The “Melosira years” of Lake Baikal: Winter environmental conditions at ice onset predict under-ice algal blooms in spring

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Abstract

Winter primary production in seasonally ice-covered lakes historically has not been well studied, but it is increasingly recognized as an important component of lake metabolism. Lake Baikal in Siberia is not only the World’s oldest, deepest, and most biologically diverse lake, but also where large under-ice blooms of the diatom Aulacoseira baicalensis (formerly Melosira) occur in some years. The phenomenon of “Melosira years” is noteworthy both for the intensity of the diatom blooms, in which total under-ice production can be a majority of total annual production, and for the enigmatic regularity of their occurrence every 3–4 yr. The degree to which these episodic blooms might be controlled by external forcing and endogenous lake processes has been debated for decades. We used a 50-yr time series of phytoplankton observations to statistically model the occurrence of Aulacoseira blooms as a function of meteorological and climatological predictor variables. The results support the hypothesis that a confluence of meteorological conditions in the preceding fall season, which favor clear ice formation with minimal snow cover, also favor Aulacoseira blooms in the following spring. Further, we observe that this confluence of factors is related to relatively strong states of the Siberian High which, while not strictly periodic, do explain a significant fraction of the interannual bloom pattern. Finally, our analyses show that the timing of the peak abundance of A. baicalensis shifted 1.6 months later across the 50-yr time series, corresponding with the delay in ice-on timing that has been associated with climate change.

Freshwater scientists worldwide increasingly recognize that winter biota may play a larger role in whole-lake productivity and trophic dynamics than was previously appreciated (Salonen et al. 2009; Bertilsson et al. 2013; Hampton et al. 2015). Even with some snow cover, ice can transmit sufficient light for photosynthesis (Cota 1985), while also providing a substrate for algal growth in the photic zone (Bondarenko et al. 2006). Further, solar heating of water beneath patches of snow-free ice can drive convective mixing, sometimes but not always keeping algal cells and nutrients suspended in the photic zone (Granin et al. 2000; Jewson and Granin 2014). Indeed, phytoplankton blooms below the ice in late winter-early spring have been reported for multiple lakes including Lake Erie (Twiss et al. 2012), Grand Traverse Bay in L. Michigan (Vanderploeg et al. 1992), lakes in central Japan (Maeda and Ichimura 1973), and Lake Baikal (Yasnitsky 1930; Antipova and Kozhov 1953; Kozhov 1955). Although under-ice blooms in lakes are acknowledged, their contribution to annual productivity, and the drivers that determine their occurrence and magnitude are poorly understood.

In Lake Baikal, the substantial contribution of the under-ice algal bloom to annual primary production has long been evident because blooms are both occasionally extreme and also well documented with long-term monitoring at a sampling frequency of 10–14 d throughout the year. In spite of ice thickness sometimes exceeding 1 m, the ice clarity at Lake Baikal can allow light penetration that fuels photosynthesis during the months of February–May when day length is increasing (Straškrábová et al. 2005; Jewson et al. 2009). In

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years of unusually intense under-ice phytoplankton growth, annual rates of primary production can exceed that of low production years by twofold to ninefold (Yoshida et al. 2003). Likewise, under-ice algal biomass in Lake Baikal exhibits large interannual variation ranging from less than 0.1 g m\(^{-2}\) to values in excess of 8.0 g m\(^{-2}\), with the correlated chlorophyll \(a\) measurements varying three orders of magnitude—the highest rates of production being comparable with those for a eutrophic lake (Kozhova and Izmest’eva 1998; Popovskaya 2000).

The large under-ice blooms in Lake Baikal are often characterized by high abundance of the diatom *Aulacoseira* (formerly *Melosira*) *baicalensis*, one of the largest freshwater planktonic diatoms (Jewson et al. 2010). Achieving filament lengths greater than 1 mm, this pelagic species sometimes attaches to the underside of ice forming strings more than 10 cm long which, when dislodged by currents, sink to the lake bottom where they presumably nourish the benthos (Bondarenko et al. 2006). In this way, the production of both ice-attached and planktonic *A. baicalensis* is thought to contribute to the pelagic and benthic food webs of Lake Baikal (Bondarenko et al. 2006). For decades, the years of the most conspicuous blooms (abundance could be 100-fold higher than in non-bloom years), termed “Melosira years” in the Lake Baikal literature (e.g. Antipova and Kozhov 1953; Kozhov 1955), recurred with apparent regular periodicity of 3–4 yr.

Although the ecological importance of these under-ice blooms in L. Baikal is recognized, the mechanisms causing the blooms, and particularly their seemingly periodic nature across years, remain a mystery. Hypotheses advanced to explain the occurrence of Melosira years range from those focused mostly on internal lake dynamics (Kozhov 1955; Kozhova 1961) to those addressing primarily external, meteorological factors (e.g. Shimaraev 1971), and even to astromonic phenomena (e.g., Bondarenko and Evstafyev 2006). Kozhov (1955, 1963) was perhaps the first to address the drivers of Melosira years, and focused on dynamics within the lake. He found no evidence for nutrient controls of *Aulacoseira* blooms but suggested that water temperatures in the months leading up to ice cover might create favorable conditions for exceptional blooms if they promoted retention of a larger “seed bank” of *Aulacoseira* cells in the photic zone. In contrast, Kozhova (1961) suggested that a suite of variables within the lake were acting in concert to produce Melosira years, including light availability (e.g. in relation to snow depth and snow removal by wind), nutrients, and possibly an intrinsic biological cycle. The suggestion of a biological cycle was the first of several papers highlighting biological dynamics that could produce apparent periodicity in *Aulacoseira* blooms. For example, previous research on *Aulacoseira* suggested life history, including variation in sexual and asexual reproduction, explained much of the variability in population dynamics (Jewson et al. 2008; Jewson and Granin 2014), and indeed may have contributed to 3- to 4-yr population cycles (Jewson and Granin 2014).

Beginning in the early 1970s, external, meteorological drivers of *Aulacoseira* blooms and their influence on ice conditions became the focus of considerable research. Using 24 yr of Lake Baikal data, Shimaraev (1971) proposed that conditions in autumn prior to the bloom were important in distributing nutrients and *Aulacoseira* cells that would later seed the bloom, and also create the conditions for clear or cloudy ice that would strongly influence light availability during spring growth. This emphasis on ice and its influence on mixing conditions were echoed by Semovski et al. (1998) who modeled under-ice light conditions based on AVHRR imagery of ice-covered Lake Baikal, and compared these estimates to diatom samples between 1994 and 1998. Experimental and observational explorations of the importance of light conditions for *Aulacoseira* (Jewson et al. 2009, 2010) drew attention to not only light limitation for photosynthesis but also the role of light in promoting under-ice mixing, and thus access to nutrients in deeper water, leading to the conclusion that the light-*Aulacoseira* relationship is more complicated than previously appreciated. Both too much and too little light under ice depress *Aulacoseira* growth, and optimum conditions might be produced with a snow depth <10 cm. Mackay et al. (2006) reported that a high proportion of variation in *Aulacoseira* abundance was explained by ice coverage characteristics (white/clear/wet/snow-covered ice) and duration.

