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LETTER

# Lagging spawning and increasing phenological extremes jeopardize walleye (*Sander vitreus*) in north-temperate lakes

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## *Scientific Significance Statement*

Climate change is predicted to have varying and often unpredictable effects on ecosystems, communities, and populations. Given that many fish species rely on climatic cues to initiate seasonal behaviors such as spawning, changes in these cues have the potential to disrupt freshwater phenological processes. Although many studies have tested whether long-term changes in climate affect freshwater ecosystems, few studies have examined the influence of increasing climate variability on freshwater species. Our study provides some of the first evidence that increasing climate variability may disrupt tightly coupled ice-off and walleye (*Sander vitreus*) spawning phenology, potentially leading to a greater frequency of natural recruitment failures that could threaten a commercially, culturally, and recreationally important fishery.

## *Abstract*

The phenology of critical biological events in aquatic ecosystems is rapidly shifting due to climate change. Growing variability in phenological cues can increase the likelihood of trophic mismatches (i.e., mismatches in the timing of peak prey and predator abundances), causing recruitment failures in important fisheries. We assessed changes in the spawning phenology of walleye (*Sander vitreus*) in 194 Midwest US lakes to investigate factors influencing walleye phenological responses to climate change and associated climate variability, including ice-off timing, lake physical characteristics, and population stocking history. Ice-off phenology shifted earlier, about three times faster than walleye spawning phenology over time. Spawning phenology deviations from historic averages increased in magnitude over time, and large deviations were associated with poor

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Additional Supporting Information may be found in the online version of this article.

offspring survival. Our results foreshadow the risks of increasingly frequent natural recruitment failures due to mismatches between historically tightly coupled spawning and ice-off phenology.

Ogaa (walleye *Sander vitreus*) are part of the cultural identity of Ojibwe tribes that currently live in the Ceded Territories of the Upper Midwest United States. Ojibwe tribes in this region hold the Seventh-Generation philosophy that humans must be mindful of future generations when hunting, gathering, and fishing for sustenance and well-being (Shultz et al. 2022). Due to long-standing connections with their relatives (resources), tribal members use environmental cues to mark changes in the seasons (e.g., singing of agoozimakakii (spring peeper *Pseudacris crucifer*) marks the start of the ogaawag aamiwag (walleye) spearing season; GLIFWC Climate Change Team 2023). We have incorporated Ojibwe words and phrases to recognize that indigenous knowledge systems contribute to a fuller understanding of environmental change, an attempt at two-eyed seeing (Reid et al. 2021).

Climate change (Aanji-bimaadiziimagak o'ow aki, loosely meaning "the world is changing") affects the phenology, or seasonal timing, of a wide variety of organisms (GLIFWC Climate Change Team 2023). One of the most well-documented trends is an increasingly earlier shift in spring biological events associated with rising temperatures (Thackeray et al. 2010). Previous studies investigating phenological shifts in freshwater fish have linked warming temperatures with earlier spawning in spring-spawning species (Lyons et al. 2015). The mechanisms associated with these temporal shifts are elusive, given that the strength and direction of phenological change may vary within and among species (Thackeray et al. 2010; Samplonius et al. 2021). Spatiotemporal differences in environmental cues can further complicate expected phenological responses to climate change (Hewitt et al. 2018; Rogers and Dougherty 2019).

Although most assessments of phenological change have focused on directional temporal trends, climate change is also predicted to increase environmental variability (Feiner et al. 2022*a*). Understanding biological responses to increasing seasonal variability can be critical for predicting how species will respond to climate change (zaasigaakwii, barely holding on). For instance, differing phenological responses between predators (gaayosed/gaayosejig, s/he who hunts) and prey (miijimaawesiinh, food animals) may create trophic mismatches (gaawiin naasaab, not alike), in which the peak abundance of prey organisms is not temporally aligned with the peak abundance of their predators. Trophic mismatches can break down essential food web linkages (aandanjige, she/he changes her/his diet) and substantially influence predator offspring survival. Frequent or prolonged temporal mismatches have significant conservation implications, as reduced offspring survival can threaten ecosystem sustainability (Samplonius et al. 2021).

