langevin method (S.I. *Assessment of the Markov Property and Stationarity*). (3) Test the stationarity of the standardized time series by the augmented Dickey–Fuller (ADF) test (S.I. *Assessment of the Markov Property and Stationarity*). (4) Using the standardized time series, estimate the deterministic and stochastic components of a Langevin model (system reconstruction); (5) Calculate mean exit time for the ecosystem states of interest.

The in situ sensors detected chlorophyll for the cascade experiment and phycocyanin for the enrichment experiment. We used standardized levels of pigment fluorescence (S.I. *Dynamic Linear Models* and Figs. S-1, S-2, S-3, and S-4) as indicators of pigment concentration for both experiments. For the standardized levels reported here, the ADF test rejected the null hypothesis of non-stationarity ( $p < 0.01$  for each lake in each experiment) and data exhibited the Markov property (S.I. *Assessment of Markov Property and Stationarity*).

### Langevin analysis

Exit time develops from terms of the Langevin Eq. 1 as summarized in several works (Siegert et al. 1998; Siegert and Friedrich 2001; Rinn et al. 2016; Tabar 2019). A detailed description of exit time analysis is presented by Arani et al. (2021). We present an abbreviated explanation here. A complete worked example (Peter Lake in the enrichment experiment) is provided as R scripts: [https://github.com/SRCarpen/ExitTime\\_BinMethod\\_PeterLakeExample](https://github.com/SRCarpen/ExitTime_BinMethod_PeterLakeExample)

The time series of standardized levels  $b_t/s_t$  were used as state variables ( $x_t$ ) to estimate the drift-diffusion model known as the Langevin equation (Carpenter and Brock 2011; Rinn et al. 2016; Tabar 2019)

$$dx = D_1(x)dt + \sqrt{2D_2(x)} dW \quad (1)$$

The implementation in R is based on Rinn et al. (2016) and the Matlab code of Arani et al. (2021).  $D_1(x)$  is the deterministic core of the dynamics called the “drift” in stochastic dynamic modeling. Its roots  $D_1(x) = 0$  are the equilibria.  $D_2(x)$ , called “diffusion” in stochastic modeling, is a deterministic function that represents the intensity of the noise as a function of  $x$ . The noise source is  $dW$  where  $W$  stands for the Wiener process, and thus  $dW$  represents Gaussian white noise. The fitted drift and diffusion functions are used below in calculations of effective potential, the stationary distribution, and mean exit time.

In this paper, diffusion functions are plotted using the definition

$$D_2(x) = \frac{1}{2}\sigma^2(x) \quad (2)$$

Thus  $\sigma(x) = \sqrt{2D_2(x)}$ , and this conversion allows drift and diffusion to be compared in the same units, pigment standardized level/time.

### Potential and effective potential

Stability of dynamic systems can be illustrated by potential curves, or “ball and cup” diagrams that show stable points as valleys and unstable points as hilltops. For deterministic systems, the potential curve  $P(x)$  is the integral

$$U(x) = \int^x D_1(z) dz \quad (3)$$

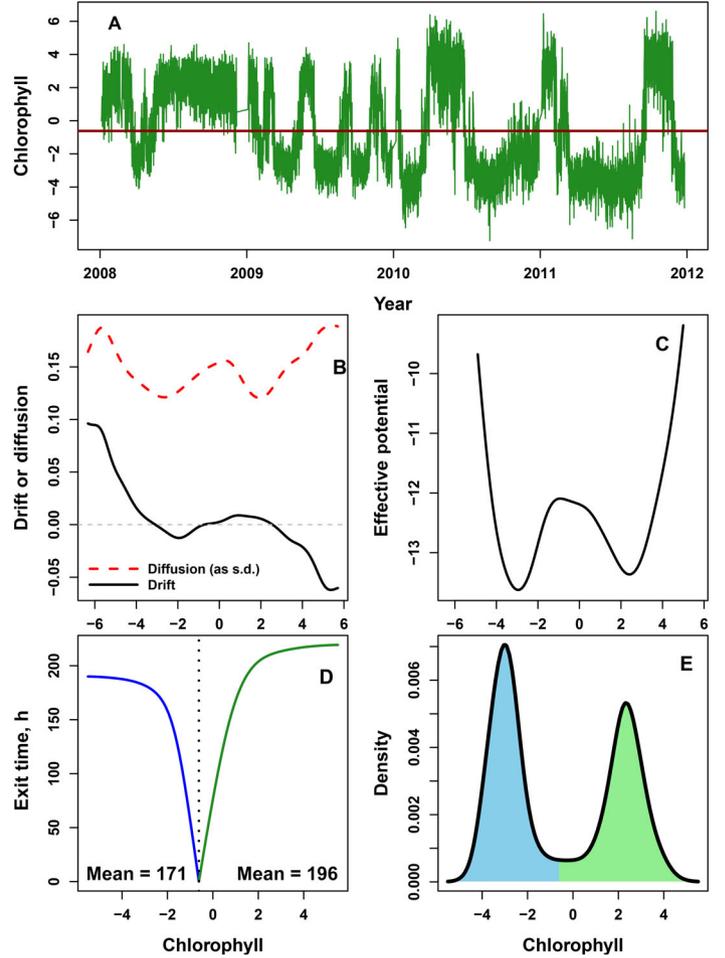
where  $z$  is a dummy variable and the integral is computed over the relevant range of  $x$ .

