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Perspective

A perspective on the ecological and evolutionary consequences of phenological variability in lake ice on north-temperate lakes

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Abstract

Climate change is leading to shifts in not only the average timing of phenological events, but also their variance and predictability. Increasing phenological variability creates a stochastic environment that is critically understudied, particularly in aquatic ecosystems. We provide a perspective on the possible implications for increasingly unpredictable aquatic habitats, including more frequent trophic asynchronies and altered hydrologic regimes, focusing on ice-off phenology in lakes. Increasingly frequent phenological extremes may limit the ability of organisms to optimize traits required to adapt to a warming environment. Using a unique, long-term ecological dataset on Escanaba Lake, WI, USA, as a case study, we show that the average date of ice-off is shifting earlier and becoming more variable, thus altering limnological conditions and yielding uncoupled food web responses with ramifications for fish spawn timing and recruitment success. A genes-to-ecosystems understanding of the responses of aquatic communities to increasingly variable phenology is needed. Our perspective suggests that management for diversity, at the intra- and interspecific levels, will become paramount for conserving resilient aquatic ecosystems.

Résumé

Les changements climatiques entraînent des modifications non seulement de la date moyenne d'étapes phénologiques, mais également de leur variance et de leur prévisibilité. Une plus grande variabilité phénologique crée un environnement stochastique dangereusement sous-étudié, particulièrement dans les écosystèmes aquatiques. Nous présentons une perspective sur les conséquences possibles pour des habitats aquatiques de plus en plus imprévisibles, dont la hausse de la fréquence d'asynchronies trophiques et la modification des régimes hydrologiques, en mettant l'accent sur la phénologie du départ de la glace dans les lacs. Des extrêmes phénologiques de plus en plus fréquents pourraient limiter la capacité d'organismes à optimiser des caractères nécessaires à l'adaptation à un milieu en réchauffement. En utilisant un ensemble de données à long terme singulier pour le lac Escanaba (Wisconsin, États-Unis) comme cas de figure, nous démontrons que la date moyenne du départ de la glace est de plus en plus hâtive et variable, modifiant ainsi les conditions limnologiques et causant des réactions trophiques non couplées qui ont des répercussions sur le moment du frai et le succès de recrutement des poissons. Une compréhension « du gène à l'écosystème » des réactions des communautés aquatiques à une phénologie de plus en plus variable est nécessaire. Notre perspective donne à penser que la conservation d'écosystèmes aquatiques résilients nécessitera une gestion axée sur la diversité tant intraspécifique qu'interspécifique. [Traduit par la Rédaction]

Climate change and phenology

Phenology is the annual timing of biological events, or the temporal dimension of natural history (Forrest and Miller-Rushing 2010). Because phenology captures the important role the physical environment plays in structuring annual organismal and population growth and development, phenology is consequential to nearly all biological processes, from cellular and genetic to communities and ecosystems (Forrest and Miller-Rushing 2010). In a warming and more varied climate, phenology is a lens through which to study the influence of climate on ecology and evolution. In terrestrial ecology, there are numerous examples of long-term changes in phenology associated with directional climate trends across taxa, from leaf-out, flowering, and fruiting of plants (Sherry et al. 2011; Vitasse et al. 2018) to the breeding of birds (Hällfors et al. 2020) and mammals (Forchhammer et al. 1998). The ramifications of changing phenology in freshwater aquatic systems are less-studied (Woods et al. 2021;

Woolway et al. 2021). Further, the implications of increasingly unpredictable phenology, driven by projected increased in climatic variability (Benson et al. 2012; Fischer et al. 2021), have been largely ignored in most ecosystems (Liu and Zhang 2020).

Limnology is unique in that it uses the term *phenology* to describe the timing of physical events that structure lake habitats as well as biological events. This convention is becoming more common, with numerous studies on the phenology of lake ice[1] and the phenology of stratification (Hadley et al. 2014; Read et al. 2014; Woolway et al. 2021). In lakes, these physical phenological shifts are mostly investigated as directional trends, with warming leading to longer ice-free seasons, increasing surface water temperatures, and longer periods of thermal stratification (Magnuson et al. 2000; Schindler 2009; Shimoda et al. 2011). Changes to physical lake habitat are in turn influencing biological phenology, with noted shifts in phytoplankton blooms (Thackeray et al. 2008; Anneville et al. 2018), zooplankton population dynamics (Winder and Schindler 2004), and fish spawning and recruitment (Lyons et al. 2015; Hansen et al. 2017; Feiner et al. 2019).

In lakes, climatic triggering of productivity, growth, reproduction, and trophic interactions define a historically predictable succession of community and species interactions (Sommer et al. 2012). In temperate lakes, this succession of events is often initiated by spring ice-off, where climate change-induced variation in ice-off phenology has the potential to disrupt successional patterns that alter ecosystem dynamics. For instance, northwestern Ontario lakes have experienced a noted increase in the variability of ice duration, ice-off date, summer surface water temperature, and importantly, minimum optimal oxythermal habitat from 1970 to 2013 (Guzzo and Blanchfield 2017). Similarly, Lake Peipsi, the fourth-largest lake in Europe, has experienced increasing stochasticity in winter water surface temperatures since 2007 (Öğlü et al. 2020). In a global analysis of lake ice variability in 184 Northern Hemisphere lakes, Kratz et al. (2000) found that the standard deviation of freeze and thaw dates was higher from 1971 to 1990 than from 1951 to 1970. However, Benson et al. (2012) concluded from an analysis of lake ice records from 150-year (1856–2005) and 100-year periods (1906–2005) that the increase in frequency of extreme ice years was due to changes in the long-term means (i.e., changes in average ice phenology over time) and not due to changes in variability (i.e., changes in the interannual variance of ice-off timing). In four large Northern Hemisphere lakes, ice-on and ice-off dates over the past century have at times been highly variable (e.g., 1920s) and at other times relatively stable (e.g., 1950s; Fig. 1), which is likely the reason behind the conflicting conclusions of Kratz et al. (2000) and Benson et al. (2012) on the trend of ice variability. In a timeseries that includes the 21st century, it appears that recent interannual variations in ice-on and ice-off dates are trending high (Figs. 1*b* and 1*d*), while changes in the dates themselves show only comparatively moderate change (Figs. 1*a* and 1*c*). This increase in variability matches the conclusion of Weyhenmeyer et al. (2011) that the variability in the timing of lake ice is higher in regions with shorter ice durations (i.e., warmer climates) and that an increase in variability might be a warning sign of critical transitions in lake ecosystems.

