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Climate Change–Driven Regime Shifts in a Planktonic Food Web

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abstract: Predicting how food webs will respond to global environmental change is difficult because of the complex interplay between the abiotic forcing and biotic interactions. Mechanistic models of species interactions in seasonal environments can help understand the effects of global change in different ecosystems. Seasonally ice-covered lakes are warming faster than many other ecosystems and undergoing pronounced food web changes, making the need to forecast those changes especially urgent. Using a seasonally forced food web model with a generalist zooplankton grazer and competing cold-adapted winter and warm-adapted summer phytoplankton, we show that with declining ice cover, the food web moves through different dynamic regimes, from annual to biennial cycles, with decreasing and then disappearing winter phytoplankton blooms and a shift of maximum biomass to summer season. Interestingly, when predator-prey interactions were not included, a declining ice cover did not cause regime shifts, suggesting that both are needed for regime transitions. A cluster analysis of long-term data from Lake Baikal, Siberia, supports the model results, revealing a change from regularly occurring winter blooms of endemic diatoms to less frequent winter bloom years with decreasing ice cover. Together, the results show that even gradual environmental change, such as declining ice cover duration, may cause discontinuous or abrupt transitions between dynamic regimes in food webs.

Keywords: seasonally forced model, climate warming, ice coverage, top-down control, freshwater plankton community.

Introduction

The dynamics of most communities and ecosystems are determined by both biotic interactions and abiotic seasonal forcing (Altizer et al. 2006; White and Hastings 2019). Because of nonlinearities, these factors interact in complex, nonadditive ways, so that knowledge of each alone is insufficient to predict the resulting dynamics. Mathematical models provide a powerful approach to understand how biotic interactions play out in seasonal environments (Evans 1988; Klausmeier and Litchman 2012; Bewick et al. 2016), particularly when their output is compared with long-term observational data. For example, the complex multiannual dynamics of measles before vaccination has been shown to result from periodic forcing of interactions among susceptible, exposed, infected, and recovered individuals (Earn et al. 2000). Another example comes from the rocky intertidal, where a complex cyclical succession among barnacles, algae, and mussels was explained by a seasonally forced patch occupancy model (Benincà et al. 2015).

Understanding how time-varying abiotic forcing and biotic interactions combine to govern the dynamics of ecological communities is becoming more pressing in the face of accelerating anthropogenic global change, as biotic interactions can mediate species responses to climate change, either enhancing or dampening the negative (or positive) effects on their abundance (Suttle et al. 2007; HilleRisLambers et al. 2013; Alexander et al. 2015). While several studies have shown that biotic interactions may alter species sensitivity to changing climate, a mechanistic mathematical framework to explain and predict such effects, especially in seasonal environments, is still lacking. Here we develop a food web model embedded in a seasonal environment and investigate how climate-induced change in seasonal abiotic forcing modifies food web dynamics, which can have consequences for higher trophic levels and ecosystem functioning. While our model is tailored to describe a freshwater planktonic food web, the general approach and insights should be applicable to other seasonal food webs undergoing climate change.

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Freshwater ecosystems may be particularly vulnerable to climate change, as some of them are warming faster than terrestrial ecosystems and aquatic organisms have limited ability to migrate (Woodward et al. 2010). In addition, the planktonic food webs at their base, consisting of phytoplankton producers and zooplankton consumers, are relatively simple and have served as model systems for several fundamental ecological theories (e.g., resource competition and ecological stoichiometry; Tilman 1982; Sterner and Elser 2002). Among freshwater ecosystems, temperate lakes with seasonal ice cover were shown to be warming faster than other lakes (O'Reilly et al. 2015), accompanied by a decrease in the duration of ice cover (Magnuson et al. 2000; Sharma et al. 2019). Empirical studies have documented numerous changes following the ice cover decline, such as shifts in mixing regime or the weakened control of phytoplankton biomass by zooplankton (lack of "clear water phase"; Straile 2000; Gaedke et al. 2010; Shatwell et al. 2016). The challenge is to develop a mechanistic theory that takes into account the changes in abiotic forcing, such as decreasing ice cover, on food web interactions to explain the observed patterns.

Lakes that are seasonally ice covered often harbor distinct winter communities, including cold-adapted phytoplankton that bloom directly under the ice (Kozhova and Izmest'eva 1998; Moore et al. 2009; Twiss et al. 2012; Dokulil et al. 2014; Özkundakci et al. 2016). Forecasting the effect of warmer winters on lake phenology and community composition requires understanding the interseasonal relationships determined by the simultaneously acting abiotic forcing and biotic interactions (Salonen et al. 2009; Klausmeier and Litchman 2012; Hampton et al. 2015; O'Reilly et al. 2015; Powers and Hampton 2016), including a better characterization of under-ice plankton dynamics. However, studies of under-ice phytoplankton and their consumption by higher trophic levels are extremely scarce (Hampton et al. 2015). Winter gaps in many long-term data sets limit insight not only into the under-ice processes but also into the connection of prewinter to postwinter community patterns (Salonen et al. 2009; Hampton et al. 2015; O'Reilly et al. 2015) and the overall understanding of ecosystem functioning.

A unique long-term data set on Lake Baikal plankton dynamics that started in the 1950s presents a notable exception in terms of winter coverage, providing an opportunity to investigate the link between changing winter conditions and food web dynamics (Kozhova and Izmest'eva 1998; Hampton et al. 2008; Moore et al. 2009; Katz et al. 2015). Lake Baikal, located in Siberia, Russia, and stretching from 52° to 56° north latitude, experiences on average 110 days of ice coverage per year (Moore et al. 2009), but the duration of ice cover has steadily declined over the last several decades. Along with this decline, the dynamics of winter phytoplankton community have changed as well. Typically, Lake Baikal has pronounced under-ice phytoplankton blooms dominated by often-endemic diatom species (Kozhova 1981, 1987; Hampton et al. 2008; Shimaraev and Domysheva 2013; Silow et al. 2016). From the 1980s, there has been a disruption of the relatively regular occurrence of winter bloom years and a corresponding decline in the abundance of large endemic under-ice blooming diatom species (Izmest'eva et al. 2011; Katz et al. 2015). Katz et al. (2015) showed a link between the winter bloom years—the "Melosira years"—and climate conditions that produce the clearest ice and thus highlight conditions for endemic diatoms such as *Aulacoseira* (formerly *Melosira baicalensis*) while recognizing that internal processes likely contribute to the magnitude and variability of the blooms (e.g., Jewson and Granin 2015).

The transition from regular to infrequent winter blooms in Lake Baikal is an example of a regime shift—"a relatively sharp change from one regime to a contrasting one, where a regime is a dynamic 'state' of a system with its characteristic stochastic fluctuations and/or cycles" (Scheffer 2009, p. 357). Could this observed regime shift be explained by the interactions of food web dynamics with the declining ice cover? To investigate this question and explore the general influence of changing environmental forcing on food web dynamics, we developed a seasonally forced food web model with winter and summer phytoplankton under shared grazer pressure. While not designed to reproduce the detailed empirical dynamics, general mechanistic models can help us test conceptual predictions and provide insights into the mechanisms that generate empirical patterns.