The potential  $U(x)$  does not account for the noise of the system. Studies of resilience should account for the possibility that random events may change the shape of the potentials (Horsthemke and Lefever 1984). Effects of noise are included in the effective potential,  $U_E(x)$  (Arani et al. 2021) and we use his function here

$$U_E(x) = - \int^x \frac{D_1(z)}{D_2(z)} dz + \log(D_2(x)) \quad (4)$$

### Exit time

For both lakes in both experiments, the drift function  $D_1$  describes a curve with two stable equilibria separated by an unstable equilibrium (main text Figs. 1–4). The expected exit times from each stable basin can be estimated by solving the



**Fig. 1.** Resilience analysis of manipulated Peter Lake during the Cascade experiment. **(A)** Chlorophyll (standardized level) vs. year during the experiment. Solid horizontal line denotes the unstable threshold. **(B)** Drift (black) and diffusion (red) functions vs. chlorophyll standardized level. **(C)** Effective potential vs. chlorophyll standardized level. **(D)** Exit time (h) vs. chlorophyll standardized level, with probability-weighted means, for the two stable basins. Vertical dotted line is the threshold between the basins. **(E)** Stationary probability density vs. chlorophyll standardized level. Shading denotes the low-chlorophyll (blue) and high-chlorophyll (green) basins.

backward Fokker–Planck equation with appropriate boundary conditions for each basin:

$$D_1(x) \frac{dT}{dx} + D_2(x) \frac{d^2T}{dx^2} = -1 \quad (5)$$

The solution of this equation, given the boundary conditions, is mean exit time  $T(x)$  if the starting state of the system is  $x$ . For each basin, we use an absorbing boundary at the middle unstable equilibrium where small random disturbance can cause a shift between basins. For the outer boundaries (left boundary of the left basin, right boundary of the right basin) we use a reflecting

boundary to indicate that no shift occurs. If the boundary is absorbing,  $T(x) = 0$  at the boundary, i.e., the exit time is 0 at the unstable edge between basins. If the boundary is reflecting, the derivative  $\frac{dT}{dx} = 0$  at the boundary, i.e., there is no change in  $T(x)$  at the reflecting boundary. For calculations, we chose the left reflecting boundary slightly above the lower limit of the data and the right reflecting boundary slightly below the upper limit of the data.

We solved the boundary-value problem (5) with the `bvpSolve()` package in R using function `bvptwp()` (Mazzia et al. 2014). An R script to illustrate the method using a simple ecological model is found at [https://github.com/SRCarpen/Exit\\_Time\\_R](https://github.com/SRCarpen/Exit_Time_R)

Solving for  $T(x)$  yields mean exit time as a function of  $x$ . It is useful to have a single representative value of exit time for an entire basin. We estimated a basin-wide mean exit time for the full width of each basin as the probability-weighted mean of  $T(x)$  with probabilities taken from the normalized stationary density of the Fokker–Planck equation which is computed from  $D_1$  and  $D_2$  (Horsthemke and Lefever 1984; Arani et al. 2021). For example, the mean of  $T(x)$  is  $\int p(x)T(x)dx$  where  $p(x)$  is the stationary probability that sums to 1 over all values of  $x$ . We integrated the stationary density using the `hcubature()` function of the `hcubature()` package in R (<https://bmaras.github.io/cubature/>).