We contend that overlooking important changes in climatic variability misses critical phenological shifts that limit adaptability to new climate conditions (Vázquez et al. 2017). In our perspective, we first review and evaluate implications of phenological variability for lake ecosystem function and resilience on ecological and evolutionary timescales. We focus on north-temperate lakes, which represent ideal ecosystems to study phenological change because characteristic annual patterns emerge from the tight coupling of climate to lake hydrodynamics and biological responses (Caldwell et al. 2020). Furthermore, in north-temperate lakes that freeze in winter, the rapid transition in the spring from ice-covered to open water (ice-off) sets in motion a succession of cyclical patterns of productivity that drive food web dynamics, while also being an easy to measure, and therefore widely recorded, event. Although our hypotheses in this perspective are drawn from our experiences researching north-temperate lakes, our observations and recommendations may be applicable to other inland waters.

Following our conceptualization of the potential influences of phenological variability on the ecology and evolution of north-temperate lake ecosystems, we present evidence of the influences of phenological variability from long-term datasets available from Escanaba Lake, a north-temperate lake in northern Wisconsin where ice phenology and biological data have been extensively monitored for the past 75 years (Sass et al. 2021). We focus on altered ecosystem dynamics in early and late ice-off years and build the case that increasing variance in ice-off dates is likely to decrease ecological resilience and evolutionary rescue capacities in aquatic systems facing climatic change.

Implications of phenological variability

Trophic asynchrony and mismatch

Phenological events in lakes are initiated by a variety of environmental cues (Chmura et al. 2019; Fig. 2). Photoperiod, light, and thermal cues serve as circadian and circannual cues that initiate emergence from dormancy, molting, and reproduction (Dupuis and Hann 2009; Jones and Gilbert 2016). For instance, zooplankton emergence from diapause and molting in many aquatic insects is often tightly tied to specific photoperiods (Stoks et al. 2014; Jones and Gilbert 2016), and thermal conditions during the growing season exert strong controls on growth and development rates of organisms at all levels of the food web—warmer temperatures increase algal, zooplankton, and larval fish growth rates, shorten hatching times, and ultimately affect survivorship (Kitchell et al. 1977; Butterwick et al. 2005; Drake 2005). Among these environmental cues, only photoperiod is independent of climate. A lake at 42°N will always receive 12.7 h of sunlight on 1 April, frozen or not. In contrast, the magnitude of light penetrating

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[1] Web of Science title search for “lake ice phenology” returned 29 papers, all published post-1998.

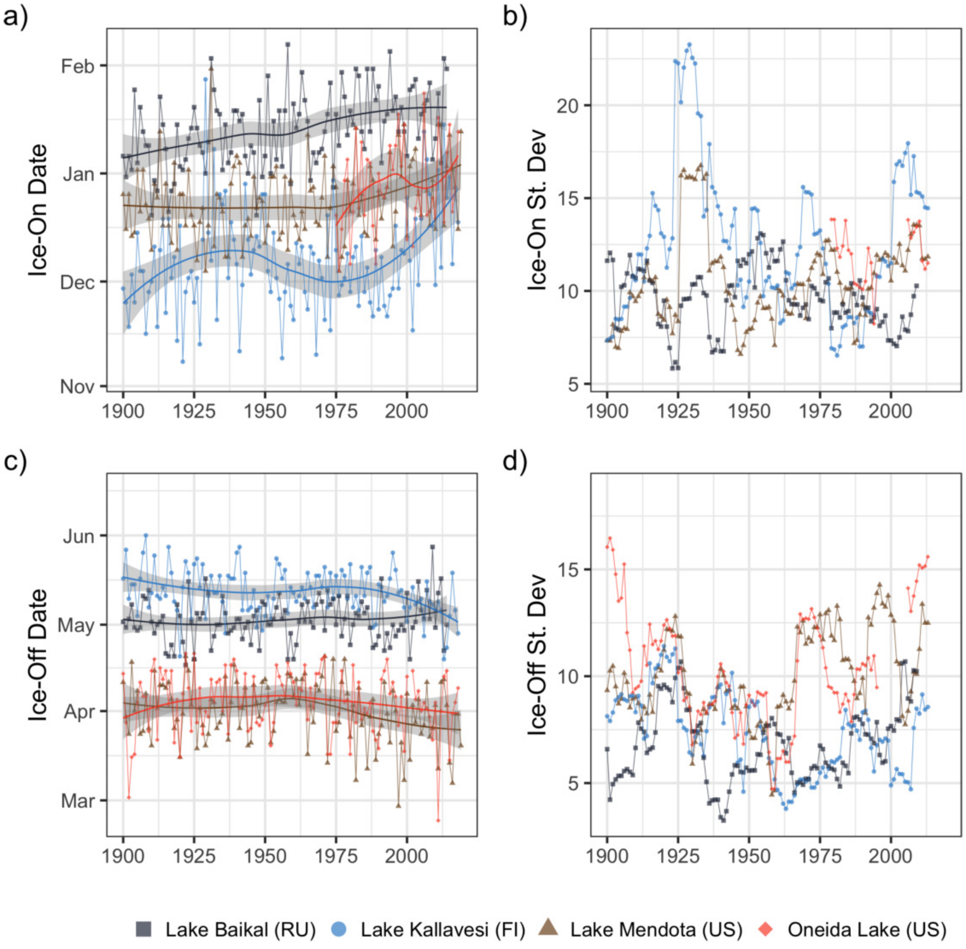
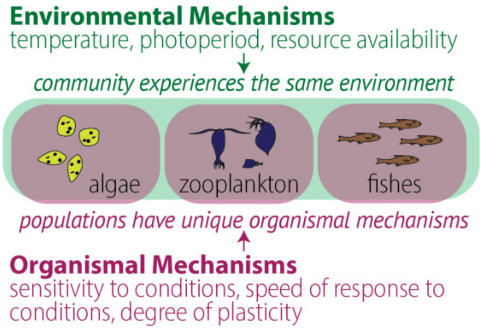


Fig. 1. For four large Northern Hemisphere lakes, (*a*) lake ice freeze dates (ice-on), (*b*) 10-year rolling standard deviation of ice-on dates, (*c*) lake ice thaw dates (ice-off), and (*d*) 10-year rolling standard deviation of ice-off dates. Data adapted from Woolway et al. (2020). [Colour online.]

