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Research Article

Synchrony of alewife, *Alosa pseudoharengus*, year-class strength in the Great Lakes region

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Abstract

Fish recruitment is interannually variable and challenging to predict. Annual recruitment is often regionally synchronized among populations and identifying drivers of such synchrony may help shed light on recruitment dynamics. We investigated interannual variation of alewife *Alosa pseudoharengus* recruitment by estimating year-class strength for populations from three of the Laurentian Great Lakes (lakes Huron, Michigan, and Ontario) using annual assessment survey data from 1968 to 2022. We first determined the age when year-class strength was set for each dataset. We then used a mixed-modeling approach incorporating age, year-class, and sampling year to estimate year-class strength for each study lake. Thereafter, we evaluated regional synchrony in year-class strength across the three lakes and evaluated potential climatic drivers of synchrony. Our results suggest that alewife year-class strength is set by age-1. Our model-derived indices of alewife year-class strength were synchronized among the three lakes, and we identified spring-summer degree-days as a potential regional driver of synchrony. This analysis highlights the potential for strong influence of climatic conditions on fish recruitment in large freshwater systems.

Key words: spatial synchrony, recruitment, climate, freshwater

1. Introduction

Elucidating drivers of fish recruitment is a challenge for fisheries researchers and managers, especially in large freshwater systems where a suite of abiotic and biotic factors can interact to regulate recruitment. Recruitment is often highly variable among years (Ricker 1954; Houde 2008), as small changes in survival rates during early life can greatly influence subsequent year-class strength and population dynamics (Houde 1987, 1989). Evidence of inter-population synchrony in recruitment can help to identify potential drivers of recruitment variation. Synchrony in recruitment of fish populations has been observed in both freshwater (Grenouillet et al. 2001; Phelps et al. 2008; Honsey et al. 2016; Bunnell et al. 2017; Honsey et al. 2020) and marine systems (Fox et al. 2000; Hollowed et al. 2001) with climatic conditions (i.e., the "Moran effect"; Moran 1953) and larval dispersal identified as potential drivers of synchrony (Bunnell et al. 2010). Although climatic conditions have been shown to contribute to recruitment synchrony in both freshwater and marine systems, previous estimates of the spatial scales of intraspecific recruitment synchrony in freshwater systems were less than 50 km compared to 500 km in marine environments (Myers et al. 1997; Feiner et al. 2019). In contrast, more recent studies in large freshwater systems (i.e., the Laurentian Great Lakes, hereafter Great Lakes) suggest that the spatial scale of synchrony can be much broader than 50 km (Bunnell et al. 2010; Honsey et al. 2016). Intraspecific recruitment synchrony among Great Lakes populations has been observed within bloater *Coregonus hoyi* (Bunnell et al. 2010), yellow perch *Perca flavescens* (Honsey et al. 2016), and cisco *Coregonus artedi* (Myers et al. 2015). Furthermore, climatic conditions also appeared to contribute to recruitment synchrony across multiple species in Lake Michigan (e.g., rainbow smelt *Osmerus mordax*, alewife *Alosa pseudoharengus*, and yellow perch; Bunnell et al. 2017). Hence, a growing number of studies have revealed the potential of annual regional climatic conditions to regulate the recruitment dynamics of Great Lakes fishes.

Recruitment of non-native alewife populations in the Great Lakes has been relatively well studied across decades and lakes. Alewife constitute a substantial component of Great Lakes food webs, serving as key forage for economically valuable salmonid fisheries (Jude et al. 1987; Jacobs et al. 2013; Leonhardt et al. 2020). Given their importance within the food web, multiple efforts to understand alewife recruitment variability within lakes have been undertaken, particularly in lakes Ontario and Michigan (e.g., Henderson and Brown 1985; O'Gorman et al. 2004; Madenjian et al. 2005; Höök et al. 2008). These studies have identified different potential drivers of recruitment, including predation by salmonids (Madenjian et al. 2005), spring-summer temperatures (Madenjian et al. 2005; Höök et al. 2008; Collingsworth et al. 2014; Bunnell et al. 2017), and winter severity (O'Gorman et al. 2004; Collingsworth et al. 2014). In most of these studies, seasonal water temperature has been included among key explanatory variables, which would suggest that large interannual differences in regional temperature could act to synchronize alewife recruitment across the Great Lakes basin. Nonetheless, only one study has evaluated alewife recruitment between lakes (Collingsworth et al. 2014), and their objective was not to explicitly test for synchrony, but rather to investigate whether two unique lake-specific models had common environmental drivers. Furthermore, the collapse of alewife in Lake Huron around 2003 (Riley et al. 2008) has led fishery managers across the Great Lakes to prioritize understanding of factors that underlie alewife recruitment variability and population persistence.