Our model revealed a complex interseasonal relationship between phytoplankton and zooplankton dynamics, mediated by the length of the ice-covered period. Because of this complex interseasonal relationship, a decrease in the ice-covered period leads to significant changes in bloom patterns, ranging from pronounced yearly winter blooms to biennial and finally to a complete absence of under-ice blooms. Two-year cycles highlight the fact that plankton dynamics in one year influence the starting conditions in the following year in addition to abiotic forcing, such as climatic drivers of ice clarity and light environment. The model results agree with the observed shift in phytoplankton bloom patterns in Lake Baikal (Popovskaya et al. 1997; Popovskaya 2000), suggesting that changing environmental forcing may alter biotic interactions and lead to regime shifts in food web dynamics.

Methods

Model Description

We used a system of differential equations to investigate the interaction between zooplankton and winter and summer phytoplankton as well as its dependence on the duration of the ice-covered period. The model consists of two groups of primary producers, winter phytoplankton (P_{W}) and summer phytoplankton (P_{S}); a limiting resource (R); and a shared consumer (C). (Equations are given in table 1, and state variables and parameter values are given in table 2.) The fraction of ice-covered days per year (length $\tau = 365$ days) is given by the parameter φ. The two groups of phytoplankton differ in their competitive ability, with P_{W} being the superior resource (nutrient) competitor during the ice-covered period (φ) and P_{S} being the superior resource competitor during the ice-free period ($1 - \varphi$). Accordingly, the superior (inferior) resource uptake parameter a_{sup} (a_{inf}) is assigned to P_{W} and P_{S} depending on the season. That is, for simplicity we assume that these parameters are mirror images of each other. The consumer is assumed to be only indirectly influenced by seasons through changes in prey availability.

We use a biomass-based model where biomass is expressed as nitrogen content (mg N L^{-1}) and all rates are defined on the per-unit biomass (table 2). All food uptake processes are assumed to follow a type II functional response. The limiting resource R is assumed to be nitrogen, one of the main limiting nutrients in Lake Baikal (O'Donnell et al. 2017). Importantly, the model results do not depend on the identity of the limiting nutrient but are generally representative of biomass dynamics under general nutrient limitation. Assuming a closed system, the total amount of nutrients (R_{tot}) is the sum of freely available nitrogen R and nitrogen bound in biomass (P_{W}, P_{S}, C). Parameterization for phytoplankton is based on published scaling relationships for physiological rates (Edwards et al. 2012) with respect to average phytoplankton cell size observed in Lake Baikal. Parameterization for the consumer represents the copepod species *Epischurella baikalensis* (formerly *Epischura baikalensis*; Bowman et al. 2019), the dominant zooplankton species in Lake Baikal that accounts for more than 90% of zooplankton biomass, and is based on direct measurements of size and weight (Afanasyeva 1998), which were used to derive physiological rates on the basis of body size scaling relationships (de Roos and Persson 2013).

Model Analysis

The model dynamics were studied numerically, using Mathematica's NDSolve function, on log-transformed equations to better capture low densities (this was compared with the untransformed equations with a large AccuracyGoal setting). This solver automatically handles discontinuities at season changes. Model dynamics were investigated across a range of values of the ice-covered period per year, φ. For a given φ, we found the long-term attractor by numerically solving for log-transformed population densities at the start of a year that resulted in the same log-transformed densities at the end of the year using Newton's method, after a minimum 100-year warm-up. We then checked the stability of this cycle by calculating its Floquet multipliers (Klausmeier 2008). To find 2-year cycles, we projected 2 years ahead. We then tracked

Table 1: Dynamic equations for the seasonally forced food web model

No.	Dynamic equation	Description
(1.1)	$R = R_{\mathrm{tot}} - P_{\mathrm{S}} - P_{\mathrm{W}} - C$	Dynamics of resource
(1.2)	$\dfrac{dP_{\mathrm{W}}}{dt} = \left(\dfrac{ea_{\mathrm{W}}R}{H_{\mathrm{P}} + R} - \dfrac{a_{\mathrm{CP}}C}{H_{\mathrm{C}} + P_{\mathrm{W}} + P_{\mathrm{S}}} - m_{\mathrm{P}}\right)P_{\mathrm{W}}$	Dynamics of winter phytoplankton P_{W}, the superior resource competitor during the ice-covered period
	$a_{\mathrm{W}} = \begin{cases} a_{\mathrm{sup}} & \text{during ice-covered period, } \mathrm{mod}(t, \tau) \in [0, \varphi\tau] \\ a_{\mathrm{inf}} & \text{during ice-free period, } \mathrm{mod}(t, \tau) \in [\varphi\tau, \tau] \end{cases}$	
(1.3)	$\dfrac{dP_{\mathrm{S}}}{dt} = \left(\dfrac{ea_{\mathrm{S}}R}{H_{\mathrm{P}} + R} - \dfrac{a_{\mathrm{CP}}C}{H_{\mathrm{C}} + P_{\mathrm{W}} + P_{\mathrm{S}}} - m_{\mathrm{P}}\right)P_{\mathrm{S}}$	Dynamics of summer phytoplankton P_{S}, the superior resource competitor during the ice-free period
	$a_{\mathrm{S}} = \begin{cases} a_{\mathrm{inf}} & \text{during ice-covered period, } \mathrm{mod}(t, \tau) \in [0, \varphi\tau] \\ a_{\mathrm{sup}} & \text{during ice-free period, } \mathrm{mod}(t, \tau) \in [\varphi\tau, \tau] \end{cases}$	
(1.4)	$\dfrac{dC}{dt} = (\nu_{\mathrm{C}}(P_{\mathrm{W}}, P_{\mathrm{S}}) - m_{\mathrm{C}})C$	Dynamics of consumer
(1.5)	$\nu_{\mathrm{C}}(P_{\mathrm{W}}, P_{\mathrm{S}}) = \sigma \dfrac{a_{\mathrm{CP}}(P_{\mathrm{W}} + P_{\mathrm{S}})}{H_{\mathrm{C}} + P_{\mathrm{W}} + P_{\mathrm{S}}} - T_{\mathrm{M}}$	Consumer net biomass production

Table 2: Variables and parameter values for the seasonally forced food web model

Variable/parameter	Value	Unit	Definition
C		mg N L^{-1}	Biomass density of consumers
P_W		mg N L^{-1}	Biomass density of winter phytoplankton
P_S		mg N L^{-1}	Biomass density of summer phytoplankton
R		mg N L^{-1}	Density of shared resource (assumed to be nitrogen)
R_tot	.2	mg N L^{-1}	Total resource density
T_M	.05	day^{-1}	Maintenance rate of consumer
m_C	.01	day^{-1}	Mortality rate of consumer
σ	.5	mg N (mg N)$^{-1}$	Conversion efficiency of producer into consumer biomass
e	1	mg N (mg N)$^{-1}$	Conversion efficiency of phytoplankton (P_W, P_S) for R
a_CP	.2	L (mg N day)$^{-1}$	Clearance rate of consumer for phytoplankton (P_W, P_S)
a_sup	.8	L (mg N day)$^{-1}$	Clearance rate of superior resource competitor (defined by season) for R
a_inf	.16	L (mg N day)$^{-1}$	Clearance rate of inferior resource competitor (defined by season) for R
H_C	.04	mg N L^{-1}	Half-saturation constant for consumer
H_P	.1	mg N L^{-1}	Half-saturation constant for phytoplankton
m_P	.05	day^{-1}	Mortality plus maintenance rate of phytoplankton (P_W and P_S)
φ	.0–.5		Fraction of ice-covered days per year
τ	365	days	Period

a periodic attractor by slightly changing the parameter φ, using linear extrapolation from previous solutions to ensure a good starting guess for Newton's method. We stopped each track when the solution became unstable (a dominant Floquet exponent equal to 1 indicates a turning point or transcritical bifurcation, and that equal to -1 indicates a period-doubling bifurcation). Model analysis was performed in Mathematica 12.1 (Wolfram); code is provided in a zip file, available online.[1] Analysis of model extensions in the supplemental PDF (available online) was performed with Matlab R2016b (MathWorks) and used a simpler brute-force strategy to generate bifurcation diagrams.