Fig. 2. Although environmental cues, such as temperature, photoperiod, and resource availability, are experienced coincidentally by entire lake communities, different taxa-specific cue reception and physiological processes regulate phenological responses, potentially causing trophic asynchronies driving ecological and evolutionary responses in lake ecosystems. [Colour online.]



the water column and water temperatures are highly dependent on ice conditions (Jansen et al. 2021). Because of this, life history events for organisms cued by photoperiod would not change in the same ways as organisms cued by light and temperature, setting up the potential for asynchronous ecological dynamics among organisms (Thackeray et al. 2016; Beard et al. 2019).

Lakes are relatively closed systems where trophic interactions are highly dependent on the dynamic interactions of resident populations. Therefore, the influence of a phenological mismatch or a high frequency of mismatch events could have substantial, lasting consequences. At the community level, trophic interactions can become decoupled if species react to changing climatic drivers at different rates than their resources or consumers (Yang and Rudolf 2010). This decoupling is known as *phenological* or *trophic asynchrony*, defined as when the seasonal peak in a resource does not align with the seasonal peak in consumer demand (Samplonius et al. 2021). *Trophic mismatch* is similar, but implies a negative consequence of asynchrony on consumer fitness or population size (Cushing 1990; Samplonius et al. 2021). These mismatches can have substantial ecological effects. For example, in Lake Washington, warmer temperatures caused the annual spring diatom bloom to advance by more than 20 days and decoupled the diatom bloom from the timing of the annual peak of *Daphnia* (Winder and Schindler 2004). de Senerpont Domis et al. (2007) modeled *Daphnia*–phytoplankton dynamics and found that warming lakes led to a mismatch between the emergence of *Daphnia* from diapausing eggs and high-quality algae production, causing a delay or even absence of the clear water phase in some temperate lakes. Similarly, warming water temperatures in Windermere caused the timing of peak zooplankton abundance to shift at a faster rate than that of peak hatching of Eurasian perch (*Perca fluviatilis*) larvae (Ohlberger et al. 2014). Differences in hatch timing of Eurasian perch and a potential prey fish (bream, *Abramis brama*) in Lake Speldrop, Germany, led to variance in Eurasian perch growth based on whether they were able to prey upon, or were forced to compete with, bream early in life (Borcherding et al. 2010). As these examples show, trophic mismatches have the potential to decrease energy flux throughout the food web via top-down and bottom-up processes, alter carbon and nutrient cycling, and result in population declines and altered communities (Thackeray et al. 2010).

To illustrate the susceptibility of a lake food web to phenological mismatch from climate variability, we provide two hypothetical scenarios of extreme ice-off in a north-temperate lake (Fig. 3). For simplicity, we conceptualize a simple (but common in North American temperate systems) aquatic community of phytoplankton, zooplankton (rotifers and *Daphnia*), and fish (planktivorous yellow perch (*Perca flavescens*) and piscivorous walleye (*Sander vitreus*)), with taxonomic variation in phenological cues among different parts of the food web. We further assume similarity in overwinter conditions leading up to ice-off, although there is evidence that winter duration and ice-on conditions may have carryover effects that influence, e.g., survivorship of zooplankton and their grazing effects the subsequent spring (Hébert et al. 2021).

Scenario 1 — Average ice-off

In an average ice-off year (e.g., mid-April), primary production (phytoplankton) is spurred by increases in light and temperature following ice-off. Rotifers, overwintering under the ice, increase in response to the increasing phytoplankton. *Daphnia*, cued by photoperiod and temperature, hatch from the sediments, increase in numbers, and begin to graze down phytoplankton populations leading to a clear water phase. Yellow perch and walleye, thermally cued to spawn (Feiner and Höök 2015), produce young-of-year (YOY) yellow perch and walleye that grow into feeding on zooplankton in time to successfully forage on large numbers of *Daphnia* before walleye transition to piscivory and begin to feed on YOY yellow perch (Feiner and Höök 2015), experiencing high growth and survival rates.

Scenario 2 — Early ice-off

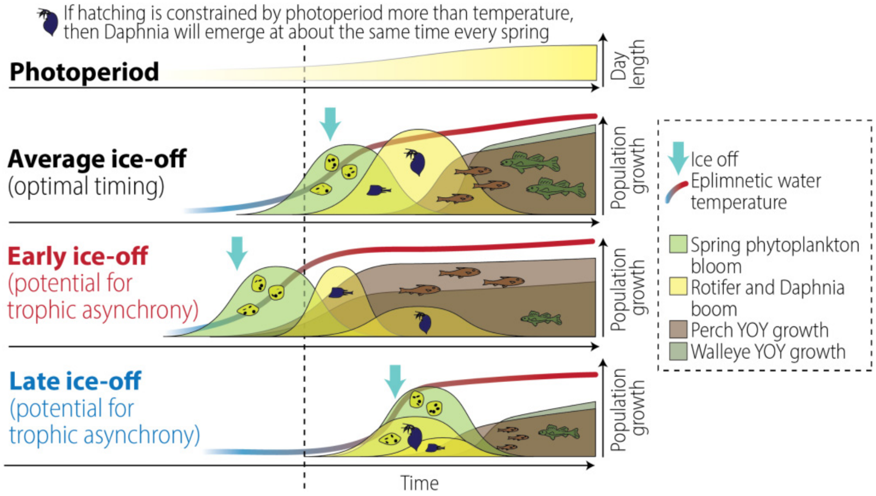
In an early ice-off year (e.g., mid-March), algal production begins to ramp up throughout March and April due to increased light but growth remains slow because temperatures remain relatively low. Rotifers increase as they feed on early algae. *Daphnia*, cued by photoperiod and temperature (Stross 1966; Cáceres 1998), emerge late relative to ice-off into already established rotifer and algal communities at a time when YOY fish, spawned at ice-off, are also beginning to feed on zooplankton (cf. Winder and Schindler 2004). Competition and predation suppress *Daphnia* population growth. Yellow perch and walleye suffer poor larval growth due to a lack of zooplankton resources (Hoxmeier et al. 2004). Poor initial YOY walleye growth causes a delayed switch to piscivory in summer (Uphoff et al. 2019). Coupled with an extended, warm spring that improves YOY yellow perch growth (Graeb et al. 2005), YOY yellow perch escape YOY walleye predation via gape limitation or by not occupying the YOY walleye foraging arena, further limiting YOY walleye growth and survival into the fall (Walters and Juanes 1993; Graeb et al. 2005).