Prior recruitment studies have used several different methods to assess lake-specific recruitment patterns including modifications to the Ricker stock-recruit model (e.g., Henderson and Brown 1985; O'Gorman et al. 2004; Madenjian et al. 2005; Collingsworth et al. 2014; Bunnell et al. 2017). Such studies have used catch-per-unit-effort (CPUE) of a single age, such as age-2 (O'Gorman et al. 2004) or age-3 (Madenjian et al. 2005; Collingsworth et al. 2014; Bunnell et al. 2017) to index recruitment in part because alewife age distributions from these surveys revealed that younger ages are not fully vulnerable to assessment gear. Similar to many other fish populations in large systems, however, it is likely that key processes that affect alewife recruitment success act on ages younger than age-2 or age-3 (e.g., Madenjian et al. 1996; Ivan et al. 2011; Bunnell et al. 2010; Collingsworth et al. 2014). Quantifying the age when year-class strength is set can shed light on drivers of recruitment success and facilitate subsequent analyses.

Moreover, evaluating multiple potential ages to index year-class strength could be beneficial given interannual sampling variability and potential changes in age-specific catchability, selectivity, and survival over time (Riley and Adams 2010; He et al. 2012; He 2019). Across the Great Lakes, alewife are sampled inconsistently across lakes using a variety of different gear types and targeted at multiple life stages. Larval alewife are only sampled periodically by studies ranging a few years (e.g., Höök et al. 2007; Weber et al. 2015; Withers et al. 2015) or consistently in select regions (e.g., near Muskegon, Michigan; Ed Rutherford, National Oceanic and Atmospheric Administration, oral communication, June 2022). Since the 1970s, the United States Geological Survey (USGS) has performed prey fish assessment surveys on lakes Huron, Michigan, and Ontario. In Lake Michigan, juvenile and adult alewife are sampled in late summer by hydroacoustic surveys and midwater trawls (Warner et al. 2008) and in the fall by bottom trawls (Madenjian et al. 2005). In Lake Ontario, alewife are sampled in the spring via bottom trawls (Weidel et al. 2019). In Lake Huron, alewife and other fishes are assessed in the fall by bottom trawls, although the alewife population crashed in the early 2000s (Riley et al. 2008). These differences in sampling methods have made it difficult to utilize datasets across lakes and to use multiple ages, including relatively young ages, to estimate year-class strength. More recently, studies of year-class strength of other species have used mixed-modeling approaches as such methods facilitate (a) consideration of additional fixed and random effects on age-specific abundances (e.g., sampling year, gear type), (b) inclusion of multiple assessment years, and (c) incorporation of multiple measures of abundance of a given cohort across ages into year-class strength estimates (e.g., Honsey et al. 2020; He et al. 2023).

Our goals were to (1) identify the age at which alewife year-class strength is set in three Great Lakes populations, (2) reconstruct alewife year-class strength for each of the three populations and investigate whether alewife year-class strength is synchronized across the region, and (3) evaluate potential regional environmental drivers of year-class strength if synchrony among the lakes was observed. To do this, we utilized a mixed-modeling approach with long-term catch-at-age datasets to provide a more accurate estimate of year-class strength and allowing for the inclusion of younger ages and multiple age abundances per year-class. We hypothesized that the age at which alewife year-class strength is set would be earlier than age-3. We also hypothesized that since past studies in multiple lakes point to the positive influence of spring-summer temperatures on alewife recruitment (e.g., O'Gorman et al. 2004; Madenjian et al. 2005; Höök et al. 2008; Collingsworth et al. 2014), recruitment of the three populations of alewife would be synchronized due to similar influences of annual regional climate conditions. Our analyses aimed to provide a better understanding of alewife recruitment drivers and dynamics across the Great Lakes.