In summary, multiple investigations of *Aulacoseira* dynamics have invoked ice conditions as a key to producing Melosira years (Kozhov 1955, 1963; Kozhova 1961; Shimaraev 1971; Kelley 1997; Semovski et al. 1998; Mackay et al. 2006; Jewson et al. 2009, 2010). Furthermore, these studies suggested that meteorological conditions, through their influence on ice conditions, helped to produce the “goldilocks” environment in which light and convection are “just right” for a Melosira year to occur. Many of these previous investigations, however, were limited by the short duration of in situ records that constrained both the range of conditions that could be observed and the power of a multivariate analysis. Here, we use 50 yr of detailed limnological data from Lake Baikal, and corresponding meteorological data to perform a more powerful multivariate analysis than has been possible previously. Our results show that a suite of environmental conditions in early winter near the time of ice onset, in turn driven in part by larger scale climate variability, predict the occurrence of *Aulacoseira* blooms in spring. The drivers are sufficiently generic that we may expect them to influence the timing and magnitude of under-ice blooms in other lakes with little snow cover and clear ice.

**Materials and methods**

**Overarching approach**

A diverse range of environmental and climate time series data were used to build multivariate predictor sets for the
occurrence of Melosira years. Melosira years were defined as those years when observed counts of *A. baicalensis* in the spring (April, May, or June) exceeded 10 cells per milliliter as per Antipova and Kozhov (1953). Blooms of *A. baicalensis* typically begin under the ice in March and can extend into June when the lake is ice-free and undergoing wind-induced mixing to depths of 250 m during spring homeothermy (Moore et al. 2009). Environmental and climate time series data were used in a multivariate logistic regression, where spring blooms of *A. baicalensis* were scored a 1, and non-blooms were scored a 0.

The multivariate predictor sets were selected to evaluate the hypothesis that climate-driven ice conditions strongly influence the occurrence of Melosira years in Lake Baikal, such that both intra-annual and longer term relationships between blooms and physical conditions can be detected. In the south basin, where data for these analyses were collected, ice cover lasts 4 months beginning in mid-January and ending in mid or late May. Models were developed along two lines; one examining the intra-annual relationship of Melosira bloom occurrence with meteorological factors that influence ice formation, and a second line of inquiry focused on the interannual, multidecadal pattern of Melosira years and its interactions with signals of longer-term climate variability. Accordingly, one set of predictor variables was comprised of meteorological variables that represent local contemporary conditions expected to correspond with intra-annual limnological processes, lacking mechanisms for year-to-year “memory.” A second set of predictors includes climate teleconnection indices (low dimension indices of large-scale, complex patterns in atmospheric circulation) which, in integrating over larger scales and longer times, are more reasoned candidates as predictors of interannual pattern of Melosira years.

Once the best performing models were estimated using the data from 1951 to 1997, their predictive performance was tested against a list of Lake Baikal *Aulacoseira* bloom years obtained a posteriori as test data from 1997 to 2009.

**Lake Baikal datasets**

Surface water temperature and algal density data have been collected on a schedule of 10–14 d at the same location on Lake Baikal, 7.2 km from the village of Bol’shie Khot at 51.880°N and 105.084°E (maximum depth 800 m) since January 1946, but with an irregular schedule prior to January 1948 (Kozhov 1963; Izmest’eva et al. 2006; Hampton et al. 2008). Discrete depths of 0 m, 5 m, 10 m, 25 m, 50 m, 100 m, 150 m, 200 m, and 250 m are typically sampled with a 10-L Van Dorn bottle for temperature measurement and phytoplankton sampling in this monitoring program; given our focus on ice-associated blooms, we used the time series of water temperature averaged from 0 m to 10 m and phytoplankton counts summed over the top 10 m. Water temperature is measured using a mercury thermometer in a Van Dorn bottle. For these analyses, we constructed the time series of monthly mean values assuming that all months are the same length ($\Delta t = 0.0833$ yr), and report temperature values as arithmetic means for each month. Because air temperature and water temperature were highly correlated at a lag of 2 months (air leading water), the monthly water temperature values were deseasoned by subtracting the long-term average for each month from the value of each monthly mean; the residuals produced a time series of water temperature anomalies.

Phytoplankton were collected and quantified starting in January 1946, and we analyzed the dataset through December 1997. Prior to 1973 phytoplankton samples were fixed in formalin, and with Lugol’s solution after 1973. Due to the hard siliceous cell wall of *A. baicalensis* and the profound differences in cell density between Melosira years and non-Melosira years it is unlikely that the change in fixative resulted in a misdiagnosis of a Melosira bloom. Thus, the time series was treated as continuous. Melosira density is reported as the log of the average density for the month plus one.

Daily values for air temperature were observations from meteorological station 30710, located near Irkutsk, Russia at 52.267°N and 104.317°E. Continuous data from January 1945 to present were downloaded from http://climexp.knmi.nl. Daily data within each month were averaged to estimate a monthly mean.

We anticipated that surface winds influence ice characteristics and snow accumulation that in turn affect the under-ice environment. Lacking consistent wind data for this period and spatial domain, we used a proxy. Surface winds result from pressure gradients driven both directly by large scale differences in surface level pressure (SLP), and indirectly by temperature differences (Sverdrup et al. 1942; Johnstone and Mantua 2014). At Lake Baikal, as elsewhere, large atmospheric pressure systems driving surface winds themselves advect, such that SLP measured at a fixed location will have variances on daily to monthly time scales expressing the passage of pressure gradients. The monthly variance in SLP was used as a proxy for winds by leveraging the inference that lower variance reflects fewer pressure systems traversing the lake and fewer wind events in the month, parallel with prior use of SLP as a proxy index for surface winds (Johnstone and Mantua 2014). SLP were obtained from the National Centers for Environmental Prediction and the National Center for Atmospheric Research (NCEP/NCAR) reanalysis model data, downloaded from National Oceanographic and Atmospheric Administration’s (NOAA) Earth System Research Laboratory (http://www.esrl.noaa.gov/psd/data/reanalysis.shtml). Reanalysis data were obtained for daily averages of 6-hourly estimates over a region that covered the area sampled for water temperature and algal density (103.75°E to 106.250°E; 51.25°N to 53.75°N) for the period 1 January 1945 to present. All of the values for that spatial domain were...
averaged, and daily values were then averaged to obtain a monthly mean and a monthly variance (of daily means) in SLP.

Time series of Julian day of ice-on and ice-off were obtained from the Global Lake and River Ice Phenology Database (http://nsidc.org/data/g01377). Snow depth data at an Irkutsk station were obtained from the Historical Soviet Snow Depth dataset (Armstrong 2001) (www.ncbi.nlm.nih.gov). The Irkutsk station was the available location in closest proximity (67 km) to the main Baikal biological station. While snow conditions on the lake likely differ from conditions in Irkutsk, we expected that conditions at Irkutsk would correlate positively with those at the lake and thus provide an index of Baikal snow conditions.

**Climate indices**

Previous studies suggested that *Aulacoseira* blooms occur with apparent regular periodicity of 3–4 yr (e.g., Shimaraev 1971); thus, we included several climate teleconnection indices as possible covariates or predictors that could explain larger-scale, interannual patterns of variance. In this study, we evaluated the performance of the Arctic Oscillation (AO), Pacific Decadal Oscillation (PDO), and Siberian High Index (SHI) indices as predictors, potentially contributing large-scale, temporally organizing climate processes to the monitoring data at Lake Baikal.