Scenario 3 — Late ice-off

During late ice-off (e.g., early May), algal production rapidly increases and fish spawn immediately upon ice-off. *Daphnia* receives photoperiod and temperature cues that trigger emergence simultaneously with both events into a world with limited food and limited predation. As algae increase, *Daphnia* increase but more slowly as they do not have the unlimited resources needed for exponential population growth. YOY yellow perch and walleye experience limited planktonic food resources and grow slowly, meaning walleye are again prevented from accessing critical fish prey of good size in midsummer. Algal production drives the early-season trophic interactions from the bottom-up until standing biomass is sufficient to support the food web.

As these hypothetical scenarios demonstrate, the phenology of ice-off has cascading, potentially long-term effects throughout the food web. These effects can be short, moderate, or long-lasting and may not be equivalent across scales. For example, an early ice-off year can decrease zooplankton abundances in the short term, with moderate-term (within-generation) implications for fish growth. In the case of long-lived species, such as fish, low recruitment years driven by increasingly frequent trophic mismatches will have long-term consequences for overall population sizes. However, our imagined lake was an admittedly simple example ecosystem. Facing increasing occurrences of phenological variability, the resilience and adaptive capacity of a lake could rather be determined by its response diversity. Conceptually, response diversity theory suggests that an ecosystem will be more resilient to environmental changes if there is a high diversity of possible responses to those changes either within species (Des Roches et al. 2018) or among species that occupy the same functional group (Ives et al. 1999; Elmqvist et al. 2003). In food webs that have low diversity of alternative prey and

Fig. 3. Three hypothetical scenarios of trophic responses to (from top) average, extremely early, and extremely late ice-off in a north-temperate lake, focusing on the emergence of the dominant spring zooplankton *Daphnia* species, which, if cued by photoperiod, will emerge at the same time every spring (dashed line), setting up potential trophic asynchronies with lower trophic levels (spring phytoplankton bloom) and higher trophic levels (young-of-year [YOY] yellow perch and walleye) that have different responses to phenological cues, such as warming epilimnetic water temperatures (gradient line) and ice-off (blue arrow). [Colour online.]



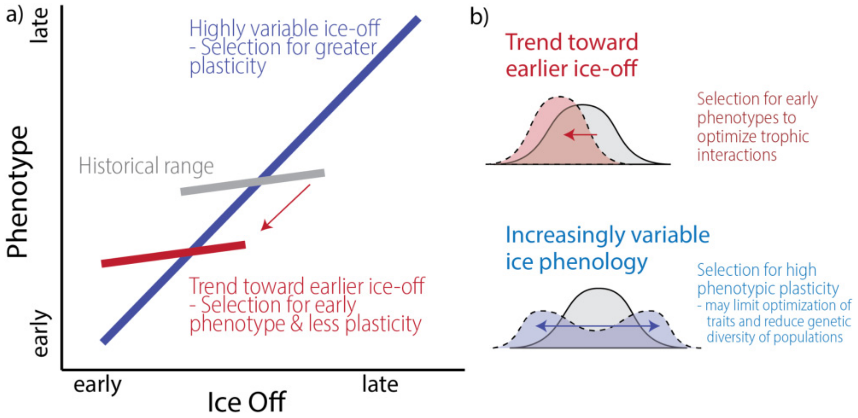
low dispersal capabilities (as in our scenarios above), low response diversity will leave the ecosystem susceptible to phenological mismatches. Alternatively, ecosystems with a high diversity of possible responses to environmental change among functionally similar species (e.g., if another zooplankton species with thermally or light energy-regulated phenology inhabited our example lake; Ślusarczyk and Flis 2019) or with high rates of dispersal potential (Havel and Shurin 2004; Kappes et al. 2014; Incagnone et al. 2015) may be more resilient to disturbance (Ives et al. 1999; Elmqvist et al. 2003).

It is important to note that these dynamics may be exacerbated for small aquatic populations that are already under harvest, habitat loss, and climate pressures, which exemplify many vital but currently struggling fish populations in lakes today (Lynch et al. 2016; Sass et al. 2017). For example, walleye natural recruitment and production have declined over time in Ceded Territory of Wisconsin lakes (Hansen et al. 2017; Rypel et al. 2018; Embke et al. 2019). Climatic variables have often been implicated, including an increase in surface water temperatures (Lester et al. 2004), growing degree days (Hansen et al. 2015*a*), loss of thermal–optical habitat (Lester et al. 2004; Hansen et al. 2019), and changes in fish species composition favoring warmwater species (e.g., largemouth bass, *Micropterus salmoides*; Hansen et al. 2015*b*; Kelling et al. 2016; Sullivan et al. 2020). Similar trends and environmental associations have been observed for yellow perch recruitment (Brandt et al. 2022). The confluence of increasing frequency of phenological extremes with associated trophic mismatches may further weaken the resilience of springtime, broadcast-spawning coolwater fishes where recruitment dynamics are largely driven by environmental conditions and threaten the long-term sustainability of these recreationally, culturally, and economically important resources (Carpenter et al. 2017; Hansen et al. 2019; Tingley III et al. 2019).

Life history and evolution

In a new reality of increasingly frequent climatic extremes occurring on annual or shorter timescales, selection pressures become complicated (Vázquez et al. 2017; Chmura et al. 2019; Visser and Gienapp 2019). The evolutionary effects of increasingly frequent extreme events are further muddied by a lack of knowledge about the genetic basis for phenology in many aquatic taxa and the prevalence of complicated gene × environment interactions ultimately driving trait expression. However, sufficient evidence exists showing evolutionary responses of phenology to selection across multiple taxa (e.g., as reviewed in Forrest and Miller-Rushing 2010; Pau et al. 2011) that we may consider some potential scenarios where phenological variance may alter phenotypic expression through genetic, environmental, and gene × environment interactions (i.e., phenotypic plasticity). In the simplest scenario, phenological extremes may act as a pulsed annual disturbance event, which selectively sweeps early or late phenotypes, similar to influences proposed by the intermediate disturbance hypothesis (Wilkinson 1999; Fig. 4). That is, early ice-off events have the potential to select for individuals that spawn, molt, and (or) emerge early, while warmer water and earlier stratification in these years may lead to increased fitness for individuals that are more tolerant to or express faster growth rates at higher temperatures. Opposing selection pressures exist in late ice-off years that favor genotypes for late spawning and tolerance of cold temperatures. In the most extreme case, sufficiently strong genetic selection gradients and high heritability of phenological traits (Lyberger et al. 2021) could result in extreme years eliminating particular genotypes from the population annually, potentially causing disruptive selection (Kingsolver and Diamond 2011) and the breakdown of important local adaptations to previously predictable phenological cues (Fig. 4). Through such a

Fig. 4. Shifts in the mean timing and variability of phenological events such as ice-off may have different evolutionary implications. Consistent trends toward earlier ice-off may cause directional selection toward "early" pheno- and genotypes (shifted red reaction norm in panel (*a*); shifted and narrowed red distribution in panel (*b*)). In contrast, high variability in ice-off date may act as a continual disturbance, selecting for higher plasticity (elongated and steeper blue reaction norm in panel (*a*)), or, with intense selection gradients, disruptive selection for pheno- and genotypic extremes (blue distribution, panel (*b*)), which could reduce the ability of populations to adapt to new phenological regimes. [Colour online.]



mechanism, a regime of extreme phenology acts as a period of high disturbance that could winnow standing genetic and phenotypic diversity in phenology that would be potentially vital for responding to increasingly unpredictable environments (Freshwater et al. 2019*a*, 2019*b*), or overwhelm long-term climatic trends, reducing adaptive evolutionary rates (Kingsolver and Buckley 2015) and the potential for "evolutionary rescue" (Gienapp et al. 2014).