2. Methods

2.1. Data collection

The datasets used for our analyses were compiled from the USGS annual bottom trawl prey fish assessment surveys for lakes Huron (fall, 1976–2004, Hondorp et al. 2024), Michigan (fall, 1973–2022, Hondorp et al. 2024), and Ontario (spring, 1978–2022, Weidel et al. 2023). The Lake Huron dataset only included data through 2003 as alewife were rarely sampled in later years (Riley et al. 2008). Lake-wide age-specific densities (number/ha) of alewife were calculated for each sampling year using established USGS methods. For more details describing the methods and summarization of each survey, see Riley et al. (2008), Weidel et al. (2019), Madenjian et al. (2005), and Collingsworth et al. (2014).

2.2. Age when year-class strength is set

Pairwise Pearson correlations were used to evaluate at which age alewife year-class strength is set (e.g., Ivan et al. 2011). Lake-specific, age-paired correlations for each year-class (e.g., age-0 in 1971 vs. age-3 in 1974, etc.) were performed for ages 0–3 using log-transformed relative abundances to more closely approximate normality. Normal Q-Q plots were used to verify the assumptions of normality. The year-classes included in these pairwise correlations were 1974–2002 for Lake Huron, 1971–2020 for Lake Michigan, and 1977–2020 for Lake Ontario. The portmanteau lack-of-fit test was performed on the lagged residuals of each correlation pairing to test for significant temporal autocorrelation (Box and Jenkins 1976). If any outliers within each correlation were detected using Cook's distance (D_i; Hair et al. 1998), they were subsequently removed. An observation was considered an outlier if the $D_i$of the observation was larger than the threshold of $4/(n—k-1)$ where n is the number of observations and k is the number of independent variables (Hair et al. 1998). The age at which year-class strength was set was determined to be the youngest age that significantly correlated with age-3 as this is the known age when alewife are fully vulnerable to the trawl assessment gear in lakes Michigan and Huron (Madenjian et al. 2005; Collingsworth et al. 2014). These calculations were performed in JMP Pro version 15.1.0 (SAS Institute Inc.).

2.3. Year-class strength estimation

Year-class strength of alewife was indexed by fitting a linear mixed-effects model to the trawl data set for each study lake. The mixed-model incorporated abundances for cohorts over multiple years, and separated age-specific effects (i.e., mortality and selectivity) and year-specific effects (i.e., sampling effort, catchability, variable predation mortality across years, etc.) from the year-class effect. (Parsons and Pereira 2001; Maceina and Pereira 2007; Honsey et al. 2020; He et al. 2023). Annual cohorts were only included if catches of two or more ages (across ≥2 years) were available for that cohort (Honsey et al. 2020). Ages 1–3 were included in the mixed-models to incorporate the earliest age that year-class strength was reliably set across all three lakes (Section 3.1 of Results) and additional ages up to when the year-class fully recruits to the fishing gears (He et al. 2023). After evaluation of different model structures (including inclusion of ages greater than 3; see Supplementary Materials), the following model was fit:

$$\log\left(\mathrm{CPUE}_{ijk}\right) = \mathrm{A}_i + \Upsilon_j + \psi_k + \varepsilon_{ijk} \tag{1}$$

where CPUE_{ijk} is the catch per unit effort of alewife of age i from year-class j in year k; $A_i$is a normally distributed random effect for age; Υ_j is the fixed effect parameter for each year-class j; and ψ_k is the normally distributed random effect for each sampling year k (Honsey et al. 2020; He et al. 2023). Before running the models, $\log_{10}$(CPUE) abundances were standardized to $N(0,1)$ to make the catch estimates comparable among lakes. The assumption of the model was that the year-class strengths of alewife were influenced by random variation in both age-specific (e.g., selectivity, mortality) and year-specific (e.g., catchability) processes. The year-class parameter was used to estimate year-class strength for each year-class (He et al. 2023). The best linear unbiased predictor (BLUP, Robinson 1991) from the sampling-year random effect was used to infer sampling-year effects, such as shifts in catchability or selectivity. These and further calculations were performed in R version 4.3.2 (R Core Team 2023) with the "lme4" package (Bates et al. 2015).

2.4. Synchrony analysis

To assess recruitment synchrony across the three study lakes, pairwise Pearson correlation coefficients were calculated for year-class strength estimates between lakes for overlapping year-classes. A positive coefficient (r) indicated year-class strength was positively synchrony between lakes (i.e., year-class strength is high (strong) or low (weak) during particular years across all lakes).