Indigenous knowledge holders have observed decreases in ice thickness on inland lakes over time, which may contribute to early ice-off (baakibii'an, the annual timing of the melting of lake ice in spring; GLIFWC Climate Change Team 2023). Ice-off prompts increases in lake primary productivity and the production of food resources for larval fish (Dugan 2021), suggesting early or more variable ice-off phenology may have cascading effects on lake food webs. In spring-spawning freshwater fish, for example, variable ice-off phenology may alter the timing of the temporally limited peak abundance of appropriately-sized prey, ultimately reducing fish growth and survival (Galarowicz and Wahl 2005).

We used a spatially and temporally expansive dataset of spawning phenology in walleye from north-temperate lakes in the Upper Midwest USA to address questions about climate-driven phenological change in freshwater aquatic ecosystems. We asked the following questions: (1) Is walleye spawning or ice-off phenology shifting over time?; (2) Is there a relationship between walleye spawning and ice-off phenology?; (3) Do trends in walleye spawning phenology vary with lake characteristics or walleye stocking history?; and (4) Is the potential for trophic mismatches changing over time, and what are the influences on the survival of walleye offspring? Our findings reveal climate effects on fish populations through decoupled phenological cycles in freshwater ecosystems, which has important conservation implications for species likely to be affected by the phenological influences of climate change (Thackeray et al. 2016).

## Methods

### Spawning and ice phenology data

Walleye are a culturally, recreationally, commercially, and ecologically important north-temperate freshwater fish. Previous studies have shown that walleye exhibit spring-spawning behavior cued by ice-off (baakibii'an; Schneider et al. 2010), increasing water temperature (ani-giizhoogamin, water is starting to warm), and photoperiod (apiichi-waaseyaa, be a certain amount of sunlight; Feiner and Höök 2015). Walleye have declined across the Upper Midwest over the past several decades due to natural recruitment declines, habitat loss (banaajitaakamig, spoiled, ruined, destroyed land), warming water, fish community change, and production overharvest (onzaami-mamoon, too much harvest; Embke et al. 2019; Sass et al. 2021; Dassow et al. 2023). In response, walleye have been widely stocked in the region (Feiner et al. 2022*a*).

Walleye spawning phenology data were collected by the Wisconsin Department of Natural Resources (WDNR), the Minnesota Department of Natural Resources (MNDNR), and the Great Lakes Indian Fish and Wildlife Commission (GLIFWC). Annual mark-recapture adult walleye population estimates and tribal spearfishing harvest dates were used to identify peak spawning activity in 194 Upper Midwestern lakes over several decades (1940s to present, Fig. 1; for