### Uncertainty of exit time

To assess uncertainty of exit time, we first bootstrapped the autoregressions by randomizing the errors ( $\epsilon_t$ , Eq. S-1a) with replacement and adding them to the predicted  $y_t$  to generate pseudodata (Efron and Tibshirani 1993). The pseudodata series were fit to the Dynamic Linear Model (Eqs. S-1) and standardized levels were used to estimate drift and diffusion (Eq. 2), exit times (Eq. 5) and the stationary probability distribution. One hundred bootstrap cycles were run, and the distribution of exit times was corrected for bias (Efron and Tibshirani 1993).

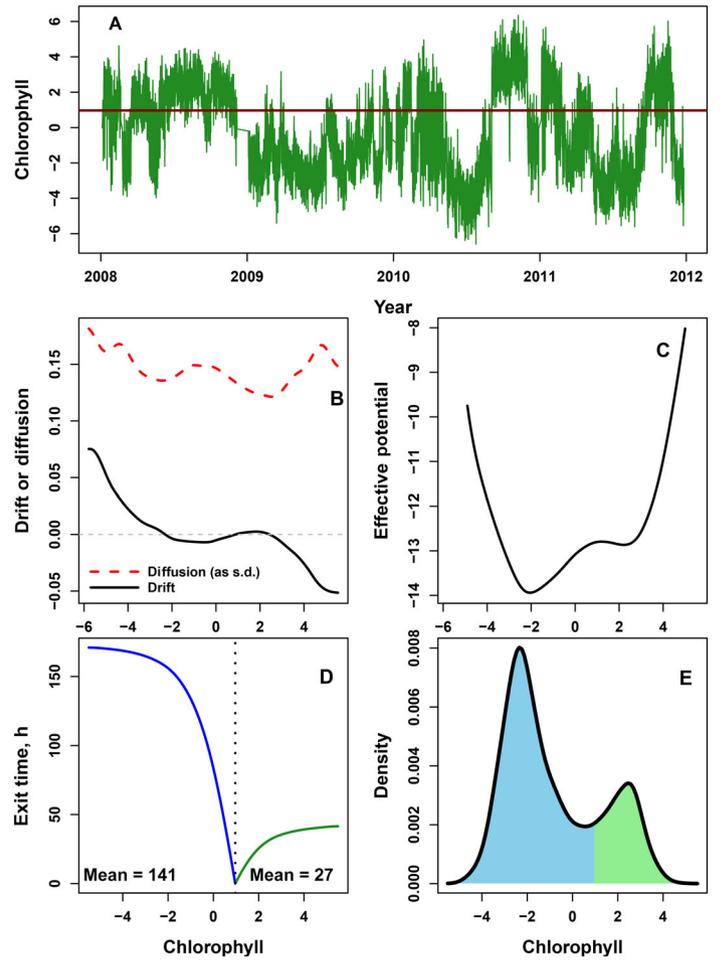
## Results

### Alternate states and resilience: Cascade experiment

Chlorophyll concentration time series during summer stratification for manipulated Peter Lake and reference Paul Lake were measured during the summer stratified seasons of 2008–2011 (Figs. S1, S2).

Standardized levels of chlorophyll (Fig. 1A) in Peter Lake were used to estimate components of a Langevin model (Fig. 1A). Diffusion (variability) is larger than the deterministic rate of change (drift) (Fig. 1B). We plotted sigma (Eq. 2) so that both components have the same units.

Chlorophyll dynamics in Peter Lake are dominated by noise. Nonetheless the drift function indicates three equilibria (three crossings of the line  $y = 0$ ). The left and right equilibria are stable, because a small increase in chlorophyll decreases the rate of change causing chlorophyll to decrease toward the



**Fig. 2.** Resilience analysis of Paul Lake, reference ecosystem for the Cascade experiment. **(A)** Chlorophyll (standardized level) vs. year during the experiment. Solid horizontal line denotes the unstable threshold. **(B)** Drift (black) and diffusion (red) functions vs. chlorophyll standardized level. **(C)** Effective potential vs. chlorophyll standardized level. **(D)** Exit time (h) vs. chlorophyll standardized level, with probability-weighted means, for the two stable basins. Vertical dotted line is the threshold between the basins. **(E)** Stationary probability density vs. chlorophyll standardized level. Shading denotes the low-chlorophyll (blue) and high-chlorophyll (green) basins.

equilibrium point, and a small decrease in chlorophyll increases the rate of change, restoring chlorophyll toward the equilibrium point. The center equilibrium is unstable because small changes of chlorophyll in either direction cause chlorophyll to shift away from the center equilibrium. Thus, the center equilibrium is a threshold separating two alternate stable equilibria. The alternate equilibria represent the minnow dominated (higher chlorophyll) and bass dominated (lower chlorophyll) states. The effective potential (Eq. 4) shows two distinct stability basins (Fig. 1C).