Data Analysis

The long-term data set for phyto- and zooplankton from Lake Baikal used in this study extends from 1951 to 1999. Because of a change in the sample preservation method from formalin to Lugol's solution in 1973 (Hampton et al. 2008), counts from samples before 1973 are considered representative for diatoms because they are equally well preserved in both but not for other phytoplankton groups. Based on data from 1973 to 1999, diatoms typically make up more than 60% of the phytoplankton spring bloom in Lake Baikal and make up 50% of total phytoplankton biomass on a yearly average (Mokry et al. 2010), although a decline in diatom abundance has been observed during recent decades (Izmest'eva et al. 2011). Summer algal biomass is typically dominated by nondiatom picophytoplankton (Moore et al. 2009). To enable the investigation of the complete time period covered by the data set, the analysis of phytoplankton bloom dynamics was performed on diatoms only. Accordingly, in our analysis we focus on characteristic winter/spring dynamics, where diatoms may be a proxy for a more complex community of potential prey that *Epischurella* eats. The year 1991 is missing from the phytoplankton data set (Hampton et al. 2008).

For the analysis, diatom cell count data were converted to corresponding biovolume values (μm^3 L^{-1}) on the basis of reported cell sizes (Database on Biovolume Metrics from the Academy of Natural Sciences of Drexel University 2001; Rioual and Mackay 2005; Belykh et al. 2006; Genkal and Bondarenko 2006; Olenina et al. 2006; Kremer et al. 2014). Count data (ind L^{-1}) for nauplii, copepodite, and adult stages of the Lake Baikal dominant zooplankton species *E. baikalensis* were converted to corresponding biomass data (mg dry weight L^{-1}) on the basis of body size reported by Afanasyeva (1998), multiplying the number of individuals by 0.00027 for nauplii, by 0.008 for copepodites, and by 0.1 for adults. Total diatom biovolume and total *Epischurella* biomass per sampling date were calculated for data from the upper layer (0–50 m). Phytoplankton were sampled at 0-, 10-, and 50-m depths, whereas zooplankton were sampled at 0–10-, 10–25-, and 25–50-m depth layers. Because of inconsistent sampling frequency from the 25–50-m depth layer across the time series, for *E. baikalensis* only the counts from the upper 25 m are included in this analysis (see also Hampton et al. 2014). Diatom and *Epischurella* data used in this study have been deposited in the Dryad Digital Repository (https://doi.org/10.5061/dryad.4b8gthtbb; Wollrab et al. 2020).

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[1] Code that appears in *The American Naturalist* is provided as a convenience to readers. It has not necessarily been tested as part of peer review.

To explore whether there are distinct annual patterns of phytoplankton dynamics between 1951 and 1999 in Lake Baikal, we performed a cluster analysis. The characteristic bloom patterns of the resulting clusters were compared with model predictions of bloom patterns dependent on ice duration and consumer abundance. Data on the timing and duration of ice coverage of Lake Baikal were taken from the Global Lake and River Ice Phenology Database (http://nsidc.org/data/g01377). Based on the observation that winter phytoplankton development in Lake Baikal starts with the onset of ice (Kozhov 1963; Kozhova 1987; Hampton et al. 2008), for each year sampling dates from the day of ice-on onward were included in the analysis of the yearly bloom development. Monthly means were calculated for $\log_{10}$-transformed diatom biovolume data. A matrix of monthly average diatom biomasses per year (transformed back to original values) was used to calculate a corresponding Bray-Curtis dissimilarity matrix indicating interannual differences in seasonal diatom abundance patterns. This dissimilarity matrix was then used to cluster years according to their seasonal diatom abundance.

The most parsimonious set of clusters was derived following Shimadzu et al. (2013) using the relationship between the number of clusters and distance between clusters. Therefore, for all clustering steps, two separate regression lines were fitted to the set of previous and subsequent clustering steps with respect to the between-cluster distance. The residuals of both regression lines were summed, and the clustering step at which the sum of residuals reached a minimum value determined the number of clusters to be differentiated.

To enable a comparison between the long-term data and model predictions on how the under-ice bloom formation depended on the pre-ice consumer abundance, the integrated *Epischurella* biomass of the preceding ice-free period, starting from the day of ice-off in the previous year and ending on the day of ice-on in the current year, was calculated using the trapezoid function of package pracma in R. In addition to the measured values, interpolated values were used for the start and the end point of the ice-free period (i.e., at day of ice-on and at day of ice-off). To avoid the confounding effects of different length of the ice-free period across the years, the integrated *Epischurella* biomass was divided by the corresponding length of the ice-free period to obtain the *Epischurella* biomass averaged over the ice-free period. A post hoc Tukey test was used to determine the between-cluster differences for $\log_{10}$-transformed average *Epischurella* biomass of the preceding ice-free period.

The ice-covered fraction of each year was calculated by dividing the length of the ice-covered period (days) by 365 days. As for *Epischurella*, a post hoc Tukey test was used to investigate the between-cluster differences for the fraction of ice-covered days per year and to compare with model predictions of whether the under-ice bloom formation depends on the length of ice coverage expressed as a fraction of the year. In addition to cluster analysis, we used linear regression to investigate whether the phytoplankton biovolume at the day of ice-off correlated with the integrated *Epischurella* biomass in the previous year, using interpolated values. Values were interpolated using a Hermite spline function, splinefun (method monoH.FC), available in R.

All data analyses were performed in R version 3.3.2 (R Core Team 2016) using the packages car, ggplot2, lubridate, mgcv, plyr, pracma, and vegan.

Results

To distinguish the blooms of winter phytoplankton from blooms of summer phytoplankton in the model results, we will refer to those as "winter" and "summer" blooms, respectively. Correspondingly, for the long-term data from Lake Baikal, phytoplankton blooms occurring in the first half of the year are also referred to as "winter" blooms.