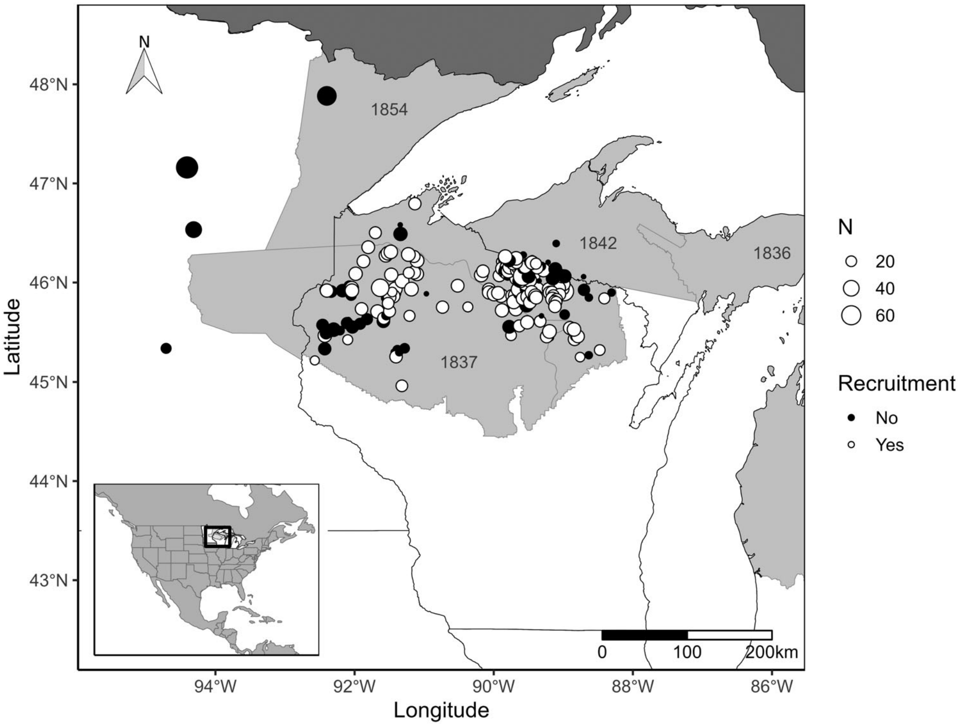

**Fig. 1.** The locations of the 194 Michigan, Minnesota, and Wisconsin, USA, lakes used in our analyses. The lakes are color-coded according to the availability of walleye (*Sander vitreus*) recruitment data (black = not available, white = available) and sized based on number of years of spawning observations. The shaded areas represent the Ojibwe Ceded Territories from the treaties of 1836, 1837, 1842, and 1854.

complete details on fish sampling, *see* Supporting Information Material S1). After performing power analysis, we limited our analyses to lakes with ≥ 11 yr of spawning observations to eliminate uncertain rates of change derived from small sample sizes (Supporting Information Material S1; Figs. S1, S2).

Ice-off phenology data was collected from two sources. Where available, we used observed ice phenology data from the Global Lake and River Ice Phenology database (Benson et al. 2000), which covered ~ 7% of lakes and lake-years. For lakes that lacked long-term observed ice-off records, we used modeled ice-off dates derived from a USGS region-wide machine-learning model that used North American Land Data Assimilation System (NLDAS) meteorological inputs combined with lake characteristics (lake position, clarity, size, depth, hypsography, etc.) to predict daily water column temperatures from 1979 to 2022, from which ice-off dates could be derived (https://www.sciencebase.gov/catalog/item/6206d3c2d34ec05caca53071; *see* Corson-Dosch et al. 2023 for details). Modeled data performed well in reflecting ice phenology when compared to observed data (correlation between observed and modeled ice-off dates; $r = 0.71$; $p < 0.001$).

## Lake characteristics and stocking histories

We examined the effects of lake characteristics, including size, depth, location, lake class, and walleye stocking history, on spawning phenology. Lake surface area, latitude, and maximum depth were acquired from agency databases and lake reports. Lake class was based on a WDNR lakes classification system (Rypel et al. 2019) that categorized lakes based on temperature, water clarity, depth, and fish community. Walleye stocking history was characterized by the relative contributions of naturally produced and stocked fish to adult recruitment using the walleye stocking classification system developed by the Wisconsin Technical Working Group (*see* also Sass et al. 2021). Wisconsin lakes were divided into three groups: natural recruitment (NR), a combination of stocking and natural recruitment (C-ST), and stocked only (ST).

## Data analysis

Across lakes, time series ranged from 11 to 75 yr of observations (median = 25 yr). We included all 194 lakes in our analyses concerning the first three lake physical characteristics (surface area, maximum depth, latitude). We used 170 and 185 Wisconsin lakes in our analyses concerning lake class and stocking status, respectively, based on available data. All data are publicly available (Feiner et al. 2023). We completed all statistical tests in R version 4.2.3 (R Core Team 2023).

To address our study objectives pertaining to changes in walleye spawning phenology, we fit a set of five Bayesian hierarchical mixed models in Stan (Stan Development Team 2023) using R package "rstanarm" (Goodrich et al. 2023) using default priors, 1000 warmup iterations, and four chains. Model 1 (defined below) was run for 20,000 steps to achieve convergence (based on visual inspection of trace plots, R-hat near 1.0, and effective sample size > 1000). All other models converged after 10,000 iterations. Model coefficients were examined using 10,000 random draws from posterior distributions. The set of models included:

1. Models with either walleye spawn day of year (DOY) or ice-off DOY as the response, random intercepts for the lake, a fixed effect of year, and random slopes to allow the effect of year to vary by lake to examine potential temporal trends in walleye and ice phenology. These models revealed minimal evidence for among-lake variation in slopes ($\sigma_{\text{year}} < 0.002$, *see* Results), which led to poor model performance when covariates were later added. Therefore, random slope terms were not included in subsequent models.
2. A model with walleye spawning DOY as the response, random lake intercepts, and ice-off DOY as the fixed predictor (where a slope near 1 indicates tracking of ice-off timing by walleye).
3. A model with walleye spawning DOY as the response, random lake intercepts, fixed effects of year, lake maximum depth, lake surface area, and lake latitude, and interactions between year and each environmental covariate to assess the effects of lake characteristics on spawning phenology. Lake maximum depth, surface area, and latitude were only moderately correlated ($r \sim 0.5$), which allowed us to assess their potential effects on spawning phenology in a single model.
4. A model with walleye spawning DOY date as the response, random lake intercepts, and fixed effects of year, lake class, and their interaction to assess the effects of lake class on spawning phenology.
5. A model with walleye spawning DOY as the response, random lake intercepts, and fixed effects of year, stocking status, and their interaction as predictors to assess the effects of stocking history on spawning phenology.

We examined temporal trends in phenological variability and its effect on walleye recruitment using similar methods. We quantified spawning phenological variability as the deviation from average conditions by calculating the absolute difference between each lake and year's peak spawning DOY and the long-term mean spawning DOY for that lake. This metric captured the deviation in spawning phenology from historical norms and allowed us to directly assess the hypothesis that mistimed spawning, in either direction, negatively influenced walleye recruitment through match–mismatch dynamics (e.g., Galarowicz and Wahl 2005). Previous studies have similarly examined the potential negative effects of phenological change by quantifying phenological variability on an absolute scale (e.g., Post and Forchhammer 2007), illustrating the possible ecological consequences of deviation from phenological norms in either direction. Walleye natural recruitment was indexed as age-0 walleye CPE (number of age-0 walleye captured per km of shoreline electrofished) from WDNR and GLIFWC fall electrofishing surveys (*see* Hansen et al. 2015 for details). We excluded lake-years where stocking of age-0 fish occurred before age-0 surveys to ensure our analysis was only examining the effect of spawning date deviation on naturally produced fish ($N = 122$ lakes). To assess whether deviations were increasing in magnitude over time, we first fit a Bayesian hierarchical gamma regression (log-link) using deviation as the response, year as a fixed predictor, and random intercepts by the lake. We then examined the potential effect of spawning phenology deviations on walleye recruitment success using a similar gamma regression with age-0 walleye CPE as the response, random lake intercepts, and spawning phenology deviation as the fixed predictor.

## Results

Walleye spawning dates trended earlier over time by about 0.37 d per decade (effect of year = −0.037 ± 0.015 (SE) d/yr), the probability that this effect was less than zero ($p(\beta < 0) = 0.99$) with minimal trend variability among lakes (random slope SD = 0.002; Fig. 2a; Supporting Information Table S1). There was a clearer, and much more rapid, shift toward earlier ice-off dates across lakes, where ice-off dates occurred about 1.1 d per decade earlier over time (effect of year = −0.11 ± 0.014 d/yr, $p(\beta < 0)$