Exit time as a function of the initial value of chlorophyll is zero at the unstable equilibrium, because a small perturbation of chlorophyll at that point can shift the ecosystem in either

direction (Fig. 1D). Exit times rise as chlorophyll moves either direction from the unstable equilibrium.

To obtain an average exit time over each basin, we calculate the weighted averages where the weights are the normalized stationary densities for starting values of chlorophyll (Fig. 1D, E). The two states of the ecosystem are apparent in the stationary probability distribution. The mean exit times of the low and high chlorophyll basins are 171 h and 196 h, respectively.

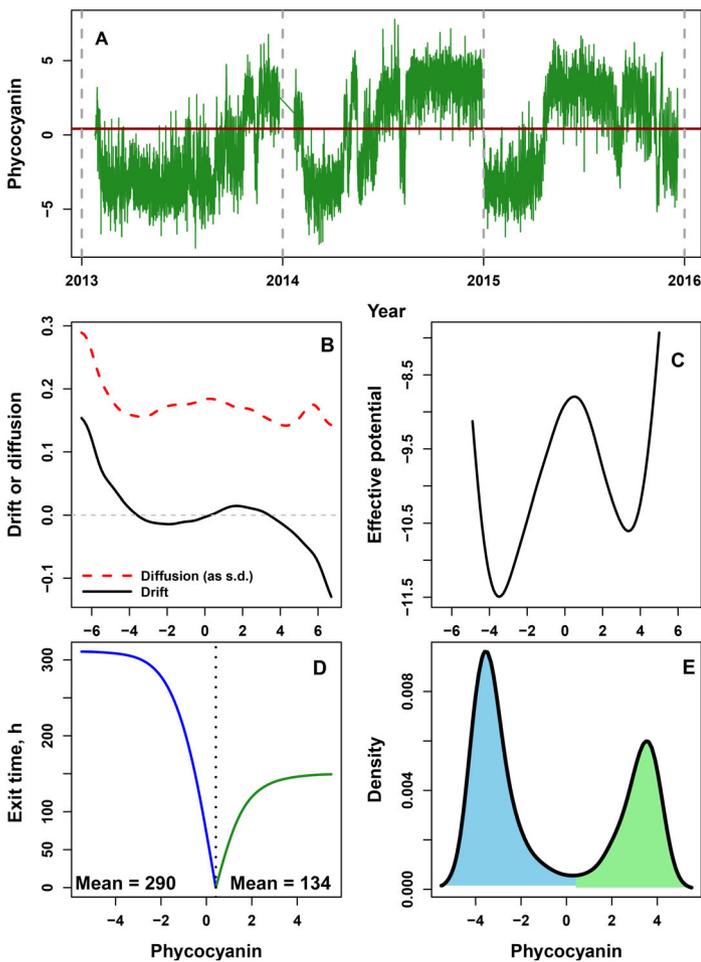
Fluctuations of chlorophyll in Paul Lake represent the baseline variability of an unmanipulated ecosystem (Fig. 2A). Although the diffusion is much larger than the drift, alternate equilibria are discernible (Fig. 2B). Mean exit times of low and

high chlorophyll equilibria are 141 and 27 h, respectively (Fig. 2D,E).