2.5. Regional climate indices

To assess the potential drivers of alewife year-class strength synchrony, climatic conditions were examined at the regional level. Based on previous studies, there is evidence that warmer spring-summer temperatures positively influence alewife recruitment success (Madenjian et al. 2005; Collingsworth et al. 2014) while colder winter temperature negatively influence recruitment success (O'Gorman et al. 2004). A warmer spring-summer can lead to earlier hatching and faster growth rates (Houde 1969; Höök et al. 2008), potentially improving survival rates. A cooler winter prior to spawning has been observed to influence egg development and offspring quality in some fishes such as percids (Farmer et al. 2015; Feiner et al. 2016), and a cooler winter post-hatch potentially reduces overwinter survival of young-of-the-year alewife (Dunlop and Riley 2013). Finally, increased spring precipitation has the potential to increase nutrient loading and productivity and reduce visibility for predators (Reichert et al. 2010).

To assess which climate conditions potentially drive synchrony in alewife recruitment, four indices were considered including (1) winter severity pre-spawn, (2) spring-summer degree-days post-hatch, (3) spring precipitation pre-spawn, and (4) winter severity post-hatch (hereafter first winter). Daily maximum and minimum air temperatures and precipitation were collected from 12 weather stations across the region from the National Oceanic and Atmospheric Administration's Climate Data Online Service (http://www.ncdc.noaa.gov/cdo-web/; Fig. 1). If a particular weather station had any data gaps, then a second weather station in close proximity (i.e., within the same city) was used to fill those missing dates. Indices were calculated by location for each year then averaged across all locations to calculate annual indices. Air temperature data were used as they are often highly correlated with surface water temperatures (Macan and Maudsley 1966; Chezik et al. 2014*a*) and are more readily available than surface water temperature data across the broad spatial and temporal scales considered through this study. The threshold temperature of 0 °C for degree-days was based upon the recommendation from Honsey et al. (2022) and Chezik et al. (2014*b*). Spring-summer degree-days at age-0 (DD_0) were calculated as the sum of daily average temperatures above 0 °C from May 1 to July 31. Winter severity pre-spawn and post-hatch were calculated as the number of days between September and May in which the average air temperature was below 0 °C (similar to Honsey et al. 2020). Regional spring precipitation was calculated by averaging precipitation data from each site for each month within each year followed by averaging the monthly regional averages across months of interest (April-May) for each year (Honsey et al. 2016). Regional average year-class strength was calculated by averaging year-class strength estimates among study lakes for a given year. The indices and regional year-class strength were calculated