AO and PDO monthly time series were obtained from public data servers at the Joint Institute for the Study of Atmosphere and Ocean (http://jisao.washington.edu/). Prior work has suggested that climate indices such as the PDO and AO, which are representations of patterns in pressure, temperature and flow, interact physically and statistically (Strong and Magnusdottir 2009; Katz et al. 2011). Therefore, we used both the winter averages (NDJFMA) of PDO and AO index values, and a binary 0 or 1 to represent their relative phases. For example, the PDO was in a “cool” phase from 1961 to 1975, and in a “warm” phase from 1988 to 1992 (Hare and Mantua 2000; Bond et al. 2003); in this analysis, a binary PDO index was created that was 1 from 1961 to 1975, and 0 from 1976 to 1988, and similarly coded for the other “cool” and “warm” eras.

SHI is the standardized time series of SLP averaged over the area defined by 40°–60° N and 80°–120° E, and is normally averaged for the months of December, January, and February to provide a winter (DJF) index of pressure systems in eastern Siberia (Trenberth and Paolino Jr. 1980; Panagiotopoulos et al. 2005). We estimated SHI from monthly SLP observations (Trenberth and Paolino Jr 1980), updated and available from the Climate Explorer at the Royal Netherlands Meteorological Institute (KNMI; http://climexp.knmi.nl). The standard representation of SHI is problematic for two reasons. First, the DJF index occurs contemporaneously or in some cases after the ice forms on Lake Baikal, and so is expected to have little predictive power within a season. Therefore, we constructed an alternative SHI (SHI<sub>D</sub>) composed of the standardized average of SLP over the same geography, but additionally including November (NDJF) to use in our statistical analysis. Second, the SHI is not stationary, with the mean value drifting downward beginning in the mid-1980s (Panagiotopoulos et al. 2005). Thus, we also differenced the NDJF SHI at lag 1 yr (= SHI<sub>D</sub>) to produce a more stationary time series that reflects relative change of this early-winter index of SLP year to year (Supporting Information Fig. S1).

**Statistical analysis and model cross-validation**

To examine intra-annual factors associated with diatom blooms, we constructed logistic regression models that estimated the likelihood of a Melosira year as a function of environmental predictors. Anticipating that these spring bloom events were the consequence of environmental states in the previous fall and winter (see below), we evaluated and employed time lags in our models. Consequently, the continuous monthly data in the predictor sets were reduced to single samples from specific months within each year, and were discontinuous year to year; none of the ordinal predictor data decimated in this manner demonstrated significant temporal autocorrelation.

When combined with the large number of potential predictor variables and their various interaction terms, the variety of potential lags among the predictor variables created a diverse and potentially unwieldy number of candidate models to be evaluated. To avoid using exhaustive model selection to indiscriminately search for candidate hypotheses (Burnham and Anderson 2002), we performed a preliminary screening of bivariate and trivariate relationships using graphical methods (Winfree 2001). This approach, used to evaluate numerous aspects of interacting periodic, or near-periodic systems, allows rapid screening of interacting sets of potentially entraining driver variables; it leverages the power of visual inspection to detect pattern, but lacks the power of an explicit statistical test (Winfree 2001). In this case, *Aulacoseira* counts were plotted against all environmental predictors over a range of lags, and the resulting plots were evaluated visually for the presence of recognizable structure in the data, such as bimodal distributions, break-points, or separable relationships in bloom and nonbloom years (i.e., “V”-shaped distributions or helices when projected in three-dimensional). Candidate lags were identified for each of the predictor variables, and these served as the starting point and limited subset of the potential model space for a model selection process that evaluated all combinations of main effects, 2-way and 3-way interaction terms.

Models were ranked using corrected Akaike Information Criteria (AICc) (Burnham and Anderson 2002), where a given model was deemed superior to an alternative if ΔAICc > 2, and the “best” model had the lowest AICc. The magnitude and direction of the effects of consistent predictors were estimated by model-averaging the top performing models (ΔAICc < 2) using Akaike weightings in the model averages (Burnham and Anderson 2002). Goodness of fit in logistic
regression is an unresolved issue, and several approaches have been suggested to evaluate model performance (Cohen et al. 2013; Tjur 2009). Here, we evaluated goodness of fit with both a coefficient of determination ($r^2$ in the sense of Cohen et al. 2013) and a coefficient of discrimination (sensu Tjur 2009); however, in this case both were highly correlated so results are reported as coefficient of discrimination ($r^2_{corr}$) (Tjur 2009).

Significance tests for $r^2$ in logistic regression specifically, and post hoc hypothesis tests in combination with information theoretic measures in general, are also a matter of some debate. For example, given that observations are binary but the model outputs are continuous bounded odds ratios of observing the events, the meaning of fractional variance explained is ambiguous—that is, the events either happened or they did not, regardless of the odds of their occurrence. An alternative measure of model performance is the area under the curve (AUC) of a receiver operator characteristics (ROC) curve (Mason and Graham 2002). Originally developed in analysis of communications, ROC curves plot the rate of correctly forecasting an event against the rate of falsely forecasting an event that did not occur; the better the forecasting model, the greater the ratio of correct to incorrect forecasts, and the larger the AUC. Expectations for AUC follow a Mann–Whitney $U$-distribution (Bamber 1975; Mason and Graham 2002), and AUC is incorporated into the test statistic as:

$$ U = \text{AUC} \times n_1 n_2 $$

where $n_1$ and $n_2$ are the number of observations with events and nonevents, respectively (Mason and Graham 2002). Significance was evaluated by permuting the observations, recalculating the AUC, and generating a distribution of $U$ values; the fraction of area above the observed test statistic value within the permuted distribution was the probability of this test statistic value, or a higher one, occurring by chance.

The analyses were initially performed on $A. \ baicalensis$ monthly time series data which spanned 1948 to 1997; subsequent to this we obtained a list of Melosira years for the period 1997–2009. We were then able to use the earlier time series as “training data” to estimate the statistical relationships between meteorological data and diatom blooms. The quality of the resulting statistical models was then evaluated with cross validation, where meteorological variables were used to “forecast” blooms in the period 1997–2009 and compared with a list of bloom and nonbloom years for $A. \ baicalensis$ for this period where we lacked monthly diatom counts. Measures of model performance over the 1997–2009 “test data” included Precision, which is the ratio of True Positives to the sum of True Positives and False Positives. True Positives are years the model forecast a diatom bloom and it happened and False Positives are years the model forecast a diatom bloom and it did not happen. Model performance was also evaluated with Accuracy, defined as the ratio of the sum of True Positives and True Negatives to Total Outcomes. True Negatives are years the model forecast no bloom and it did not happen (Fawcett 2006). All statistical methods were performed in the R environment for statistical computing (Ver. 3.0.3) (R Core Team 2015).

**Results**

Evaluation of monthly $Aulacoseira$ time series reveals much of the same temporal structure that has lead previous researchers to identify the presence of “periodic,” or perhaps more accurately, episodic under-ice blooms. Aggregating monthly values into a time series of annual sums (Fig. 1a) reveals a pattern of Melosira years similar to those reported previously (Kozhova 1961; Evstafyev and Bondarenko 2007; Silow et al. 2011), but examination of superimposed monthly means reveals a more diverse pattern of $Aulacoseira$ bloom dynamics. The large-scale, interannual patterns in the data are essentially the same; a power spectrum estimated for both monthly and annual data demonstrated similar distributions of energy in the overlapping range of harmonics (Fig. 1b). Both datasets revealed large power in the 3.6 and 4.2 yr/cycle bands that have previously been cited in defining the “periodic” pattern of Melosira years, and in relating the timing of diatom blooms to larger scale periodic phenomena (e.g., Kozhova 1961; Votintsev 1961).