Model Results

The model shows that with decreasing ice cover, the food web transitions through different dynamic regimes. When the ice-covered period decreases from half a year ($\varphi = 0.5$) to complete absence of ice coverage ($\varphi = 0$), the model predicts a shift from regular annual winter phytoplankton blooms for $0.401 < \varphi < 0.5$, to 2-year cycles for $0.2271 < \varphi < 0.401$, and then to the complete absence of winter bloom for $\varphi < 0.2025$ (fig. 1*A*). In the narrow range of $0.496 < \varphi < 0.5$ there are three alternative annual cycles (fig. S1*A*–S1*C*; figs. S1–S8 are available online). Counterintuitively, for $0.37 < \varphi < 0.5$ the winter phytoplankton has larger average biomass than summer phytoplankton even though it has a shorter season where it is the superior competitor, which can be attributed to top-down control by the grazer (fig. S1*D*). The 2-year cycles observed for $0.2271 < \varphi < 0.401$ can be described as a winter bloom year followed by a delayed winter bloom year for $\varphi > 0.3$ (fig. 1*B*) and as a winter bloom year followed by a non-winter-bloom year for $\varphi < 0.3$ (fig. 1*C*). For a small region of $0.2025 < \varphi < 0.2301$, there are smaller winter blooms, with a narrow range of 2-year cycles ($0.212 < \varphi < 0.2179$) embedded in a range of annual cycles. The regime shift from annual to biennial winter blooms at $\varphi = 0.3$ is abrupt, and the regime shift from biennial winter blooms to annual blooms at $\varphi = 0.2271$ is discontinuous (for precise definitions of different regime shifts, see "Discussion"). There is a complete absence of winter blooms for $\varphi < 0.2025$. Figure S1 shows more examples of different dynamical regimes, and figure S2 zooms in to the region between $0.226 < \varphi < 0.231$.

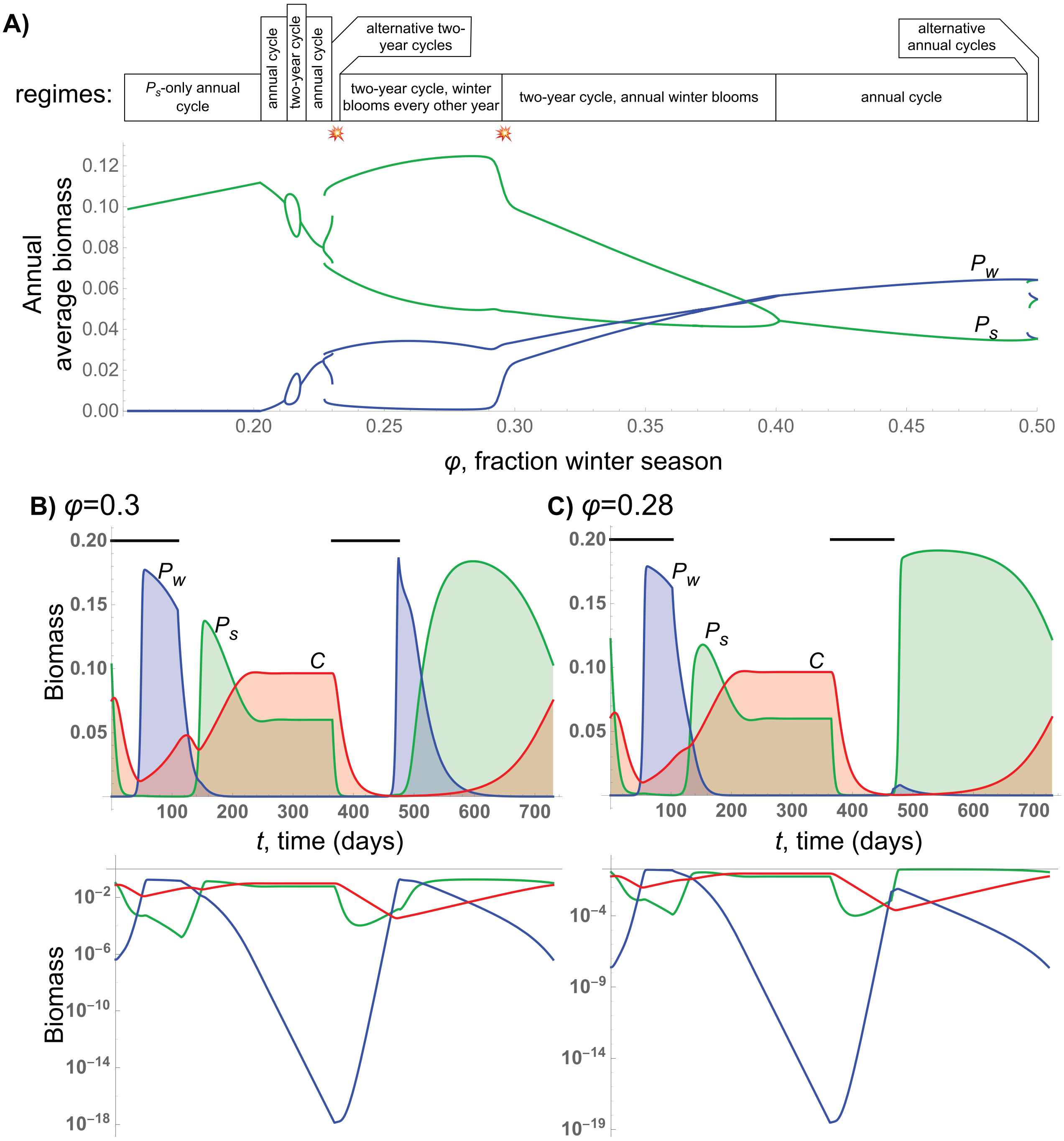

Figure 1: *A*, Dynamic regimes and annual average biomass of winter phytoplankton (blue) and summer phytoplankton (green), dependent on the fraction of the winter (ice cover) season, φ. In areas of 2-year cycles, the different averages of years 1 and 2 are shown. Significant regime shifts are indicated with a flash. *B*, *C*, Community dynamics of P_W (blue), P_S (green), and the consumer C (red) in two consecutive years on a linear (*upper graph*) and a logarithmic (*lower graph*) scale for selected periods of ice coverage (indicated by horizontal black lines). *B* illustrates a large winter bloom in the first year and a delayed winter bloom in the second, and *C* illustrates a large winter bloom in the first year and no winter bloom in the second. See figure S1 for more examples of the dynamics.

The observed differences in the bloom dynamics for different φ can be explained by a complex relationship among the length of the ice-covered period, phytoplankton dynamics, and phytoplankton effects on zooplankton growth. In winter bloom years, the increase in zooplankton biomass during the winter bloom leads to stronger consumer control of summer phytoplankton, resulting in a less pronounced peak and shorter duration of the summer bloom (fig. 1*B*, 1*C*). At the same time, the enhanced consumer biomass further decreases winter phytoplankton during the ice-free period, resulting in lower initial densities of winter phytoplankton in the following ice-covered period, which subsequently delay or prevent winter bloom.

If the reduction in winter phytoplankton biomass during the ice-free period is not too great, pronounced winter blooms occur on a yearly basis. However, with the decreasing length of the ice-covered period, strong top-down control during the (longer) ice-free period leads to a stronger reduction in winter phytoplankton, delaying (fig. 1*B*) or even inhibiting (fig. 1*C*) winter bloom formation in the following year. In years with no or delayed winter blooms, zooplankton development during the ice-covered period is strongly reduced, which leads to a more pronounced, long-lasting summer bloom but also to less suppressed winter phytoplankton biomass at the end of the year. This leads to more favorable starting conditions for the development of a pronounced winter phytoplankton bloom the next year, giving rise to the observed 2-year cycles for $0.2271 < \varphi < 0.401$. In years with no winter bloom, zooplankton biomass decreases to very low levels during the ice-covered period so that a large, long-lasting summer phytoplankton bloom develops right after the ice-off.