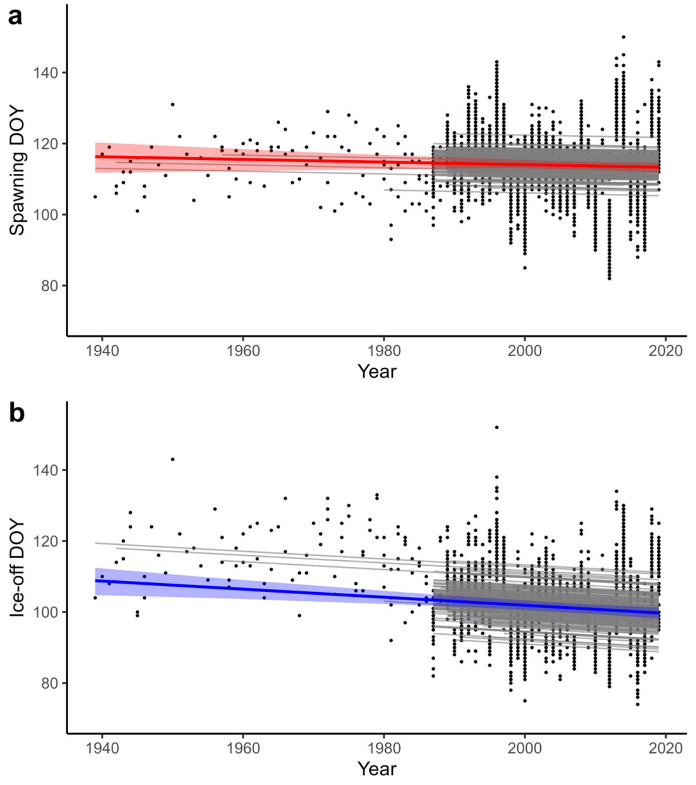

**Fig. 2.** Temporal trends in (**a**) walleye (*Sander vitreus*) peak spawning dates and (**b**) ice-off dates across 194 lakes based on hierarchical regression models. Black points are observed data, thin gray lines are lake-specific trends, and colored lines and shaded areas are the global relationship and 95% credible interval.

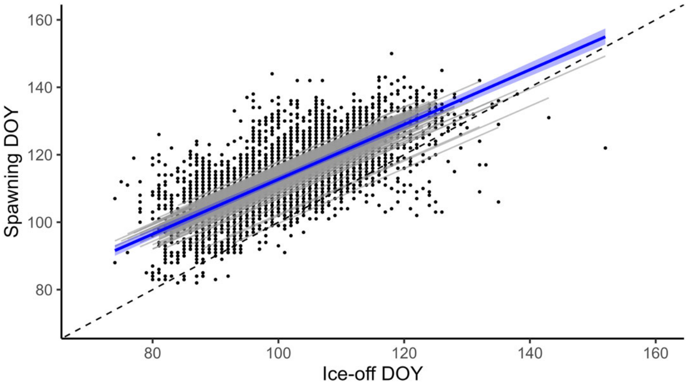

**Fig. 3.** Relationship between walleye (*Sander vitreus*) spawning dates and ice-off dates across 194 Upper Midwestern lakes. Black points are observed data, thin gray lines are lake-specific trends, and colored lines and shaded areas are the global relationship and 95% credible interval (CI) from a hierarchical linear regression model. Dashed line represents a 1 : 1 relationship to demonstrate that the ice-walleye relationship is less than 1 (slope and CI: 0.81, 0.79–0.83).

$= 1.00$; Fig. 2b; Supporting Information Table S2). Changes in ice-off dates were also largely coherent among lakes (random slope SD $= 0.002$). Walleye and ice-off DOY were strongly related within lakes, but the slope of this relationship was substantially less than one (slope $= 0.81 \pm 0.011$, $p(\beta < 1) = 1.00$; Fig. 3; Supporting Information Table S3).

None of the surface area, latitude, maximum depth, or lake class characteristics influenced trends in walleye phenology (Supporting Information Figs. S3, S4; Supporting Information Tables S4, S5). Lakes supported by natural recruitment trended toward earlier spawning over time (NR, year slope $= -0.046 \pm 0.018$, $p(\beta < 0) = 0.99$) while lakes supported partially by stocking (C-ST slope $= -0.026 \pm 0.022$, $p(\beta < 0) = 0.84$) or wholly by stocking (ST slope $= -0.019 \pm 0.027$, $p(\beta < 0) = 0.73$) showed less evidence of temporal trends. However, contrasts in these slopes showed little evidence for pairwise differences (Supporting Information Fig. S5; Supporting Information Table S6).

Deviations in walleye spawning phenology increased substantially over time by $\sim 2.2\%$/yr (mean slope $= 0.022 \pm 0.001$ SE, $p(\beta > 0) = 1.00$), which amounted to a $\sim 92\%$ increase over the past three decades (from $\sim 6.5$ to $\sim 12.5$ d; Fig. 4a; Supporting Information Fig. S6; Supporting Information Table S7). Age-0 walleye CPE was negatively related to the magnitude of spawning phenology deviations, declining by $\sim 3.3\%$/d of additional deviation from average timing (mean slope $= -0.033 \pm 0.004$ SE, $p(\beta < 0) = 1.00$) and by more than half across the range of deviations observed (Fig. 4b; Supporting Information Table S8).