However, closer examination reveals additional information in the higher resolution monthly data. First, not all bloom years are the same; 1982 for example, was characterized by a single, discrete spring peak, but 1961 was characterized by several, smaller peaks occurring throughout the spring (Fig. 1a). In addition, over the course of the 50-yr time series, the spring bloom of $A. \ baicalensis$ occurred progressively later in the year. The slope of the relationship between month of peak $A. \ baicalensis$ counts and year (Fig. 2a) was positive and significant, indicating a shift of 1.6 months later for maximum $A. \ baicalensis$ abundance ($r^2 = 0.18, p < 0.001$). This shift coincides with the progressive delay in ice-on timing (Magnuson 2000) (Fig. 2b), and provides further support for hypotheses that $A. \ baicalensis$ blooms are related to ice formation. The correlation between day of ice-on and month of diatom bloom was positive and statistically significant ($r^2 = 0.14, p < 0.001$), but the different temporal resolutions (daily vs. monthly) limit more detailed interpretation of this correlation.

Any hypotheses that link spring blooms of $A. \ baicalensis$ with prior fall or winter conditions must accommodate predictors that could lead the blooms by time lags as large as 6–8 months. Two- and three-dimensional embeddings of predictor variables against diatom density generated a number of candidate predictors and time lags, as well as indications...
that variables were interacting. One example is the changing geometry of point distributions when the density of peak *A. baicalensis* counts in the spring were plotted against air temperature at lags of 4, 5, and 6 months prior (Fig. 3a–c). In this case, the distributions of points corresponding to peaks in diatom density in non-Melosira years (<2.36 = ln (10 cells mL\(^{-1}\)) were relatively flat; the distribution of points for Melosira years (>2.36) showed little indication of a functional relationship when lagged 4 months, some indication at 5 month, and little indication again as the lag was shifted 6 months earlier. When air temperature was lagged 5 months, it was common for low temperature values to be associated with both Melosira years and non-Melosira years. Such a division suggests that if a predictive relationship were present, it likely would include interactions of air temperature and other predictors. Performing this same geometric evaluation of air-temperature, water temperature residuals, and variance in SLP suggested predictive relationships with 3- to 6-month lags; lags did not reveal obvious structure with any of the other potential predictor variables.

### Intra-annual patterns of Melosira years

The most parsimonious models predicting Melosira years with meteorological variables were complex and contained numerous interactions, but performed well in predicting Melosira years (Fig. 4a). The three top models that were statistically similar ranged from 11 to 15 parameters (Table 1). All of the top three models had superior goodness of fit to the interannual models (described below), and similar goodness of fit among themselves based on area under the ROC curve (Fig. 4b). The second-most parsimonious model, although not significantly so (\(\Delta AICc = 1.14\)), had superior goodness of fit based on coefficient of discrimination \(r^2_{corr} > 0.99\), and better forecasting performance suggested
by AICc (Table 1, Fig. 4c); the other top models ranged from 75% to 80%.

All top models contained main effect terms for environmental variables thought to contribute to ice quality: air temperature, water temperature anomalies, and variance in SLP. Averaged models produced main effects for water temperature, wind, and snow depth that were negative, and strongly positive for phase of PDO and neutral for air temperature. However, interaction terms containing air temperature all had much larger negative effect sizes. All of the top models also contained main effects for snow depth and the phase of PDO. They differed in the number of 2-way and 3-way interactions. Indeed, in each of the top models, almost half of the parameters involved the PDO index (Table 1), with no other climate teleconnection indices present in the most parsimonious models. The best models all had lags of 5 months for air temperature (e.g., December predicts April), 4 months for surface pressure variance, and 3 months for snow depth and water temperature anomalies; no lags in the other predictors were seen in the best models.

Determining the most parsimonious model is challenging given the complexities of the best performing models and the potential model space. The most parsimonious model will be the lowest point on a surface defined by the AICc scores for all possible models. We evaluated the distinctiveness of our top models based on the steepness of the information criteria landscape around the best performing models—the more distinctively parsimonious the best performing models were, the steeper, or “peakier” the AICc landscape of adjacent models would be. A plot of the AICc scores from 500 best performing models reveals that the AICc landscape adjacent to the best models is quite steep (Fig. 5), and this increases our confidence that the top models are indeed the most parsimonious in spite of their complexity, and that a much simpler, but still competitive model has not been missed.

**Interannual patterns of Melosira years**

The top five models (Table 2) using climate teleconnection indices to predict interannual patterns were indistinguishable on the basis of AICc; all were within 1.3 AIC units, and all had modest effective coefficients of discrimination. However, all top models shared similar, statistically significant goodness of fit at the 0.05 level based on ROC. Of these top models, all contained a SHI<D main effect and most also contained either an AO, PDO, or both main effects. The top performing model additionally contained an AO: PDO interaction term (Table 2). Model averaging of the top five models resulted in positive effect sizes for SHI, PDO, and AO: PDO interaction term, and a negative AO effect size; all had confidence intervals that did not span 0.

Comparing the observed pattern of Melosira years to the predicted sequence based on the best model in Table 2 over the period 1948 to 1997, 6 of 14 bloom years, and 33 of 35 nonbloom years, or 79.6% of the total observations were correctly identified by the model (Fig. 6a). Although the model did not identify (odds ratio of a Melosira year <0.5) the Aulacoseira blooms in 1950, 1960, 1961, 1964, 1971, 1982, 1991, and 1994, and predicted unobserved blooms in 1955, and 1980, the model did predict increased odds of a bloom in 1950, 1961, and 1982 relative to adjacent years.

**Model cross-validation**

When the model that appeared to have the best forecast performance (AUC = 0.888) was applied to meteorological data from 1997 to 2009, it produced a time series of forecasts of Melosira years that was almost entirely accurate (Supporting
Information Fig. S2). The forecast time series included one false negative (2002), and no false positives. Thus, this model’s precision over the 13-yr test data period was 1.0 (5 out of 5), and the accuracy was 0.92 (12/13); this degree of association was statistically significant ($X^2 = 6.3$, $p = 0.012$).