For $\varphi < 0.2025$, winter blooms completely disappear as a result of the combination of a short duration of the ice-covered period and consumer control during the extended ice-free period, while summer bloom formation starts right after ice-off. With a further decrease in the ice-covered period, consumer biomass during the ice-covered period does not decrease as much, leading to shorter and less pronounced summer blooms due to increased top-down control. In the complete absence of seasonality ($\varphi = 0$), the consumer-summer phytoplankton reach a stable equilibrium (not shown).

Cluster Analysis of Interannual Differences in Diatom Development

The cluster analysis on the observed monthly averaged diatom biovolume from Lake Baikal spanning from 1951 to 1999 revealed four distinct patterns of annual diatom biomass development: (1) a “no-bloom” cluster, characterized by no distinct phytoplankton bloom throughout the year (fig. 2*A*); (2) a “fall bloom” cluster, with no winter bloom but a bloom in fall with peak abundance in October (fig. 2*B*); (3) a “typical winter bloom” cluster, characterized by high winter bloom development with peak abundance in April (fig. 2*C*); and (4) a “delayed winter bloom” cluster, with peak abundance in May (fig. 2*D*). The peak abundance in the delayed winter bloom is, on average, slightly lower than the typical winter bloom. It should be noted that the analysis of the most parsimonious set of clusters suggested five distinct clusters; however, one of those clusters consisted of only a single year (1966) with no winter bloom and a bloom development in fall with peak abundance in September. Because of similar qualitative characteristics, we added the year 1966 to the fall bloom cluster. A nonmetric multidimensional scaling ordination on the same dissimilarity matrix supports the distinctness of the identified clusters (see fig. S3).

In line with model predictions, the average biomass of the grazer *Epischurella* in the preceding ice-free period is significantly lower in typical winter bloom years than in years with no or delayed winter blooms (fig. 2E; post hoc Tukey test, $P < .05$). A direct comparison of $\log_{10}$-transformed average *Epischurella* biomass of the preceding ice-free period (mg L^{-1}) and the $\log_{10}$-transformed diatom biovolume (μm^3 L^{-1}) at day of ice-off the same year over the whole study period also shows a significant negative correlation (fig. 3; $F_{1,45} = 11.12$, $P < .01$). Therefore, as in the model, higher *Epischurella* density in the preceding ice-free period precludes pronounced winter phytoplankton blooms. Although not significant, the length of the ice-covered period in delayed winter bloom years is lower than in no-bloom years (fig. 2*F*; post hoc Tukey test, $P < .1$).

Figure 4 shows the sequence of the no-bloom or fall, typical, and delayed winter bloom years from 1951 to 1999. While the first three patterns (no-bloom, fall, and typical winter bloom) appear throughout the investigated period, delayed blooms do not appear before 1974 but appear frequently after. There is no indication that the occurrence of the delayed winter bloom years is driven by the change in fixation method in 1973 to Lugol’s solution, which, in principle, could have led to an increase in the detection of small diatom cells but the size class distribution of the delayed bloom cluster is well within the range of the size classes detected for other clusters (fig. S4). In fact, the appearance of delayed winter blooms coincides with a significant shift in the Pacific Decadal Oscillation (PDO) from a cold to a warm phase (Hare and Mantua 2000) and is accompanied by less frequent occurrence of typical winter bloom years in Lake Baikal (fig. 4*A*; Izmest’eva et al. 2011; Katz et al. 2015). To ease the comparison of *Epischurella* abundances and ice duration with the occurrence

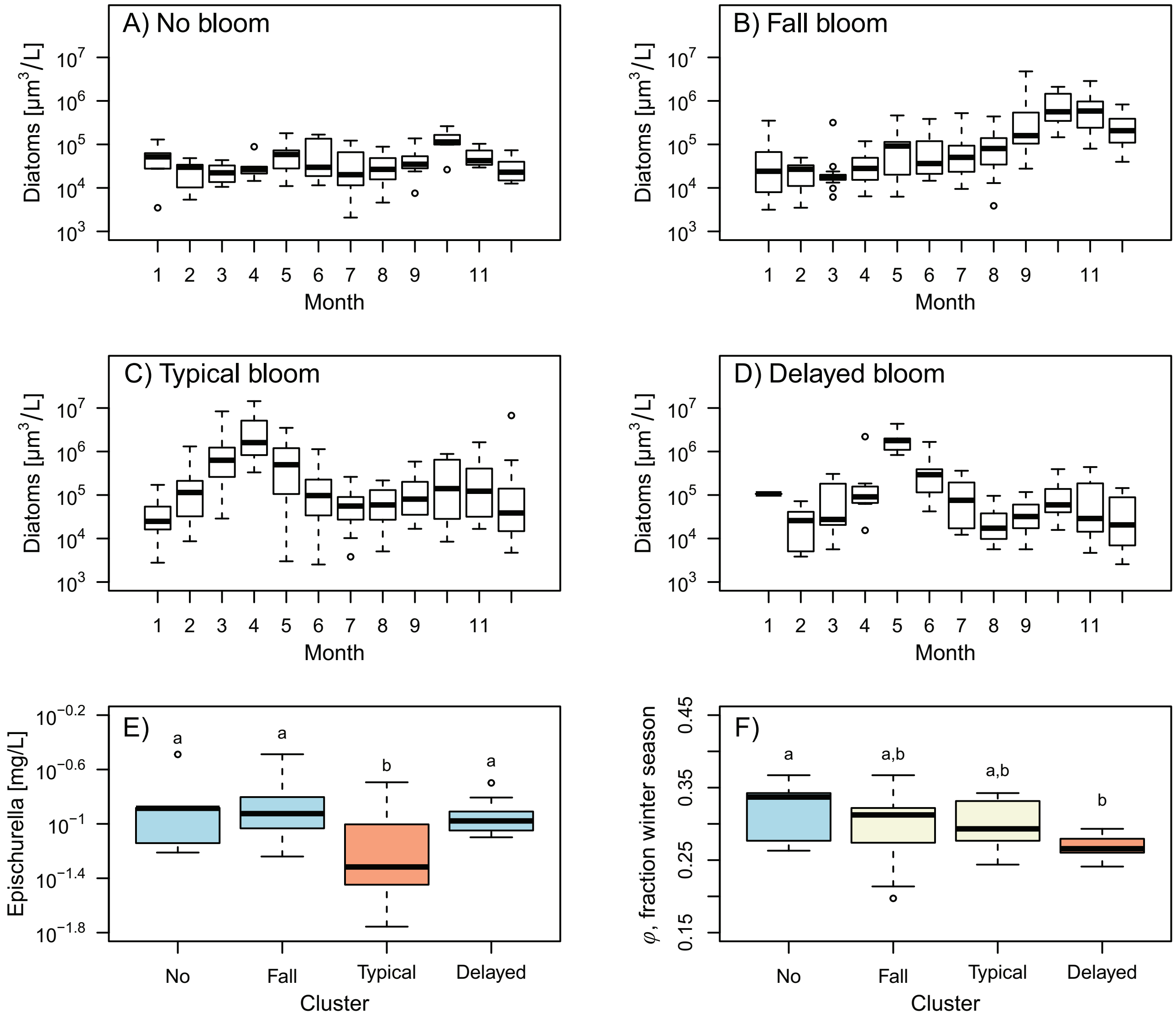

Figure 2: *A–D*, Distinct bloom patterns of yearly log$_{10}$-transformed diatom biovolume (μm^3 L^{-1}) for Lake Baikal from year 1951 to year 1999 as indicated by cluster analysis, differentiating no-bloom (*A*), fall bloom (*B*), typical winter bloom (*C*), and delayed spring bloom (*D*) years. *E*, *F*, Between-cluster differences with respect to log$_{10}$-transformed average *Epischurella* biomass (mg L^{-1}) of the preceding ice-free period (*E*) and ice duration (proportion of ice-covered days per year; *F*). Different letters indicate significant differences in the distribution of *Epischurella* biomass or ice duration between clusters.

of certain bloom clusters, for each year we show the log$_{10}$-transformed average *Epischurella* biomass of the preceding ice-free period (fig. 4*B*; mean $= 10^{-1.0}$ mg L^{-1}) as well as the ice duration (fig. 4*C*; mean = 107 days) as deviations from their average values.