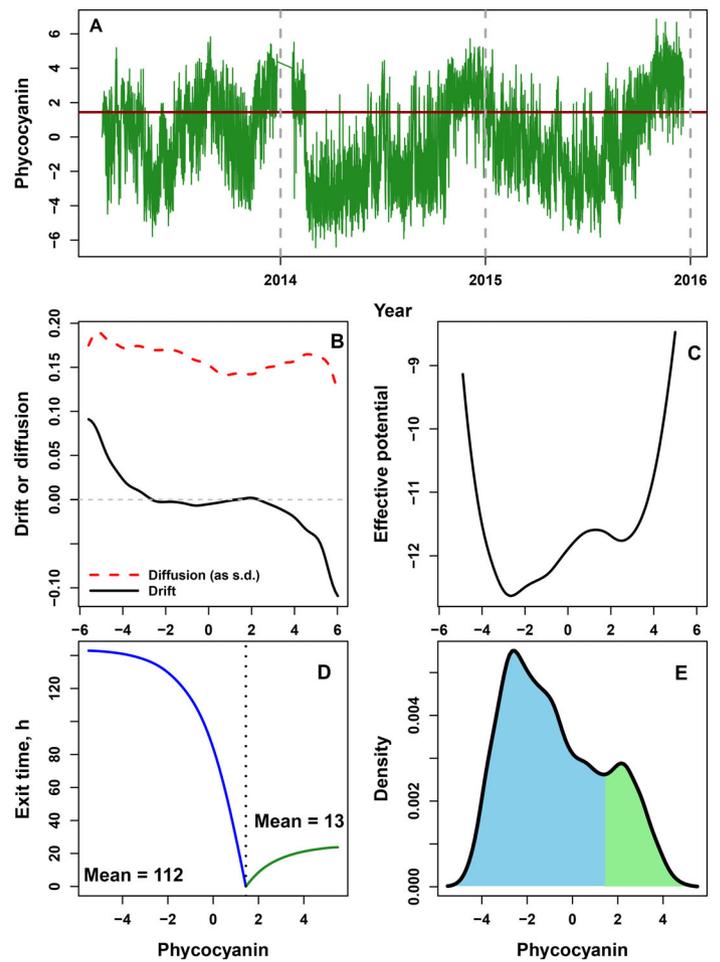
### Alternate states and resilience: Nutrient enrichment experiment

Phycocyanin RFU were highly variable in manipulated Peter Lake (Fig. 3) and reference Paul Lake during the enrichment experiment (Fig. 4).

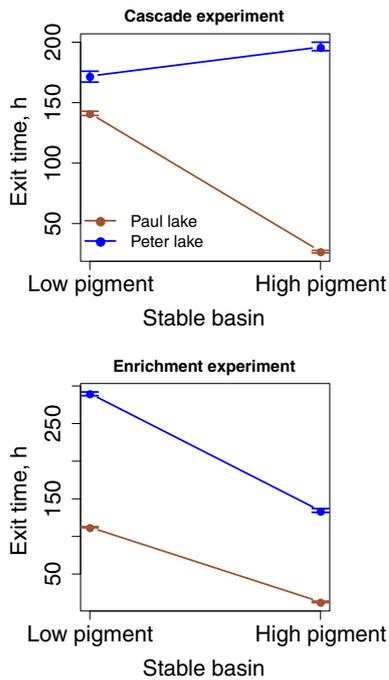
Standardized levels of phycocyanin in Peter Lake suggest shifts from low- to high-pigment levels during each year (Fig. 3A). Diffusion (as sigma (Eq. 2), in the same units as drift) was notably larger than drift (Fig. 3B). The effective potential



**Fig. 3.** Resilience analysis of enriched Peter Lake during the enrichment experiment. (A) Phycocyanin (standardized level) vs. year during the experiment. Solid horizontal line denotes the unstable equilibrium. (B) Drift (black) and diffusion (red) functions vs. phycocyanin standardized level. (C) Effective potential vs. phycocyanin standardized level. (D) Exit time (h) vs. phycocyanin standardized level, with probability-weighted means, for the two stable basins. Vertical dotted line is the threshold between the basins. (E) Stationary probability density vs. phycocyanin standardized level. Shading denotes the low-phycocyanin (blue) and high-phycocyanin (green) basins.



**Fig. 4.** Resilience analysis of Paul Lake during the enrichment experiment. (A) Phycocyanin (standardized level) vs. year during the experiment. Solid line denotes the unstable equilibrium. (B) Drift (black) and diffusion (red) functions vs. phycocyanin standardized level. (C) Effective potential vs. phycocyanin standardized level. (D) Exit time (h) vs. phycocyanin standardized level, with probability-weighted means, for the two stable basins. Vertical dotted line is the threshold between the basins. (E) Stationary probability density vs. phycocyanin standardized level. Shading denotes the low-phycocyanin (blue) and high-phycocyanin (green) basins.