**Discussion**

The variables that emerged as important in these models were consistent with hypotheses that ice quality, determined during ice formation in the late fall is a critical driver of blooms in the following spring. The negative coefficients for air temperature, windiness (i.e., variance of surface air pressure) and water temperature in the months of ice formation are consistent with our understanding that relatively clear ice transmits light to the diatoms below. Similarly, snow accumulation on the ice will limit light transmission (Jewson et al. 2009; Jewson and Granin 2014), and our top models contained negative coefficients for snow depth. However, snow may play a more nuanced role in the spring blooms in mediating heat flow into the under-ice water (Jewson et al. 2009) and driving under-ice water circulation. Indeed, the snow cover can be patchy in distribution and result in spatially heterogeneous timing and intensity of diatom dynamics intra-annually (Jewson et al. 2009; Jewson and Granin 2014). On balance however, the enigmatic appearance of 3–4 yr cycles in Melosira years, the focus of numerous previous studies, may be best explained by large-scale climate oscillations that influence local conditions, particularly those represented by the SHI, without entirely precluding the internal processes that likely contribute to the magnitude and variability of the blooms (e.g., Jewson and Granin 2014).
The best performing models identified here make a strong case that abiotic factors that contribute to ice quality drive the temporal pattern of Melosira years, but the use of logistic functions treats all Melosira years as binary (i.e., did it happen or not?), and limits the inferences we draw to those addressing temporal pattern. Consequently, we are not able to address different amplitudes of *Aulacoseira* population blooms, nor why some high-density years consist of one large peak while others consist of smaller, numerous peaks. Given that our models did not consider biotic factors as predictors, it is tempting to suggest that biotic factors or spatial heterogeneity in dynamics may influence amplitude and other bloom characteristics. Recent work has suggested important interactions between life history transitions (sexual vs. asexual reproduction), population dynamics, and nutrient cycling in *A. baikalensis* (Jewson and Granin 2014). This suggests that while we failed to identify a biotic factor in the interannual pattern of Melosira years, biotic factors likely play important roles in determining the intra-annual trajectories of individual *Aulacoseira* blooms.

### Intra-annual environmental determinants of Melosira years

The growth process for lake ice has multiple steps that together determine the qualities of the ice. Characteristics of both primary and secondary ice growth determine net ice clarity and are affected by environmental conditions (Michel and Ramseier 1971; Ashton 1989; Kouraev et al. 2007; Kirilllin et al. 2012). Primary ice forms first as a skin that spreads horizontally over the water surface; secondary ice crystals grow vertically down from the primary ice into the water. Additional, superimposed ice that forms from precipitation or flooding (Michel and Ramseier 1971), which can limit light transmission, seems not to be a significant ice growth determinant.

### Table 1. Performance of the best three models that predict L. Baikal Melosira years with meteorological variables and climate teleconnection indices ranked by AICc. PDOB is the binary phase of the Pacific Decadal Oscillation, AT is air temperature, WT is water temperature anomaly, WN is wind proxy (= monthly variance in daily SLP), SD is snow depth. Although the best performing models were relatively close based on AICc, model number two below was superior based on $r^2$ and AUC, and it was identified as the “top model.”

| Model                              | AICc  | $r^2$  | AUC   | $p$   |
|------------------------------------|-------|--------|-------|-------|
| WT+AT+WN+SD+PDOB                  | 48.41 | 0.751  | 0.868 | 4E-04 |
| WT:SD+WN:SD+AT:PDOB                  | 49.55 | 0.999  | 0.888 | 6.8E-04|
| AT:PDOB+WT:PDOB+SD:PDOB+WN:PDOB+ | 49.79 | 0.798  | 0.877 | 4E-05 |
| AT:WD+WN:PDOB                  | 50.01 | 0.710  | 0.793 | 3E-05 |
| WT:WD+WN:PDOB                  | 50.01 | 0.710  | 0.793 | 3E-05 |
| SD:PDOB                  | 50.01 | 0.710  | 0.793 | 3E-05 |

### Table 2. Performance of the best five models that predict Lake Baikal Melosira years using climate teleconnection indices, ranked by AICc. For comparison, a model with no predictive power that randomly forecast events would on average produce an AUC of 0.5 (Mason and Graham 2002). PDOB is the binary phase of the Pacific Decadal Oscillation, the AO is the monthly AO index, and the SHI is the differenced NDJF SHI as described in the text.

| Model                              | AICc  | $r^2$  | AUC   | $p$   |
|------------------------------------|-------|--------|-------|-------|
| AO:PDOB+AO+PDOB+SHI               | 57.8  | 0.251  | 0.702 | 0.001 |
| SHI                               | 57.9  | 0.115  | 0.647 | 0.021 |
| PDOB+SHI                           | 58.1  | 0.151  | 0.647 | 0.021 |
| AO+SHI                            | 58.5  | 0.147  | 0.661 | 0.012 |
| AO+PDOB+SHI                       | 59.1  | 0.178  | 0.674 | 0.006 |
process on Lake Baikal (Todd and Mackay 2003; Kouraev et al. 2007), possibly due to the dry winter climate (Moore et al. 2009).

Greater ice clarity is associated with larger ice crystals, which are in turn associated with primary ice formation during conditions of calm winds and large temperature gradients between the air and water (Michel and Ramseier 1971; Ashton 1989). Lake Baikal achieves homeothermy in late fall-early winter (November–January) with surface water temperatures around 4°C (Kouraev et al. 2007), but even if surface waters supercool prior to ice formation, these waters may only get to ~1°C (Kirillin et al. 2012); thus, variability in the air-water temperature gradient will largely be determined by the much greater interannual variability in late-fall air temperatures. While wind enhances the cooling of surface waters and the convection of heat away from the lake, it also can disrupt ice crystal formation, resulting in disoriented ice crystals, frazil slush, trapped bubbles, and potentially roughened water surface, with overall lower ice clarity (Michel and Ramseier 1971; Kirillin et al. 2012). Thus, clear primary ice is associated with low air temperatures, and also low wind speeds, consistent with our top models.

The growth of clear secondary ice is related also to the growth of large ice crystals, which in turn result from both clear primary ice formation, and small, but sustained air:water temperature gradients (Michel and Ramseier 1971). Key to the formation of clearer, thicker lake ice is the relative slowness of secondary ice formation in order to produce larger ice crystals, as happens when the ice and associated stratified water temperatures form and heat is principally conducted with diffusive processes. When lake ice forms slowly, the thermal gradient in the water below the ice can become modest, with relatively large masses of cold water remaining below the water-ice boundary; conversely, when the ice forms quickly, the thermal gradients can be steeper with relatively warm water limiting the growth of the secondary ice sheet (Kirillin et al. 2012). Therefore, lower water temperature anomalies observed in the months following

**Fig. 6.** (a) Time series plot of Melosira year occurrence (Melosira year = 1; non-Melosira year = 0) from 1948 to 1997 (black), with the fit of the best logistic regression model for that time series based only on climate indices from Table 1 (red). The logistic model forecasts the probability of the event in question occurring; thus, values greater than 0.5 on the y-axis suggest that *Aulacoseira* blooms are more likely than not to occur. (b) ROC curve for the top model plotted in 6a, which in this case is 0.702. (c) Histogram of AUC scores when the model fits are permuted and AUC is recalculated. The gray, dashed, vertical line shows the position of the observed AUC score for the fitted model; the area under the tail greater than the gray line shows the exact probability of seeing that high an observed AUC just by chance (= the p value), in this case 0.001.
primary ice formation and during secondary ice growth, would be consistent with more extensive, clearer secondary ice growth. Consistent with our knowledge of this phenomenon, our averaged model terms indicated that Melosira years were more likely in years with negative water temperature anomalies.