Discussion

Our model shows that a gradual shift in seasonality, by mediating food web interactions, can lead to abrupt regime shifts in community dynamics. The predicted shifts from annual winter blooms, to 2-year cycles with winter bloom years alternating with delayed or no winter bloom years, to the complete absence of winter blooms with decreasing length of the ice-covered period highlight how seasonal forcing defines the temporal arena of the game played between interacting species. The model also highlights the fact that phytoplankton groups adapted to certain conditions (e.g., ice-covered period) may persist as those conditions become less common but ultimately disappear when they become too short in duration (the extinction of

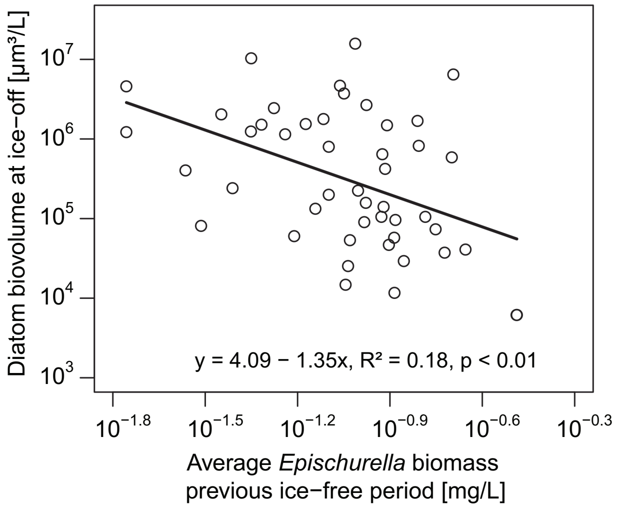

Figure 3: Correlation between $\log_{10}$-transformed average *Epischurella* biomass of the preceding ice-free period (mg L^{-1}) and the $\log_{10}$-transformed diatom biovolume (μm^3 L^{-1}) at day of ice-off for the years 1951–1999.

winter phytoplankton when the ice cover duration $\varphi = 0.2025$).

A regime shift has been defined as "a relatively sharp change from one regime to a contrasting one, where a regime is a dynamic 'state' of a system with its characteristic stochastic fluctuations and/or cycles" (Scheffer 2009, p. 357). Regime shifts can be classified as smooth, abrupt, or discontinuous (Collie et al. 2004; Scheffer 2009). In a smooth regime shift, the quantitative behavior changes approximately linearly with respect to the parameter, so a large change in the environmental parameter is required to result in a large change in the dynamic state. At an abrupt regime shift, the behavior changes nonlinearly, so even a small change in the environmental parameter can result in a large change in the dynamic behavior. Finally, at a discontinuous regime shift, the response is so nonlinear that it doubles back on itself, leading to multiple attractors and hysteresis (Scheffer 2009).

Our model illustrates all of these types of regime shifts (fig. 1*A*). For most of the range of φ, the behavior changes smoothly. Even across the bifurcation point between annual and 2-year cycles at $\varphi = 0.401$, the annual abundances do not vary greatly. There are two notable exceptions. First, the transition from alternating winter and delayed winter blooms to biennial winter blooms around $\varphi = 0.3$ is an abrupt regime shift, since this pronounced change in the dynamics occurs over a narrow range of parameter values. Second, the transition from biennial winter blooms to small annual winter blooms around $\varphi = 0.23$ is a discontinuous regime shift, due to the existence of multiple attractors and the discontinuous changes at the bifurcation points (see fig. S2 for a zoomed-in range of parameters). However, note that the range of parameter values with multiple attractors is quite narrow ($0.2271 < \varphi < 0.23$), corresponding to a range only 1.1 days wide, so there is little practical distinction between this discontinuous regime shift and an abrupt one.

Abrupt and discontinuous regime shifts may require certain model complexity, such as nonlinear interaction terms (Collie et al. 2004; Scheffer 2009; Wollrab and Diehl 2015) or more interacting species. To investigate what is responsible for the regime shifts we see, we looked at two variants of the model, one with linear functional responses (fig. S5) and one without grazers (fig. S6). Both of these simpler models show a smooth decrease in winter phytoplankton with decreasing length of the ice-covered period. Therefore, it appears that both nonlinear functional responses and the presence of predator-prey interactions are required for abrupt and discontinuous regime shifts in this system.

However, our main model is a simplification of the actual system, so correlations with observations have to be taken cautiously. To test the robustness of our model predictions, we examined the effect of some extra bits of realism (figs. S7, S8). The exact transition points between different regimes are influenced by the choice of the physiological parameter values. For example, reducing the nutrient/prey uptake rate of winter phytoplankton and consumer or taking into account reduced physiological rates at low temperatures would shift the observed thresholds to higher φ values—that is, even a smaller decrease in the length of the ice cover would lead to the absence of winter blooms (fig. S7). If we increase the physical realism of the seasonal forcing by including a well-mixed season (when the water column is not stratified) between winter and summer stratification periods, during which phytoplankton growth is set to zero, mimicking light limitation during the mixed period, the transition point is shifted to lower φ values for the default parameterization or remains similar in case of decreased winter growth (fig. S8). The investigation of model dynamics for different parameter settings, either with or without a well-mixed period, showed that the main outcome was preserved under all scenarios, namely, transitions from regular winter blooms to irregular and finally to a complete absence of winter blooms.

These models also predict an earlier disappearance of the winter bloom compared with the model with abiotic forcing only (fig. S6). This suggests that biotic interactions, such as predator-prey, can exacerbate the negative effects of climate change on the abundance of vulnerable, winter-adapted taxa. Studies in other systems also suggest that various biotic interactions may mediate species