## Discussion

Using an expansive dataset, we found a slight trend toward earlier peak spawning dates in walleye (ogaa) throughout the Upper Midwest US ($\sim 0.4$ d/decade). Although this result does indicate a small shift in walleye spawning phenology, previous studies have shown much more rapid trends toward earlier spawning in other Midwestern percids. For example, Lyons et al. (2015) found a change of 6.2 d/decade in Lake Michigan yellow perch (*Perca flavescens*). Our results also counter previous findings suggesting that fishes generally exhibit marked phenological shifts (Thackeray et al. 2016). The minimal shift in walleye spawning phenology we observed has several implications for our understanding of walleye spawning cues. Trends in walleye spawning phenology may be less directly responsive to ice phenology than originally predicted (Watts et al. 2022). The nearly static nature of spawning dates may also suggest a larger role for photoperiod in moderating spawning dates than previously thought (Feiner and Höök 2015).

Ice-off dates shifted earlier at a rate of $\sim 1.1$ d/decade, or about three times faster than the change in walleye spawning

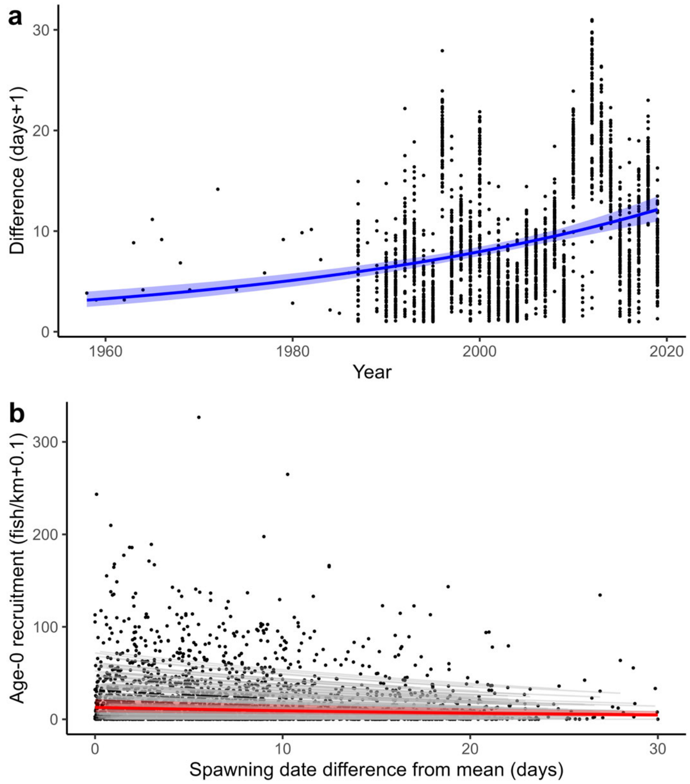

**Fig. 4.** Trends in (**a**) walleye (*Sander vitreus*) spawning phenology deviation, defined as the absolute difference in days between the date where peak spawning occurred and the lake-specific long-term average, and (**b**) the relationship between walleye spawning deviation and walleye recruitment (age-0 walleye/km captured in nighttime electrofishing), observed across 122 lakes in the Upper Midwest. Black points are observed data, thin gray lines are lake-specific trends, and colored lines and shaded areas are the global relationship and 95% credible interval from hierarchical gamma regressions (among-lake intercept variation was minimal in panel (**a**), so lake-specific lines are obscured behind global trend). A small constant was added to each response variable to aid in model fitting.

phenology. This dramatic difference between spawning and ice-off phenological change may demonstrate a threat to walleye populations, given the importance of their temporal coupling for the maintenance of trophic synchrony between juvenile walleye and the peak abundances of their prey (Hartman and Margraf 1992; Galarowicz and Wahl 2005). Supporting this, walleye spawning somewhat lagged ice-off phenology within lakes, as a 1 d shift in ice-off date was associated with only a 0.8 d shift in peak spawning date. Therefore, although ice-off is directly related to climatic conditions each year (Hewitt et al. 2018), our results suggest that walleye phenology may be unable to maintain the same degree of interannual flexibility necessitated by the observed climate variability. These findings highlight the potential detrimental effects of increasing climate-driven extremes in abiotic phenological events and constrained interannual plasticity of biotic responses. Because ice-off cues the boost in primary productivity that stimulates the production of prey for larval walleye (Dugan 2021), a misalignment of ice-off and peak walleye spawning in years with extreme climatic conditions may decrease prey availability during times when larval walleye are most abundant (gawanaandam, he/she starves). This temporal mismatch (gaawiin naasaab, not alike) could further erode recruitment success in naturally reproducing populations (Siddon et al. 2013) and threaten already declining walleye populations (zaasigaakwii, barely holding on).