The relationship between snow and Aulacoseira blooms is likely more complex. As noted, on-ice snow thicknesses of 10 cm or more can exclude light from penetrating the under-ice area and supporting primary production (Jewson et al. 2009). In addition, precipitation that occurs at the time of primary ice formation can affect ice crystal development, producing lower light transmission in the ice sheet (Michel and Rameise 1971). Later in the winter when the ice has formed, however, the presence of snow in discrete patches has been suggested to be important in creating discontinuities in light and shade in the water below the ice, producing lateral thermal gradients that drive convection in the top 30 m of water (Zhadanov et al. 2001). Indeed, recent work has also indicated a seasonal variation in the depth of snow-mediated circulation, which in turn interacts with seasonal changes in cell size and population growth rates in A. baikalicensis, with implications for distributions of observed population sizes and nutrient availability in the upper water column during winter-time algal growth (Jewson and Granin 2014).

Although Aulacoseira is known to adhere to the under-ice surface (Bondarenko et al. 2006), higher densities have been seen 25–30 m below the ice sheet correlated with a deeper layer of uniformly cold water that appears to be convectively mixed (Jewson et al. 2009). Convective mixing on that scale would be important, and if generally true the role of snow in creating and maintaining the thermal gradients that drive convection is likewise important. Complex relationships between environmental factors, such as snow accumulation limiting light transmission, but facilitating convection suggests (1) that one might not be surprised by a large number of interaction terms in the best performing statistical models of the system, and (2) that it is likewise unsurprising that modeling of the relationships between meteorological variables and Aulacoseira blooms in the lake has been challenging in the past.

The scarcity of blooms between 1975 and 1988 is particularly suggestive of an influence of large-scale climate drivers, and the phase of PDO in particular, on the Melosira year phenomenon. This period has been noted as a period of PDO “warm” phase with significant transition in climatic pattern at both the beginning and end of the period (Trenberth and Hurrell 1994; Hare and Mantua 2000). The PDO is recognized as a major driver of ecological phenomena in a diversity of other systems (e.g. Beamish et al. 1999; McFarlane et al. 2000), in affecting East Asian Winter Monsoon (e.g., Wang et al. 2008; Park et al. 2012), and the seasonal timing of water temperature changes in Lake Baikal itself (Katz et al. 2011). There are however, a number of other, more proximate, regional-scale climatic drivers that can affect meteorological states associated with Aulacoseira blooms. As early as 1999, for example, climate drivers such as the North Atlantic Oscillation were identified as important indicators of general conditions at Lake Baikal and even specifically with ice break-up events (Livingstone 1999).

Interestingly, although the best performing models in this study were complex, the fact that the PDO phase is a dichotomous factor means that in each case we are operationally considering two models—one simpler than the other. When the PDO is in its cool phase, the value of the parameter is zero and those interaction terms containing PDO are non-functional, leaving a more simple model. In the intervals where PDO is in its warm phase, a more complex model is recruited by adding a number of PDO interaction terms, resulting in the observed, relatively irregular Aulacoseira blooms in these periods (e.g., 1976–1989), without relying on specific values of the PDO index. Thus, PDO in this case can be viewed as a “gating” term that interacts with other regional and local conditions, rather than a direct interactor via fluctuations in atmospheric pressure systems (Gershunov and Barnett 1998; Verdon and Franks 2006; Katz et al. 2011).

Decadal temporal pattern in Melosira years
The temporal spacing of Melosira years early in the time series (pre-1976), with blooms approximately 3 yr apart, gave the impression of periodicity. When inspecting the whole time series however, the pattern is more appropriately characterized as episodic with an average interevent interval of 3.8 yr; periodic phenomenon being more correctly defined by a clear interevent period (Bendat and Piersol 2011). The long gap with only one bloom between 1975 and 1988, and the series of couplet years between 1988 and 1999 disrupt a consistent period, an observation only possible because of the length of high quality monitoring data at hand. The original reports of the periodic blooms of Aulacoseira were developed with data collected at more irregular intervals from 1945 to 1950 (Kozhov 1963) and consistent, quantitative data only from 1950 to 1951 (Kozhov 1955), 1950 to 1953 (Votintsev 1961), and 1950 to 1961 (Shimaraev 1971). Given the luxury of hindsight, nearly a half century more data and accessible research on meteorology, we now can build on the creative scientific insights of previous investigators to advocate for a relatively minor change in how the Melosira years are characterized.

The intra-annual, meteorological models performed well and have illuminated within-year dynamics that lead to thick, clear ice that would likely promote Aulacoseira blooms. Compared with climate indices that average across several months, however, those predictors lack the “memory” to support hypotheses to address the episodic temporal pattern of Melosira years that have been sustained across multiple decades, nor the apparent eras such as the 1976–1988 period.
The interannual climate index-based models (summarized in Table 2), do suggest that large-scale atmospheric patterns, the SHI in particular, play an important role in determining the pattern of Melosira years.

The Siberian High has been highlighted as one of the more stationary and influential atmospheric features in the Northern Hemisphere (Gong and Ho 2002; Panagiotopoulos et al. 2005; Jeong et al. 2011), and has been implicated as a major driver of central Asian winter climate and East Asian Winter Monsoons (Gong and Ho 2002; Cheung et al. 2012). The short-term variability of the Siberian High strength and Ural blocking events show a 2- to 3-yr negative autocorrelation in the period between 1957 and 2000 (Wang et al. 2010a,b), suggesting that together they may constitute a high-quality predictor of Melosira years. It also has been observed that variability in the Siberian High is associated with ice thickness on Lake Baikal once the influence of other climate signals has been removed (Todd and Mackay 2003). The strength of the Siberian High went into decline in the years following the mid-1970s transition (Panagiotopoulos et al. 2005), and has strengthened in recent decades (Jeong et al. 2011). This strengthening of the Siberian High in the early 1990s, and acquisition of neutral values in the early 2000s (Jeong et al. 2011), however, have come later than the resumption of frequent Melosira years (Fig. 4a). Indeed, increased North Atlantic ice melt, and associated decreased thermohaline overturning circulation and regional sea surface temperatures were also observed since the mid-1970s transition (Rahmstorf et al. 2015), but aside from short term fluctuations these trends have continued and are expected to continue into the next century (Rahmstorf et al. 2015). Given the coincidence of the onsets of these transitions and the coupling of sea surface temperatures and atmospheric circulation (e.g., Webster 1981; Rasmusson and Wallace 1983), it is tempting to suggest a mechanistic hypothesis that connects all of these dynamics, but the lack of coincident rebound in the late 1980s argues against a comprehensive hypothesis connected to the Lake Baikal diatoms. Conversely, the PDO transitioned in the late 1980s, more coincident with the resumption of Melosira years (Park et al. 2012); suggesting some level of interaction between the PDO and the intensity of the Siberian High.

Regional meteorological correlates of the SHI, an index present in all our top interannual models, are consistent with our model of intra-annual ice formation described above. Stronger Siberian High has been associated with colder air temperatures in the Baikal region as air is driven down from high altitude to the surface by pressures that may exceed 1030 hPa at surface level (Gong and Ho 2002). The strength of the Siberian High is amplified by blocking, high-pressure systems upstream from the Siberian High in the Ural Mountain region (Wang et al. 2010b). In winters with strong Ural blocking, polar winds are directed northward into the anticyclonic flow of the Siberian High, adding to its strength and resulting in profoundly colder air temperatures (Wang et al. 2010b; Cheung et al. 2012).