**Fig. 5.** Exit time for low- and high-pigment stable basins for both lakes during the cascade and enrichment experiments. Error bars show the interquartile range (25<sup>th</sup> to 75<sup>th</sup> percentile) and circle shows the median (50<sup>th</sup> percentile) of 100 bootstrap samples (S.I.).

showed two stable basins, but the high-phycoerythrin basin appears shallower than the low-phycoerythrin basin (Fig. 3C). Exit times are zero at the unstable transition point between the basins, and rise to the left and right of the transition point (Fig. 3D). The two basins of attraction are evident in the stationary probability density (Fig. 3E). The probability-weighted exit times are 290 h for the low-phycoerythrin basin and 134 h for the high-phycoerythrin basin.

Paul Lake also exhibited seasonal fluctuations in standardized level of phycoerythrin (Fig. 4A). Diffusion was much larger than the drift (Fig. 4B) but nonetheless alternate states are evident in the effective potential (Fig. 4C) and density (Fig. 4E). Exit times are 112 h for the low-pigment basin and 13 h for the high-pigment basin (Fig. 4D).

### Validation of the models

For each dataset the one-step predictions of the fitted Langevin equations compared to data had a lower negative log likelihood than a hypothetical model with constant drift (S.I. *Model Validation*). To visualize the goodness of fit we compared one-step conditional probabilities predicted by the Langevin equations with the observed one-step changes of the data for selected initial points quantiles in each lake in each experiment (S.I. *Model Validation* and Fig. S5). Predicted distributions closely matched observed distributions.

### Uncertainty of exit time estimates

Distributions of the deterministic equilibria (zeroes of the drift function) were estimated by bootstrapping (S.I. Figs. S6, S7). For Peter Lake, each bootstrapped pseudo-dataset, 100 for each experiment, had three equilibria, two stable equilibria separated by an unstable threshold. The variability of estimated equilibria is relatively narrow and equilibria are well-separated on the pigment axes (Fig. S6). For Paul Lake equilibria were distinct and variability was modest (Fig. S7).

Distributions of mean exit time from 100 bootstrap cycles were computed for both stable basins in both experiments (S.I. Figs. S8, S9). Exit time includes the stochasticity of the dynamics (diffusion). Patterns of the distributions were different among experiments, lakes, and stability basins.

In manipulated Peter Lake, exit times were longer than in unmanipulated Paul Lake based on interquartile ranges (Fig. 5). Exit time from the low-pigment basin was longer than exit time from the high-pigment basin in Paul Lake. In Peter Lake for the cascade experiment the high-pigment equilibrium had longer exit time than the low-pigment equilibrium. In the enrichment experiment, this pattern was reversed with shorter exit time in the high-pigment equilibrium.

### Discussion

The long-term condition of both lakes is the low-pigment state. In Peter Lake the manipulations caused short-term excursions into the high-pigment state, but by different mechanisms. In the cascade experiment, intervals of high chlorophyll were caused by fluctuations in grazing associated with movement of planktivorous fishes between littoral and pelagic habitats (Pace et al. 2013; Cline et al. 2014). In the nutrient enrichment experiment, intervals of high phycoerythrin were associated with accumulation of phosphorus and nitrogen in phytoplankton (Wilkinson et al. 2018). When manipulations ended, the ecosystem returned to the low-pigment pre-manipulation state. For both experiments, phase-randomized surrogate time series did not have alternate states, suggesting that alternate states were not likely to be detected by chance (S.I. *Could Alternate States be Detected by Chance?*).

In Paul Lake, fluctuations of pigment concentrations are due to the routine dynamics of phytoplankton in a variable physical-chemical environment, interacting with grazers in an ecosystem that was not manipulated. Note that Paul Lake lies upstream of Peter Lake, was sampled using a separate boat, and was not contaminated with added nutrients. Chlorophyll fluctuations in Paul Lake show occasional brief peaks in the epilimnion (Fig. S2) as seen in previous studies (Carpenter and Kitchell 1993; Carpenter et al. 2001). Weekly phytoplankton counts in Paul Lake from 1984–1997 showed both absence and occasional peaks of Cyanobacteria that are consistent with the patterns we observed in high-frequency phycoerythrin data (Cottingham et al. 1998). These fluctuations could have appeared as alternate states in our analysis.