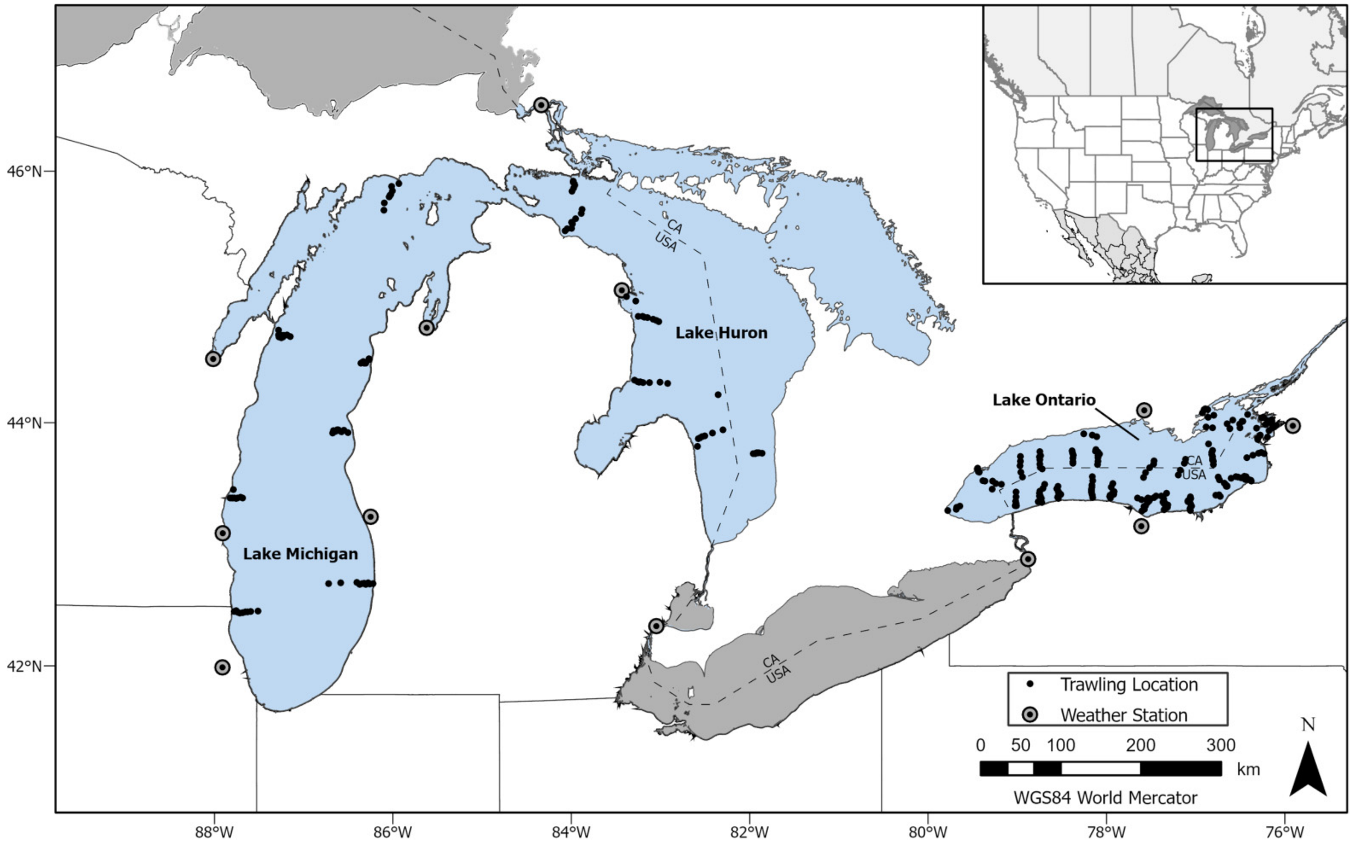


Fig. 1. Map of the four southernmost Laurentian Great Lakes with the study lakes shaded in blue. Gray circles with a black center represent the weather stations used to calculate the regional average climatic indices. The bottom trawling locations are represented by black dots within each respective lake. Map credits: (U.S. State Boundaries: Great Lakes Commission 2019; Great Lakes Shapefiles: United States Geological Survey 2010).

for two time periods: 1977–2001 when year-class strength was estimated for all three lakes and 1977–2020 when year-class strength was estimated for lakes Michigan and Ontario. Pairwise Pearson correlation coefficients were estimated using each of the four annual regional climatic indices and the regional average year-class strength for each time period. For climate and other associations, we not only note significant effects at $\alpha = 0.05$ level of significance without corrections for multiple comparisons, but also note that several correlations were robustly significant (i.e., $\alpha = 0.01$).

3. Results

3.1. Age when year-class strength is set

Results of pairwise correlations provided evidence that alewife year-class strength is set at age-1 for all three populations, and potentially by age-0 in the Lake Michigan population (Table 1). Only one correlation was significantly temporally autocorrelated and removed from the analysis: Lake Ontario age-1 versus age-2 ($\chi^2 > 18.307$). One outlier (1996) was removed from the Lake Huron age-1 versus age-3 correlation ($D_i = 0.36$). In all three lakes, age-1 relative abundance was significantly, positively correlated with age-3 relative abundance 2 years later (Fig. 2). Strong correlations were also observed between age-2 and age-3 relative abundance in lakes Michigan and Ontario (Table 1). Finally, in Lake Michigan, a strong correlation was also observed between age-0 and age-3 abundances indicating that year-class strength might be set as early as the fall of the first year of life (Table 1). Although age-0 and age-3 relative abundances were correlated in Lake Michigan, we chose not to include age-0 abundances in subsequent analyses as (a) age-0 abundances were not available for Lake Ontario, (b) correlations from Lake Huron did not support age-0 relative abundances being a strong predictor of age-3 relative abundances, and (c) potential climatic drivers of synchrony included seasonal metrics not relevant to age-0 individuals sampled in the fall (e.g., post-spawn winter temperatures). In total for all three lakes, we determined that year-class strength is set by age-1 and therefore age-1 and older capture data were used in subsequent analyses.