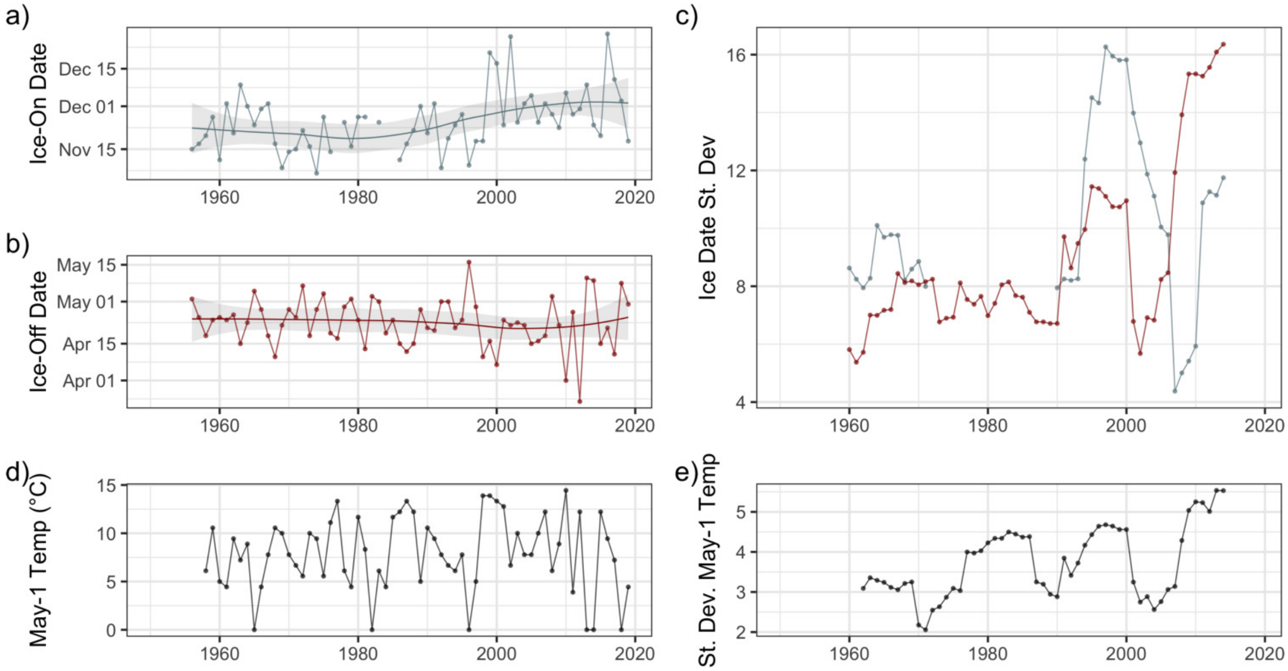
Even in the absence of directional selection on phenological phenotypes, increasing phenological extremes could influence intrapopulation variation in phenology-related traits via other mechanisms. Depending on the underlying genetic structure determining phenological phenotypes, high interannual variation in the environment could select for high levels of phenotypic plasticity (Stamp and Hadfield 2020), which can comprise a significant proportion of the diversity in phenological responses within populations (Iler et al. 2017). Such plasticity may be expressed as individuals or populations vary their responses to different phenological cues (e.g., light and temperature) under different conditions (Krabbenhoft et al. 2014; Bonamour et al. 2019), although tradeoffs may exist between levels of plasticity and adaptation to tolerate extreme conditions (Sasaki and Dam 2021). For instance, O'Dea et al. (2019) showed that not only did changes in developmental temperature influence phenotypic expression of life history traits in a meta-analysis of 43 fish species, but also that phenotypic responses varied depending on whether temperatures were cooled or warmed. Cooled temperatures led to a change in mean trait expression, whereas warmed temperatures led to an increase in trait variability. Thus, phenological variability could lead to differences in both average phenotypes and intrapopulation phenotypic variation among generations simply by altering the thermal environment organisms experience during early life (O'Dea et al. 2019).

Reproductive bet-hedging is another common phenotypically plastic strategy observed in unpredictable environments, wherein individuals vary investment in offspring to increase the chances that at least some match their environment (Vanoverbeke et al. 2009; Shama 2017). Alternatively, maternal effects offer another avenue toward increased response diversity through plasticity (Mousseau and Fox 1998). For example, warmer maternal environments experienced by *Daphnia* producing diapausing eggs cause offspring to emerge at earlier photoperiods (Toyota et al. 2019). In some cases, maternal signals may also be heritable through nongenetic mechanisms such as epigenetic changes to gene expression, which could act to maintain or release genetic variability, and thereby the evolutionary rescue capability of populations. These maternal environmental signals can confer fitness if conditions are predictable from year to year; however, maternal effects and epigenetic changes may often be maladaptive in highly variable phenological environments (O'Dea et al. 2016). While increased plasticity may confer short-term benefits, on timescales when ecological interactions and evolutionary changes merge, increased phenotypic plasticity may reduce the evolutionary response of populations to changing environments, negatively influencing long-term fitness (Pauls et al. 2013; Duputié et al. 2015). Alternatively, the evolution of phenotypic plasticity may allow populations to maintain genetic diversity in variable environments, thereby conferring long-term adaptive benefits (Xue and Leibler 2018; Rago et al. 2019).