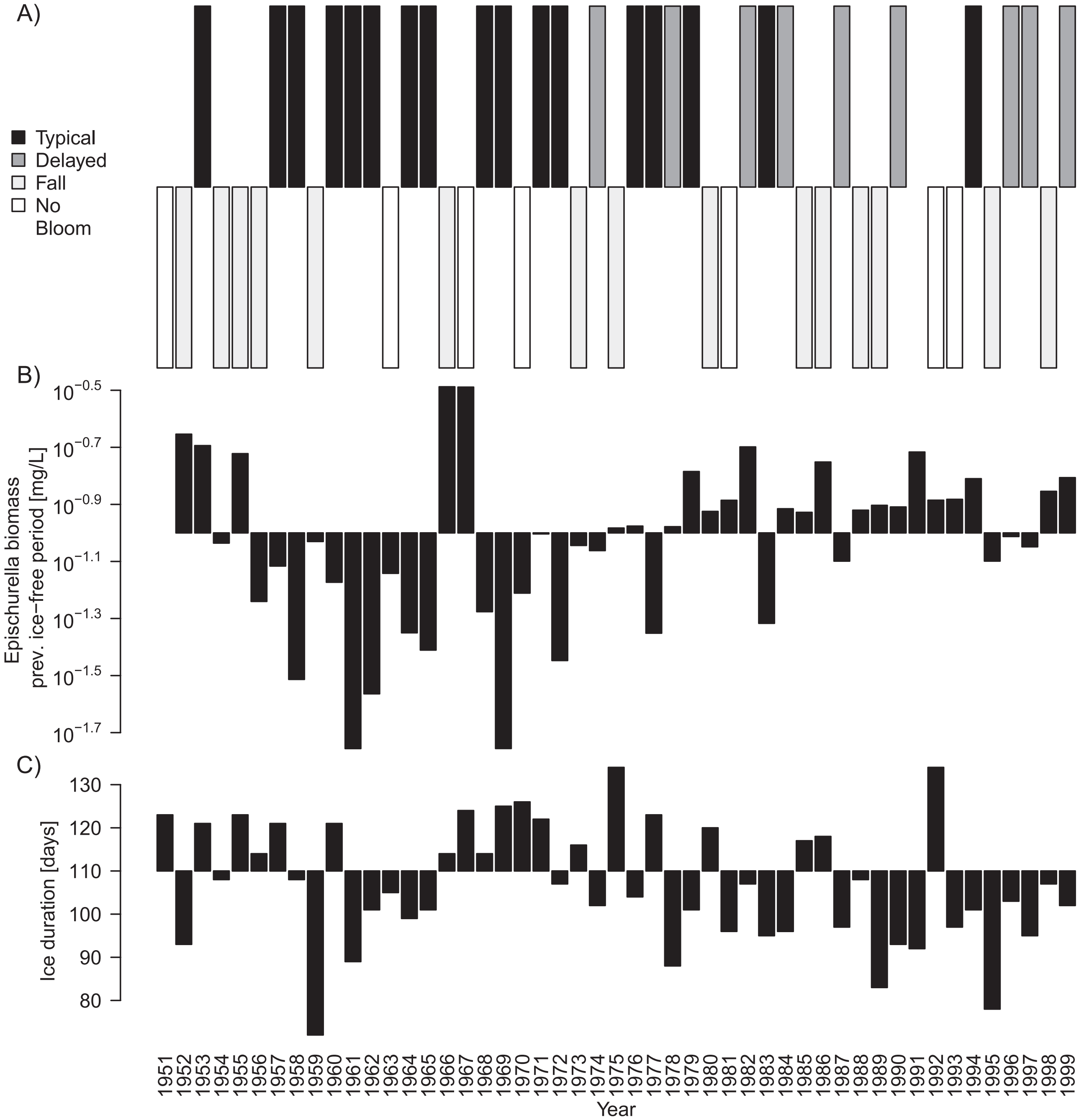

Figure 4: Time course from 1951 to 1999, showing sequence of no-bloom (white), fall bloom (light gray), typical bloom (black), and delayed bloom (dark gray) years (*A*); corresponding $\log_{10}$-transformed average *Epischurella* biomass of the previous ice-free period (mg L^{-1}) centered around the average of $10^{-1.0}$ mg L^{-1} (*B*); and ice duration of the same year (days) centered around the average of 110 days (*C*). Note that average *Epischurella* biomass indicated at year *i* illustrates the average *Epischurella* biomass of the previous ice-free period, reaching back to year $i-1$.

responses to climate change (HilleRisLambers et al. 2013; Engelhardt et al. 2020). Our model provides an example of the joint influences of biotic interactions and changing climate on the persistence of different species.

Previous studies linked the occurrence of the winter bloom years to cold and warm phases of the PDO and pre-ice weather conditions affecting ice transparency (Katz et al. 2015). In its current version, our model assumes clear ice conditions and, therefore, does not include the influence of ice clarity on light availability for phytoplankton growth. Low light levels might limit under-ice phytoplankton growth even in the absence of strong top-down control and could potentially disrupt a predicted high winter bloom year (Katz et al. 2015). This might explain the absence of winter blooms in some of the years with long ice coverage.

The observed correlation between typical winter blooms and low *Epischurella* biomass, as well as absent or delayed winter blooms and high *Epischurella* biomass in the preceding ice-free period in Lake Baikal, supports the key model prediction that consumers in the previous season inhibit winter bloom formation. Thus, while the ice clarity (not included in our model) can make a large bloom possible (Katz et al. 2015), the level of consumer pressure is likely a determinant of how large that winter bloom can become.

The described feedback mechanisms that operate across seasons and give rise to 2-year cycles depend on the ability of the consumer to control its prey species. In the absence of this top-down control, phytoplankton dynamics would just follow the length of their respective growing season (fig. S6; see also Klausmeier 2010). Top-down control might be weakened if some algae are less edible or completely inedible. There is some evidence that larger diatom species, typically occurring in Lake Baikal, are not as easily edible by *Epischurella* as other phytoplankton (Moore et al. 2019). Indeed, Bondarenko et al. (2006) have suggested that *Epischurella* in Lake Baikal actively avoids areas of highest *Aulacoseira* density under ice because of the propensity of this alga to form mucus-rich aggregations that may interfere with copepod feeding. However, our own observations of the gut content of *Epischurella* confirm that *Aulacoseira* is consumed (D. R. O'Donnell and E. Litchman, personal communication). Baikal's *Epischurella*, similar to other copepods, has shown strong preference for ciliates in summer assemblages, obtaining 96%–98% of their carbon from ciliates and the remainder from small diatoms such as *Synedra* (Moore et al. 2019). Whether such trophic pathways shift under ice is currently untested. Melnik et al. (2008) describe a complex assemblage of micrometazoans associated with under-ice algae in Baikal, creating considerable uncertainty about winter trophic interactions. Nevertheless, the assumption that winter phytoplankton dynamics in Lake Baikal is, at least in part, under top-down control is supported by the significantly negative relationship between the average *Epischurella* abundance during the previous ice-free period and the phytoplankton abundance at the day of ice-off. While future studies could investigate seasonal dynamics of a more highly resolved planktonic food web model, ciliates should ideally also be a part of regular monitoring programs.

During the last century, the average ice duration at Lake Baikal declined from around 120 days per year in the early 1900s to 105 ice-covered days per year by the end of the twentieth century (fig. 4*C*). Simultaneously, the typical bloom pattern reported for Lake Baikal, characterized by large winter blooms of endemic diatoms and less pronounced summer blooms, is changing toward a decreased frequency of winter bloom years (Hampton et al. 2008). The cluster analysis of phytoplankton (diatom) periodicity in Lake Baikal conducted in this study reveals significant changes in bloom patterns during the second half of the twentieth century. Most importantly, it shows a shift from the years with pronounced regular winter blooms to a less frequent occurrence of delayed bloom years in the mid-1970s. This change coincides with a shift from a cold to a warm PDO phase, which led to a significant increase in annual temperatures experienced at Lake Baikal (Hare and Mantua 2000; Katz et al. 2015) and a drop in the average duration of the ice-covered period to 105 days per year. The observed trend toward less frequent winter blooms for Lake Baikal over the investigated time period is in line with the predicted shifts in our model analysis. With a further decrease in the average length of the ice-covered period, winter blooms may disappear completely. This would put the mostly endemic, under-ice bloom-forming phytoplankton species in Lake Baikal at a disadvantage (Izmest'eva et al. 2011), with consequences for the whole food web, biogeochemical cycling, and energy transfer.