We were surprised to see alternate states in the high-frequency pigment data from Paul Lake. The experiments were designed initially to test dynamic indicators of resilience. In Peter Lake, several dynamic indicators provided early warnings of loss of resilience but no indications of declining resilience were detected in Paul Lake (Carpenter et al. 2011; Batt et al. 2013; Pace et al. 2013, 2017; Cline et al. 2014; Wilkinson et al. 2018).

We considered the possibility that cyclic fluctuations in irradiance, temperature or other variables could appear to be alternate states in sensor data. During each experiment in each lake, daily samples were taken, returned to the laboratory, and analyzed by fluorometry to measure Chl *a* concentration (Carpenter et al. 2011; Pace et al. 2017). Drift functions of the Langevin Eq. 1 for daily chlorophyll time series show alternate states for the manipulated lake, Peter Lake, but not for the reference Paul Lake (Fig. S-10 and S.I. *Alternate States in Daily Chlorophyll Time Series*). However, the diffusion component is relatively large, consistent with the sensor data. Because of the daily time step and small sample size (about 120 daily samples per year vs. 288 sensor samples per day, or about 34,560 sensor samples per year in each lake), we did not attempt to estimate exit time from the daily data. Patterns in the daily data are consistent with the alternate states we detected in Peter Lake but ambiguous with regard to the alternate states we detected in Paul Lake. Further research using high-frequency pigment measurements in a wider variety of aquatic environments is needed to improve understanding of alternate states of phytoplankton and the response of stochastic indicators such as exit time.

An exit event occurs when the pigment line crosses the unstable equilibrium that separates the two basins (Figs. 1A, 2A, 3A, 4A). Most of the intervals between exit events are short, and some quick events are hidden by the width of the plotted lines. Thus, the mean exit times range from about 1 to 10 d due to the dominance of short events (Fig. 5). These rather short mean exit times are another indication of the high variability of the time series.

To be useful an indicator of stochastic resilience should be repeatable, comparable among ecosystems, responsive to changes in resilience, and have low-to-moderate uncertainty for real-world time series. In addition, for our method the time series to be analyzed should meet the assumptions of the Langevin method. For these sensors and these lakes, the standardized levels analyzed here meet these conditions. Different data standardizations may be appropriate for different ecosystems or sensors.

In summary, resilience of phytoplankton biomass (as measured here by their pigments) in lake ecosystems may depend on slowly-changing variables such as watershed sources of nutrients and colored Dissolved Organic Carbon, sediment release of nutrients, grazer dynamics, and apex predators. Gradual trends of such variables reduce resilience and increase the likelihood that random events can cause a regime shift

(Holling 1973; Scheffer et al. 2001). Our experiments simulated gradual forcing of Peter Lake by trophic cascades or nutrients. Pigment concentration, especially in sensor optical measurements, is highly variable and this variance strongly affects resilience measured using exit time and likely other stochastic indicators. The temporal fluctuations of chlorophyll are large enough that thresholds are crossed every few days when measured by high-frequency sensors during multiyear whole-lake experiments. We suspect that a decades-long perspective of high-frequency measurements could reveal much longer exit times for past states of Peter Lake, consistent with patterns seen in paleolimnological records (Leavitt et al. 1989). Nonetheless we have shown a pathway for comparative resilience studies of lake ecosystems using resilience measures that are consistent with Holling's (Holling 1973) emphasis of random fluctuations as a key element of resilience. The challenge is to build long-term highly-resolved datasets needed to measure stochastic variables that may provide a quantitative indicators for comparing resilience among aquatic ecosystems.

#### Data availability statement

Data used here are downloadable from: (1) Carpenter, S., M. Pace, J. Cole, R. Batt, C. Buelo, and J. Kurzweil. 2018. Cascade Project at North Temperate Lakes LTER High Frequency Sonde Data from Food Web Resilience Experiment 2008–2011 ver 1. Environmental Data Initiative. <https://doi.org/10.6073/pasta/5a8c6398661fad0bc8f1f5119b1150d6>. (2) Pace, M., J. Cole, and S. Carpenter. 2020. Cascade project at North Temperate Lakes LTER—High Frequency Data for Whole Lake Nutrient Additions 2013–2015 ver 2. Environmental Data Initiative. <https://doi.org/10.6073/pasta/cbe19041db41e720d84970f43156c042>

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### Conflict of Interest

None declared.

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