Surface levels winds also have been related to the Siberian High, with wind anomalies being predominantly Northerly and weak in strength in strong Siberian High years, and the opposite in low SHI years (Todd and Mackay 2003). Those authors have pointed out, however, that the observed patterns are based on estimates with coarse spatial resolution and averaged temporal sequences. Indeed, the wind events that have the greatest significance for ice formation and break-up are more often associated with episodic, short duration events and may not be reflected by climatologies (Todd and Mackay 2003). The orography of the Lake Baikal region may also mitigate the influence of large scale winds on surface level heat flux; the north and west shores of the lake abut the Baikal and Primorskiy mountains which can achieve 2000–3000 m in height within 4km of the lake shore, and provide a formidable wind shadow to North and Northwest winds.

The SHI appearing in every top model is a strong result (Table 2) notwithstanding the goodness of fit statistics for those models. Climate teleconnection indexes such as the SHI, AO, or PDO, are low-dimension descriptions of rich, multivariate climatic patterns over very large scales. By their nature, they average what may be important variances in local conditions in both time and space. Drawing direct relationships between diverse climate patterns and specific meteorological predictors of Melosira years (e.g., air and water temperature, wind) is also challenging, because the relationships themselves are interacting, complex and have evolved Worldwide over the period from 1950 to 2000 (e.g., Torrence and Webster 1999; Panagiotopoulos et al. 2005; Lo and Hsu 2010). Given the numerous studies linking variability in North Pacific atmospheric dynamics and the Siberian High (e.g., Cheung et al. 2012; Park et al. 2012; Tubi and Dayan 2013), it seems likely that there are relevant aspects of both the Siberian High and PDO that are dynamically linked to each other, or are proxies for some as yet unidentified climatic driver, all of which are linked to the regional meteorological determinants of Melosira years on lake Baikal.

Given these complexities, our results may be surprisingly straightforward. Conditions at ice formation were strongly related to the likelihood of Melosira year occurrence, and models provided good predictive power—correctly identifying the presence or absence of a Melosira year in 12 of the 13 yr of a validation dataset. Further, we can now suggest that the apparent 3-year periodicity of Melosira years, which has presented a Baikalian enigma for decades, is better described as episodic and relates to larger-scale patterns of climate oscillations represented by activity of the Siberian High.

This empirical derivation of a time-lagged model for climate-ice-algae interactions emerges at a time when interest in under-ice biota and ecosystem dynamics is increasing (Salonen et al. 2009; Bertilsson et al. 2013), and shortening ice
duration and other associated climate change effects are altering lake dynamics in dimensions that we do not yet fully understand (e.g., Shimaraev 2002; Moore et al. 2009). Although Lake Baikal is frequently described as an outlier, and its productivity under ice may prove to be exceptionally high, the extent to which under-ice productivity contributes to annual lake dynamics in seasonally ice-covered lakes worldwide remains largely unknown. Our results suggest that the attention of physical, chemical, and biological limnologists together would be usefully focused on the critical period of ice formation and later conditions affecting snow cover, to anticipate the physical environment that will influence biotic processes under ice. Winter and spring dynamics occurring under clear, cloudy, or snow-covered ice—determined by conditions in late fall or early winter at ice formation—affect not only the biota under the ice but also the conditions as ice recedes. Fish kills and ice-off greenhouse gas emissions are at one end of the spectrum of measurable societal importance that can be attributed to under-ice lake processes, and thus warrant further study, but more nuanced winter influence on plankton and biochemistry dynamics are also at play and promise fertile areas of future investigation (Sommer et al. 2012; Jewson and Granin 2014).

References

Antipova, N. L., and M. M. Kozhov. 1953. Materials on seasonal and annual fluctuations of number of main forms of phytoplankton of Lake Baikal. [In Russian]. Proc Irkutsk State Univ. Ser Biol 7: 63–68.

Armstrong, R. 2001. Historical Soviet daily snow depth version 2 (HSDSD). National Snow and Ice Data Center, Boulder, CO. CD-ROM.

Ashton, G. D. 1989. Thin ice growth. Water Resour. Res. 25: 564–566. doi:10.1029/WR025i03p00564

Bamber, D. 1975. The area above the ordinal dominance graph and the area below the receiver operating characteristic graph. J. Math. Psychol. 12: 387–415. doi:10.1016/0022-4416(75)90001-2

Beamish, R. J., D. J. Noakes, G. A. McFarlane, L. Klyashtorin, V. V. Ivanov, and V. Kurashov. 1999. The regime concept and natural trends in the production of Pacific salmon. Can. J. Fish. Aquat. Sci. 56: 516–526. doi:10.1139/cjfas-56-3-516

Bendat, J. S., and A. G. Piersol. 2011. Random data: Analysis and measurement procedures. Wiley.

Bertilsson, S., and others. 2013. The under-ice microbiome of seasonally frozen lakes. Limnol. Oceanogr. 58: 1998–2012. doi:10.4319/lo.2013.58.6.1998

Bond, N. A., J. E. Overland, M. Spillane, and P. Stabeno. 2003. Recent shifts in the state of the North Pacific. Geophys. Res. Lett. 30: 2183. doi:10.1029/2003GL018597, 23.

Bondarenko, N. A., and V. K. Evstafyev. 2006. Eleven-and ten-year basic cycles of Lake Baikal spring phytoplankton conformed to solar activity cycles. Hydrobiologia 568: 19–24. doi:10.1007/s10750-006-0339-1

Bondarenko, N. A., O. A. Timoshkin, P. Röpstorff, and N. G. Melnik. 2006. The under-ice and bottom periods in the life cycle of Aulacoseira baicalensis (K. Meyer) Simonsen, a principal Lake Baikal alga. Hydrobiologia 568: 107–109. doi:10.1007/s10750-006-0325-7

Burnham, K. P., and D. Anderson. 2002. Model selection and multi-model inference, 2nd ed. Springer.

Cheung, H. N., W. Zhou, H. Y. Mok, and M. C. Wu. 2012. Relationship between Ural-Siberian blocking and the East Asian winter monsoon in relation to the Arctic oscillation and the El Nino-Southern Oscillation. J. Clim. 25: 4242–4257. doi:10.1175/JCLI-D-11-00225.1

Cohen, J., P. Cohen, S. G. West, and L. S. Aiken. 2013. Applied multiple regression/correlation analysis for the behavioral sciences. Routledge. pp. 736.

Cota, G. F. 1985. Photoadaptation of high Arctic ice algae. Nature 315: 219–222. doi:10.1038/315219a0

Evstafyev, V. K., and N. A. Bondarenko. 2007. An intriguing enigma of Lake Baikal. Biol. Rhythm Res. 38: 107–117. doi:10.1080/09291010600902710

Fawcett, T. 2006. An introduction to ROC analysis. Pattern Recognit. Lett. 27: 861–874. doi:10.1016/j.patrec.2005.10.010

Gershunov, A., and T. P. Barnett. 1998. Interdecadal modulation of ENSO teleconnections. Bull. Am. Meteorol. Soc. 79: 2715–2725. doi:10.1175/1520-0477(1998)079<2715:IMOE>2.0.CO;2

Gong, D.-Y., and C.-H. Ho. 2002. The Siberian High and climate change over the middle to high latitude Asia. Theor. Appl. Climatol. 72: 1–9. doi:10.1007/s007040200008

Granin, N. G., and others. 2000. Turbulent mixing under ice and the growth of diatoms in Lake Baikal. Verhein. Int. Ver. Limnol. 27: 2812–2814.