In the absence of winter blooms, phytoplankton phenology will shift to bloom dynamics typically observed in temperate lakes, which start with the onset of the stratified period (after ice-off) as described in the Plankton Ecology Group (PEG) model (Sommer et al. 1986; Sommer et al. 2012). The PEG model has been very influential in the description of regular bloom patterns for temperate lakes with moderate periods of ice coverage (Sommer et al. 1986). It describes the regular sequence of spring bloom formation through fast-growing, most edible phytoplankton species, followed by a clear water phase resulting from grazing pressure by zooplankton and a second bloom in (late) summer formed by less edible phytoplankton species (Sommer et al. 1986). A recent update of the PEG model also includes the influence of overwintering zooplankton on spring bloom formation (Sommer et al. 2012) but still assumes repeating yearly patterns, overlooking the potential for more complex dynamics playing out across seasons and years. However, previous models have shown that interannual feedbacks can result in regular and irregular multiyear cycles when the diamond food web at the heart of the PEG model is subject to annual forcing (Evans 1988; Klausmeier and Litchman 2012), similar to our model. To date, not much attention has been given to this phenomenon in empirical studies, but there is some evidence for the relevance of interannual spillover effects, as predicted by Klausmeier and Litchman (2012), where high cyanobacterial blooms at the end of the year dominate the spring bloom in the following year (Deneke and Nixdorf 1999).

The results of this study show that the length of ice cover and consumer abundance can jointly determine the timing and magnitude of phytoplankton winter bloom. The seasonally forced model gives a general insight into the connection between abiotic forcing and biotic interactions and the corresponding interseasonal relationships, which is relevant not only for Lake Baikal but for other deep lakes in the temperate zone. Deep lakes experience more pronounced declines in the duration of the ice-covered period than shallow lakes (Bernhardt et al. 2012; Kirillin et al. 2012). Coherent responses in phytoplankton and zooplankton phenology (i.e., the timing of biomass peaks) with respect to temperature regimes influenced by the North Atlantic Oscillation have been observed across large parts of Europe, supporting the close coupling between plankton dynamics and environmental forcing (Weyhenmeyer et al. 1999; Gerten and Adrian 2000; Straile 2002; Blenckner et al. 2007; Straile et al. 2012). The lack of a coherent response in phytoplankton biomass levels has been argued to be caused by interactive effects of environmental forcing and top-down control through grazers (Straile 2000). Similarly, experimental warming during spring phytoplankton development lead to lower phytoplankton spring biomass and have been explained by a stronger top-down pressure (Sommer et al. 2015). All of these studies suggest that changes in plankton dynamics resulting from changing temperature regime can be understood only when taking into account biotic interactions.

Models of species' range shifts under climate change have shown that including not only abiotic forcing but also biotic interactions changes the predictions (Preston et al. 2008; Jaeschke et al. 2012; Engelhardt et al. 2020). Theoretical studies of seasonally forced predator-prey dynamics that take into account shifts in seasonality due to climate change are rare but also show strong responses of food webs to moderate changes in climate. For example, a dynamic model of the Arctic terrestrial vertebrate predator-prey food web predicts that even a moderate change in the timing of snow melt may cause local extinctions of some predator species (Gilg et al. 2009).

Our model provides a general insight into shifts in community composition and predator-prey dynamics along gradual changes in abiotic forcing, not only for lake systems but also for terrestrial systems with seasonally adapted primary producers and general consumers. At present, mechanistic models integrating winter and summer processes over several consecutive years are largely missing but would be essential for explaining community dynamics in temperate and arctic regions (Vadadi-Fülöp et al. 2012). Future modeling studies that include other environmental factors and more complex food webs will further improve our ability to understand and predict shifts in community dynamics under climate change.

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Statement of Authorship

S.W., C.A.K., and E.L. designed the study; S.W. and C.A.K. performed the modeling work; E.A.S. and L.I. provided the empirical data; S.W. performed the statistical analyses; and S.W., C.A.K., E.L., and S.E.H. interpreted the results. S.W. wrote the first draft of the manuscript, and all authors contributed substantially to revisions.

Data and Code Availability

Biological data are part of a historic Russian data set registered with the Russian government (2005620028). Data published with this article are based on (1) phytoplankton data from Lake Baikal registered with the Russian government (2014621482; Irkutsk State University; Federal Service on Intellectual Property; Database on the State of Phytoplankton of Lake Baikal, L. R. Izmest'yeva, S. V. Shimaraeva, and E. A. Silow [2014620772; accepted June 6, 2014; registered October 23, 2014, in the database register]) and (2) zooplankton data from Lake Baikal registered with the Russian government (2015621067; Irkutsk State University; Federal Service on Intellectual Property; Database on the State of Zooplankton of Lake Baikal, L. R. Izmest'yeva, S. V. Shimaraeva, E. V. Pislegina, and E. A. Silow [2015620296; accepted April 1, 2015; registered July 13, 2015, in the database register). Biological data used in the article are available via the Dryad Digital Repository (https://doi.org/10.5061/dryad.4b8gthtbb; Wollrab et al. 2020). Data on timing and duration of the ice-covered period on Lake Baikal can be accessed through the Global

Lake and River Ice Phenology Database (http://nsidc.org/data/g01377).

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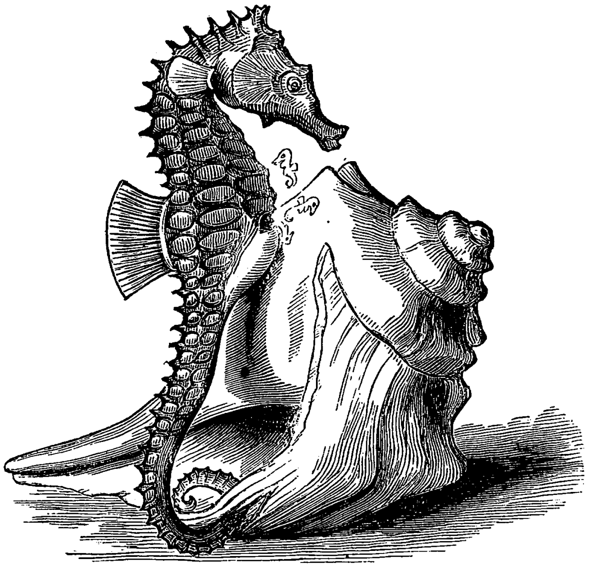

"But, perhaps, more curious is that distinction drawn from their mode of reproduction; a trait so strange, as to suggest the seemingly abnormal habits of the Marsupials,—the Opossum and the Kangaroo,—although the eccentricity of the fish is far greater than that of the land marsupial; for, in the latter, it is the female whose pouch receives the immature young, and which are therein nourished to complete their development. The parental relation of the female Lophobranch, however, is restricted to the simple emission of the unimpregnated eggs." From "The Sea-Horse and its Young" by Samuel Lockwood (*The American Naturalist*, 1867, 1:225–234).