Case study: effects of variability in ice-off phenology in a northern Wisconsin, USA, temperate lake

Increasing variability in lake ice phenology has potential ecological and evolutionary ramifications (Weyhenmeyer et al. 2011). Here, we use unique, long-term datasets from Escanaba Lake, located in the Northern Highland Lake District of northern Wisconsin, USA, as a case study to empirically inves-

Fig. 5. Escanaba Lake timeseries of (*a*) lake ice freeze dates (ice-on), (*b*) lake ice thaw dates (ice-off), (*c*) 10-year rolling standard deviation of ice-on (blue) and ice-off (red) dates, (*d*) morning water temperature on 1 May with years when the lake was still frozen shown as 0 °C, and (*e*) 10-year rolling standard deviation of 1 May water temperature. [Colour online.]



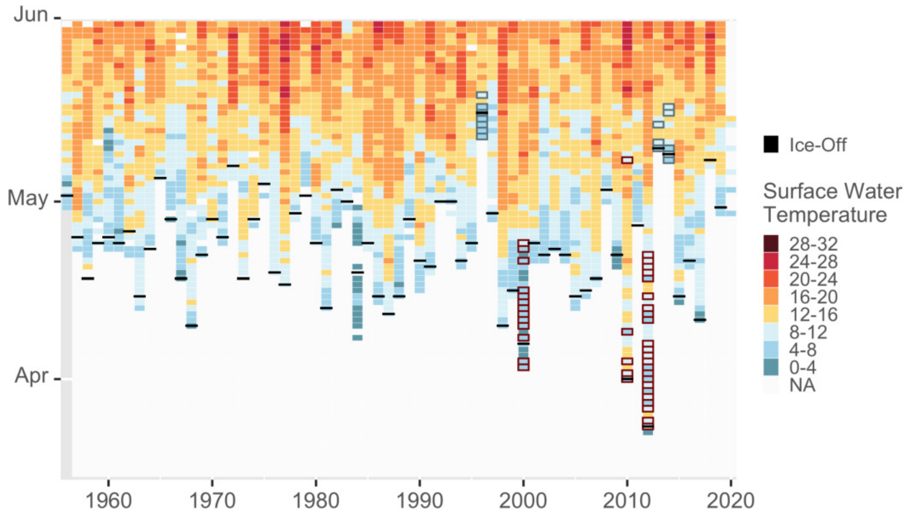
tigate patterns of increasing variation in lake ice phenology. The Wisconsin Department of Natural Resources has monitored ice phenology, environmental conditions (e.g., daily water temperature), and biological variables (e.g., fish population size and recruitment) on Escanaba Lake with few interruptions since 1956, allowing us to demonstrate the limnological and ecological repercussions of an increasing frequency of extreme early and late ice-off years. For brevity, we limit the methodological details of sample collection, which can be found in more detail elsewhere (Serns 1982; Hansen et al. 1998; Shaw et al. 2018).

To examine temporal trends in ice phenology variability, we calculated a 10-year rolling standard deviation of ice dates across the entire period of observation (1956–2020). Ice-on dates were not recorded in 1977, 1982, 1984, and 1985. We performed the same analysis using water temperatures observed on 1 May as an index of spring thermal conditions, which can have strong influences on fish growth and recruitment (Hansen et al. 1998; Redman et al. 2011). To evaluate ecological implications of ice phenology on Escanaba Lake over longer timescales, we focused on walleye, which have been comprehensively surveyed since 1947 (Hansen et al. 1998) using spring fyke netting to capture and estimate adult population size during the spawning period. The date of peak female catch offers a metric of peak spawn timing in this population (see also Schneider et al. 2010). The abundance of YOY walleye is determined using fall (water temperatures around 12 °C) mark–recapture AC electrofishing surveys of the entire shoreline as a measure of recruitment. We evaluated temporal trends in average spawn timing as well as temporal changes in the 10-year rolling standard deviation of spawn timing to test whether walleye spawning phenology has become similarly variable as ice phenology. We then related YOY recruitment to annual spawn timing mismatch (i.e., the difference between annual peak spawn timing and the overall mean) to assess the potential for mismatches to influence walleye recruitment.

Variability in ice-off phenology and spring conditions during walleye spawning

In Escanaba Lake, there has been no trend in ice-off dates and a slight shift toward later ice-on dates since 1956. However, both overall variability and the frequency of extreme years have increased substantially (Figs. 5*a*–5*c*). These patterns are largely similar to those observed in temperate lakes globally (Fig. 1). The three earliest and latest ice-off years, with one exception, have all occurred in the 21st century; the most extreme early years were 2000, 2010, and 2012, and the most extreme late ice-off years were 1996, 2013, and 2014 (Fig. 5). The average difference in ice-off date from one year to the next has roughly doubled since the 1980s (mean: 8.5 days) and 1990s (mean: 9.8 days) to the 2010s (mean: 18.2 days). Most notably, from 2011 to 2013, the ice-off date seesawed from 26 April to 22 March to 9 May. The latter is a span of 47 days. Water temperatures on 1 May exhibited coherent patterns with ice-off phenology (Figs. 5*d* and 5*e*). Notably, the lake still being frozen on 1 May was historically rare, but has occurred three times in the past decade. Therefore, there is evidence for limited coarse-grained (i.e., direc-

Fig. 6. Spring (15 March to 1 June) surface water temperature in Escanaba Lake. Ice-off dates are shown with a thin horizontal black line. Ideal walleye spawning temperature (5–10 °C) is highlighted for the three earliest (red outline) and three latest (blue outline) ice-off years to demonstrate differences in potential spawning duration in extreme years. [Colour online.]



tional) change in phenology in the region; rather, increased fine-grained (i.e., interannual) variation in climate has led to increasingly unpredictable springtime growth conditions for flora and fauna, which has implications for the rates of pheno- and genotypic changes within populations in their responses to climate change (Crozier and Hutchings 2014; Merilä and Hendry 2014).