We found little evidence for environmental effects on trends in walleye spawning phenology. We did, however, observe a potential effect of fish stocking. Lakes with walleye populations supported entirely by natural recruitment trended toward earlier spawning, while lakes supported partially or entirely by stocking showed no change (although pairwise differences in slopes were minimal). Other studies have shown how broodstock collection and aquaculture practices can have selective effects on spawning behavior (Stefanik and Sandheinrich 1999; Austin et al. 2021), suggesting additional work to unravel the potential effects of stocking on walleye phenology may be warranted, particularly given widespread walleye stocking programs in the region (Feiner et al. 2022*b*). We also note that we were not exhaustive in examining other determinants of spawn timing, such as population demography (Rogers and Dougherty 2019). Future research should continue to assess the influence of other climatic and non-climatic variables on phenology. Notably, the interplay between season length, spawning duration, and the potential for resulting trophic mismatch should continue to be explored (Guzzo et al. 2017).

The average magnitude of spawning date deviations from long-term averages more than doubled over the past four decades (from ~ 5 d in 1980 to ~ 13 d in 2020). Because recruitment success was strongly negatively related to these deviations, an increase of this magnitude would correspond to an expected 23% decrease in walleye natural recruitment. Given that walleye are presumably adapted to environmental conditions typical of average spawning dates, deviations from these conditions due to climatic extremes (e.g., early or late ice-off) may present ecological and physiological challenges for successful reproduction (Feiner and Höök 2015). Because climate change is predicted to increase climatic variability (Feiner et al. 2022*a*), our results represent some of the first research examining the threats of increasing climatic variability on long-term population sustainability. While outside the scope of this study, future research should investigate the mechanisms of potential differences in recruitment success between years with early spawning dates and years with late spawning dates, which may reveal the processes limiting recruitment success in different biotic and abiotic environmental conditions.

One major confounding factor in our study was a sampling limitation. Mark-recapture surveys and tribal harvest each spring cannot be conducted until ice-off allows lake access. Thus, it is possible that peak walleye spawning occasionally occurred earlier than was recorded. The correlation between ice-off and the beginning of sampling could also artificially inflate the relationship between spawning and ice phenology. However, because the sampling process is standardized each year and our analyses examined trends over time rather than absolute dates, this sampling limitation should not have appreciably influenced our results. In addition, the use of modeled ice-off dates derived from a machine-learning model may have also introduced error into our analyses, although preliminary results showed a highly significant correlation between observed and modeled ice-off dates in cases where both were available. This suggests that any error introduced by modeled data was minimal.

Given the mismatched trends in ice-off and walleye spawning phenology, declining walleye natural recruitment (Rypel et al. 2018; Honsey et al. 2020), and the potential for trophic mismatches due to limited plasticity in spawning phenology (Feiner et al. 2022*a*), strategies to mitigate the negative effects of climate change on walleye should continue to be explored with the assistance of local communities and tribal populations (Carpenter et al. 2017; Dassow et al. 2023). Our results also have important implications for many other taxa exhibiting phenological dependence on climate (Stenseth and Mysterud 2002). It is likely that disparate phenological responses and adaptations among organisms will play an outsized role in food web structure (Nakazawa and Doi 2012; Post 2017) and species persistence (Ramos–Jiliberto et al. 2018; Rudolf 2019) in an increasingly variable future. Our results further demonstrate the need for careful mechanistic examinations of population and community phenology to evaluate susceptibilities to phenological change and better inform management strategies that can increase ecosystem resilience (Carpenter et al. 2017) and prepare for potential shifts to new ecosystem states (Shultz et al. 2022).

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