Hampton, S. E., L. R. Izmest’eva, M. V. Moore, S. L. Katz, B. Dennis, and E. A. Silow. 2008. Sixty years of environmental change in the world’s largest freshwater lake–Lake Baikal, Siberia. Glob. Change Biol. 14: 1947–1958. doi:10.1111/j.1365-2486.2008.01616.x

Hampton, S. E., M. V. Moore, T. Ozersky, E. H. Stanley, C. M. Polashenski, and A. W. Galloway. 2015. Heating up a cold subject: prospects for under-ice plankton research in lakes. J. Plankton Res. doi:10.1093/plankt/fbv002

Hare, S. R., and N. J. Mantua. 2000. Empirical evidence for North Pacific regime shifts in 1977 and 1989. Prog. Oceanogr. 47: 103–145. doi:10.1016/S0079-6611(00)00033-1

Izmest’eva, L. R., M. V. Moore, S. E. Hampton, and E. A. Silow. 2006. Seasonal dynamics of common phytoplankton in Lake Baikal. [In Russian]. Proc. Samara Russ. Acad. Sci. Sci. Cent. 8: 191–196.

Jeong, J.-H., T. Ou, H. W. Linderholm, B.-M. Kim, S.-J. Kim, J.-S. Kug, and D. Chen. 2011. Recent recovery of the Siberian High intensity. J. Geophys. Res. Atmos. 116: 1984–2012. doi:10.1029/2011JD015904

Jewson, D. H., and N. G. Granin. 2014. Cyclical size change and population dynamics of a planktonic diatom, Aulacoseira

Katz et al.
cover variability. Asia-Pacific Symposium on Remote Sensing of the Atmosphere, Environment, and Space, p. 270–277. International Society for Optics and Photonics.

Shimaraev, M. N. 1971. Hydrometeorological factors and variation in the abundance of Baikal plankton. [In Russian]. Proc. Limnol. Inst. Sib. Branch USSR Acad. Sci. 12: 259–267.

Shimaraev, M. N. 2002. Manifestation of global climatic changes in Lake Baikal during the 20th century. Dokl. Earth Sci. 383A: 288–291.

Silow, E. A., A. V. Mokry, and S. E. Jorgensen. 2011. Some applications of thermodynamics for ecological systems, in J. C. Moreno Pirajn [ed.], Thermodynamics—Interaction studies—Solids, liquids and gases. InTech.

Sommer, U., and others. 2012. Beyond the Plankton Ecology Group (PEG) model: Mechanisms driving plankton succession. Annu. Rev. Ecol. Evol. Syst. 43: 429–448. doi: 10.1146/annurev-ecolsys-110411-160251

Straskaťová, V., and others. 2005. Primary production and microbial activity in the euphotic zone of Lake Baikal (Southern Basin) during late winter. Glob. Planet. Change 46: 57–73. doi:10.1016/j.gloplacha.2004.11.006

Strong, C., and G. Magnusdottir. 2009. The role of tropospheric Rossby wave breaking in the Pacific Decadal Oscillation. J. Clim. 22: 1819–1833. doi:10.1175/2008JCLI2593.1

Sverdrup, H. U., and others. 1942. The oceans: Their physics, chemistry, and general biology. Prentice-Hall.

Tjur, T. 2009. Coefficients of determination in logistic regression models—A new proposal: The coefficient of discrimination. Am. Stat. 63: 366–372. doi:10.1198/tast.2009.08210

Todd, M. C., and A. W. Mackay. 2003. Large-scale climatic controls on Lake Baikal ice cover. J. Clim. 16: 3186–3199. doi:10.1175/1520-0442(2003)016<3186:LCCLOL>2.0.CO;2

Torrence, C., and P. J. Webster. 1999. Interdecadal changes in the ENSO-monsoon system. J. Clim. 12: 2679–2690. doi:10.1175/1520-0442(1999)012<2679:ICITEM>2.0.CO;2

Trenberth, K. E., and J. W. Hurrell. 1994. Decadal atmosphere-ocean variations in the Pacific. Clim. Dyn. 9: 303–319. doi:10.1007/BF00204745

Trenberth, K. E., and D. A. Paolino, Jr. 1980. The Northern Hemisphere sea-level pressure data set: Trends, errors and discontinuities. Mon. Weather Rev. 108: 855–872. doi:10.1175/1520-0493(1980)108<0855:TNHSLP>2.0.CO;2

Tubí, A., and U. Dayan. 2013. The Siberian high: Teleconnections, extremes and association with the Icelandic low. Int. J. Climatol. 33: 1357–1366. doi:10.1002/joc.3517

Twiss, M. R., and others. 2012. Diatoms abound in ice-covered Lake Erie: An investigation of offshore winter limnology in Lake Erie over the period 2007 to 2010. J. Great Lakes Res. 38: 18–30. doi:10.1016/j.jglr.2011.12.008

Vanderploeg, H. A., S. J. Bolsenga, G. L. Fahnsteniel, J. R. Liebig, and W. S. Gardner. 1992. Plankton ecology in an ice-covered bay of Lake Michigan: Utilization of a winter phytoplankton bloom by reproducing copepods. Hydrobiologia 243: 175–183. doi:10.1007/BF00007033

Verdon, D. C., and S. W. Franks. 2006. Long-term behaviour of ENSO: Interactions with the PDO over the past 400 years inferred from paleoclimate records. Geophys. Res. Lett. 33: L06712. doi:10.1029/2005GL025052

Votintsev, K. K. 1961. Hydrochemistry of Lake Baikal. [In Russian]. USSR Academy of Science Press.

Wang, B., Z. Wu, C.-P. Chang, J. Liu, J. Li, and T. Zhou. 2010a. Another look at interannual-to-interdecadal variations of the East Asian winter monsoon: The northern and southern temperature modes. J. Clim. 23: 1495–1512. doi:10.1175/2009JCLI3243.1

Wang, L., W. Chen, and R. Huang. 2008. Interdecadal modulation of PDO on the impact of ENSO on the East Asian winter monsoon. Geophys. Res. Lett. 35: L20702. doi:10.1029/2008GL035287

Wang, L., W. Chen, W. Zhou, J. C. Chan, D. Barriopedro, and R. Huang. 2010b. Effect of the climate shift around mid-1970s on the relationship between wintertime Ural blocking circulation and East Asian climate. Int. J. Climatol. 30: 153–158. doi:10.1002/joc.1876

Webster, P. J. 1981. Mechanisms determining the atmospheric response to sea surface temperature anomalies. J. Atmos. Sci. 38: 554–571. doi:10.1175/1520-0469(1981)038<0053:MDTART>2.0.CO;2

Winfree, A. T. 2001. The geometry of biological time. Springer.

Yasinsky, V. N. 1930. Results of the Lake Baikal plankton observations at biological station in 1926–1928. [In Russian]. Proc. Biol. Geogr. Inst. Irkutsk State Univ. 4: 191–238.

Yoshida, T., and others. 2003. Seasonal dynamics of primary production in the pelagic zone of southern Lake Baikal. Limnology 4: 0053–0062. doi:10.1007/s10201-002-0089-3

Zdanov, A. A., N. G. Granin, and M. N. Shimaraev. 2001. The generation mechanism of under-ice currents in Lake Baikal. Dokl. Earth Sci. 377A: 329–332.

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