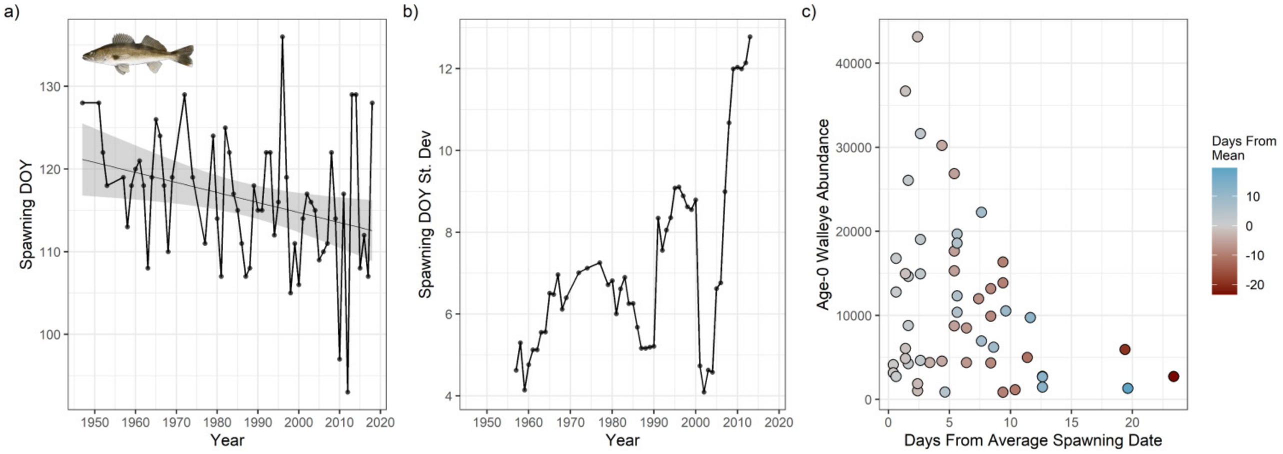
Consequences of ice-off variability for walleye spawning and recruitment

Average ice-off in northern Wisconsin takes place in late April, but can range from late March to mid-May (Dugan 2021), and Arctic warming may be responsible for increasing the variability of winter weather (Cohen et al. 2020). In Escanaba Lake, most walleye spawning activity occurs when spring water temperatures are between 5 and 10 °C (the mean ± SD water temperature on dates when spawning females were captured was 8.3 ± 3.0 °C), which aligns well with walleye from other systems (reviewed in Feiner and Höök 2015). In early ice-off years, ideal spawning temperatures took place almost a month earlier than late ice-off years, and the duration was much longer (Fig. 6). In late ice-off years, surface waters warmed extremely fast, and the window of ideal temperatures may only last a few days (Fig. 6). Furthermore, the timing of ice melt can affect lake conditions for the remainder of the year. Dugan (2021) showed in an assessment of eight north-temperate lakes in Wisconsin that lakes demonstrated clear ecological memory (e.g., carryover effects of ecological phenomena influencing later dynamics; O'Connor et al. 2014; Hughes et al. 2019) of ice-off conditions in their physical limnology. Spring epilimnetic water temperatures are higher in early ice-off years, and longer spring mixing periods in early ice-off years allow hypolimnetic waters to gain heat, resulting in warmer hypolimnia through the summer, altering habitat for fish like walleye (Lester et al. 2004).

Over time in Escanaba Lake, walleye spawning trended earlier (1.2 days per decade; Fig. 7*a*) and became more variable (Fig. 7*b*). Extreme spawning dates had deleterious effects on walleye recruitment (Fig. 7*c*). Walleye recruitment was below average when spawning occurred more than 10 days earlier or later than average. Peak recruitment years only occurred when spawning occurred within 5 days of the long-term average, and recruitment was never high when spawning was more than 10 days out of sync (Fig. 7*c*). These patterns are highly suggestive of trophic mismatches controlling walleye recruitment (indeed, larval walleye growth has been found to be sensitive to the availability of appropriately sized prey; Hoxmeier et al. 2004), although more research is needed to fully explore the mechanistic links among ice and spawning phenology and walleye recruitment overall. Nonetheless, an increasing frequency of extreme years could have long-lasting, negative effects on the viability of this and other important cold- and coolwater fish populations by increasing the frequency of poor recruitment years and making strong recruitment years rarer.

Although we have focused on spring (ice-off) phenology here, variability in fall (ice-on) phenology may also have ecosystem consequences that are coupled or decoupled with ice-off variability. In some north-temperate lakes, coldwater native, fall spawning fishes such as lake trout (*Salvelinus namaycush*), cisco (*Coregonus artedi*), and lake whitefish (*Coregonus clupeaformis*) exist at the southern extent of their range, where climate change effects are predicted and have resulted in extirpations of these species (Sharma et al. 2011; Honsey et al. 2016; Renik et al. 2020). For example, Renik et al. (2020) showed that about 30% and two-thirds of former cisco and lake whitefish populations have been extirpated from inland lakes in Wisconsin, respectively. Lake trout, cisco, and lake whitefish are fall spawners where spawning activity is cued by photoperiod and temperature, and egg hatching in spring is linked to specific water temperature growing de-

Fig. 7. Patterns in walleye spawning phenology and recruitment in Escanaba Lake, including (*a*) day of year (DOY) of peak walleye spawning activity (indexed by DOY of peak catches of spawning females), (*b*) rolling 10-year standard deviation in peak spawning DOY, and (*c*) relationship between spawning mismatch (the difference between a year's spawning date and the overall mean) and age-0 walleye recruitment in fall, where points are shaded by the direction (early—red, late—blue) and magnitude of mismatch (brighter colors—larger mismatch).



gree days (Lyons et al. 2015), which can be influenced by variability in ice-on and ice-off dates and winter limnological conditions.

Research priorities

Our perspective has illustrated how recent phenological regimes are becoming atypical of the historical context for which aquatic communities are adapted, influencing limnological and biological processes in the short and long term. Data from temperate lakes highlight the critical need to develop an understanding of how increasing climate and phenological variability, not just long-term average trends, may erode ecosystem functionality. However, in developing this perspective, it also became clear that phenological dynamics and trophic asynchronies are understudied in freshwater systems when compared to marine and terrestrial biomes. Comprehensive, long-term phenological studies occur in only a handful of freshwater systems (e.g., this study, Müggelsee, Lake Washington, and Windermere; Adrian et al. 2006; Thackeray et al. 2013; Walters et al. 2013). With clear—and in many cases substantial—changes in phenology occurring globally (Sharma et al. 2019), there is a critical need to better understand whether increasing variability in climate influences ecological and evolutionary processes in freshwater systems. We offer perspectives based on our observations for a series of research priorities focused on understanding the ecological and evolutionary consequences of ice variability on inland waters.

(1) High-resolution data during transitional seasons

Studying climate-related change requires long-term data, especially when evaluating changes in ecosystem variability over time. Multiple lines of evidence support the notion that air temperature, precipitation, and wind speeds have become increasingly variable (Groisman et al. 1999; Easterling et al. 2000; Cohen et al. 2020). To build a better understanding of whether these large-scale, climate-related, increases in variability are influencing ecosystem functioning and resident organisms, high-frequency sampling of ecosystems is required, especially in spring when organisms are developing, and ecological interactions are establishing conditions for the remainder of the growing season. Routine sampling programs typically operate on biweekly to monthly sampling intervals, and these intervals may be too low in frequency to capture phenological interactions (Dugan 2021). Manual sampling can be supplemented with high-frequency sampling using in situ sensors deployed on lake buoys (Hamilton et al. 2015). To capture the fall-to-winter and winter-to-spring transitions, buoys must be deployed under lake ice (Yang et al. 2021) and should not be restricted to "deep hole" sampling (i.e., only sampling the deepest point of the lake). Ice-out dynamics within lakes may vary spatially, which has implications for species using nearshore habitats.

(2) Trophic interactions and asynchronies

Empirically identifying trophic asynchronies in aquatic food webs is difficult, but necessary to understand whether phenology influences trophic interactions and the flow of energy through food webs through ecological memory effects on ecosystem properties (Hébert et al. 2021). To test for mismatched timing in predator and prey species, changes in the composition of fast-growing phytoplankton, zooplankton, and ichthyoplankton communities must be documented. Again, this requires high-frequency sampling across the winter–spring transition. To provide support of phenological mismatch in extreme ice-off years, evidence is required that establishes consumer–resource relationships (diet and isotopic analyses) and influences on consumer fitness (population density and growth). High-resolution studies of consumer diets could further reveal important phenological or ontogenetic shifts that control consumer performance and have potential legacy effects in long-lived species (May et al. 2019) or alter resource availability in later months via selective feeding or top-down controls (Hoffman et al. 2001).

(3) Implications of diversity from genes to ecosystems

With increasing variability in ice coverage, ecosystem fragility is a concern. As increased variability threatens thresholds for state changes, the size of systems, scales of change, and diversity of species, gene pools, and ecological function are all important. Concepts of evolutionary rescue and ecological resilience are premised on historical research establishing that highly diverse systems with functional redundancy and plasticity in genetics and food web structure will be more robust to variability and disturbance. Documenting changes in diversity, from genes to ecosystems, in response to phenological variability will be key to understanding eco-evolutionary dynamics of phenological variability (Siepielski et al. 2009; Carlson et al. 2014). This means that changes in genetic diversity should be documented in congruence with changes in community and ecological diversity, because in the same way that loss of community diversity can destabilize systems, loss of genetic diversity within and across species acts to limit the ability of species to adapt (Hoffmann et al. 2017). Numerous theoretical models have predicted that variability will lead to a loss of genetic diversity and ecological function over time, but empirical tests of model predictions are consistently called for (Gienapp et al. 2014; Vázquez et al. 2017).

Understanding the selective mechanisms driving genetic change in response to altered phenology will require basic information about the genetic underpinnings of phenology in many different taxa. Single-nucleotide polymorphism (SNP) analyses could be used to test for differences in population genetic structure and selection pressures between early and late ice-off years. These analyses could also target specific phenology-related thermal and circadian loci (Madsen et al. 2020) to test whether these regions experience greater change than other regions of the genome. Once the underlying genetic structure of phenological evolution is better documented, reciprocal transplant experiments, targeted stocking programs, and focused phenotypic assays across lakes could target research on phenological phenotypes and changes in phenotypic plasticity. At the community level, documenting changes in taxonomic and functional diversity of community components (i.e., phytoplankton, zooplankton, and forage fish) will be important, as loss and gain of species, changes in species dominance, or increases in invasive species can all occur and are predicted responses to disturbance that can destabilize ecosystem function (Miller et al. 2021).

(4) Managing for increasing variability

For lakes experiencing increasing climate variability, developing strategies to manage for diversity at the intra- and interspecific levels may become paramount for supporting resilient ecosystems (Carpenter et al. 2017; Tingley III et al. 2019). Fisheries management can implement regulations to promote demographic or phenotypic diversity in spawning date, which may ensure that some proportion of recruits experience benign environments and stabilize recruitment (Schindler et al. 2010; Freshwater et al. 2019*a*). For example, Wisconsin walleye fishing seasonally closes between two fixed dates (first Sunday in March and first Saturday in May). As walleye spawning shifts earlier, this may lead to early-spawning fish becoming susceptible to harvest, meaning that responsive regulation to shift this closed window may be necessary to fully protect spawning fish. Increasing or maintaining habitat diversity (i.e., plant diversity and landscape heterogeneity) and (or) connectivity among diverse metapopulations can increase the viability of populations and maintain important genetic diversity needed for adaptation to new phenological regimes (Sgrò et al. 2010; Sass et al. 2017; Zelnik et al. 2018). In situations where organisms are targeted coincident with major phenological cues (i.e., spawning fish and fruiting plants), phenologically informed regulations can protect vulnerable populations and prevent overharvest of segments of the phenological distribution that may disrupt genetic or phenotypic diversity (Peer and Miller 2014; Erisman et al. 2017; Tillotson and Quinn 2018). Lastly, maintaining populations within a safe-operating space by minimizing the influence of other external stressors within managerial control, through improved land use management, reduction of nutrient loads, and prevention of species invasions, can further buffer populations against climate effects outside of managerial control, such as increasing phenological volatility (Seavy et al. 2009; Carpenter et al. 2017).

Conclusions

Each of the 100 million inland waterbodies on Earth has different historical annual patterns, unique food webs, and an unknown capacity for adaptation. It is critical to begin developing a better understanding of whether the timing and variability of seasonal events (phenology) are responding to climatic changes and variability. There is a critical need for limnologists to address the ecosystem-level influences of climate variability. Does a loss of environmental predictability lead to novel trophic mismatch, and thereby new food web configurations and new opportunities for abrupt change? Could increasing variability be an early warning sign of a transition to a new ecosystem state (Dakos et al. 2012)? What are the implications of phenological extremes on the genetic structure of populations and the resilience of inland aquatic ecosystems to adapt to new climate regimes?

Advancing understanding of phenological change requires long-term data across multiple levels of biological organization and records of phenological trait distributions (Thackeray 2016; Kharouba et al. 2018; Caldwell et al. 2020). From individual waterbodies to the entirety of global inland waters, what is likely to shift, what abrupt changes might we expect, and what is at risk of collapsing? From genes to ecosystems, the influences of climate change should be viewed through the lens of climate variability, intra- and interannual (Straile et al. 2015), as well as long-term shifts in the mean (Vasseur et al. 2014).

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Data accessibility

The North Temperate Lakes Long-Term Ecological Research (NTL-LTER) data used in the manuscript are available through the NTL-LTER website and the Environmental Data Initiative. Data DOIs are cited in the manuscript. Escanaba Lake data are available upon request to GGS.

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