3.2. Year-class strength estimates

The mixed-models for: (1) Lake Huron included 28 year-classes (1974–2001) from 27 sampling years (1976–1999, 2001–2003); (2) Lake Michigan included 50 year-classes (1971–2020) from 50 sampling years (1973–2022); and (3) Lake Ontario included 44 year-classes (1977–2020) from 44 sampling years (1978–2019, 2021–2022; Fig. 3). Year-class strength in Lake Huron during the late 1970s and early 1980s was con-

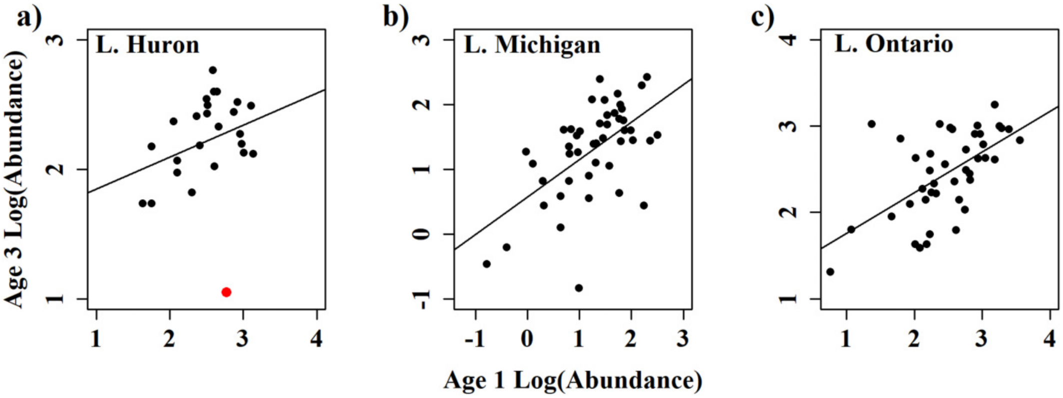
Table 1. Pairwise Pearson correlation coefficients (r) relating alewife Alosa pseudoharengus abundance across ages for year-classes from four Laurentian Great Lakes datasets.

	Lake Huron fall bottom trawl	Lake Michigan fall bottom trawl	Lake Ontario spring bottom trawl
Age 0 vs. Age 1	−0.02 [26]	+0.66 [43]∗	–
Age 0 vs. Age 2	−0.04 [25]	+0.48 [43]∗	–
Age 0 vs. Age 3	−0.35 [24]	+0.52 [43]∗	–
Age 1 vs. Age 2	+0.45 [26]∗	+0.75 [47]∗	‡
Age 1 vs. Age 3	+0.49 [24]∗ †	+0.58 [46]∗	+0.59 [42]∗
Age 2 vs. Age 3	+0.24 [26]	+0.73 [47]∗	+0.70 [42]∗

‡= Correlation removed due to significant temporal autocorrelation detected.

†= Outlier removed from correlation after detection using Cook's D (year-class 1996). Previous correlation $r = +0.28$. Significant correlations are indicated with an asterisk (∗) for $p < 0.01$. The number of year-classes included in each correlation are specified as [*n*].

Fig. 2. Comparisons of age-1 versus age-3 abundance (log(number ha^{-1})) for year-classes of alewife *Alosa pseudoharengus* in (*a*) Lake Huron ($r = 0.49$), (*b*) Lake Michigan ($r = 0.58$), and (*c*) Lake Ontario ($r = 0.59$). Outlier removed from Lake Huron comparison is indicated by red dot.



sistently weak until becoming a more consistent pattern of peaks in strong and weak years before the population crashed in the early 2000s. In Lake Michigan, year-class strength was relatively strong from 1970–1990 before becoming on average weaker in the 2000s and consistently weak after 2013. Lake Ontario consistently has had a pattern of strong and weak peaks in year-class strength throughout the entire time series. For all three lakes, the sampling-year effect remained relatively consistent around the model average (Fig. 4).

3.3. Synchrony analysis

Pairwise Pearson correlation coefficients (r), suggested that alewife year-class strength is generally synchronized in the Great Lakes region (Fig. 5). Lake Michigan was significantly synchronized with Lake Huron ($r = 0.59$, $p < 0.01$, $n = 28$) and Lake Ontario ($r = 0.33$, $p = 0.03$, $n = 44$). Lake Huron was also significantly synchronized with Lake Ontario ($r = 0.54$, $p < 0.01$, $n = 25$).

3.4. Regional climate indices

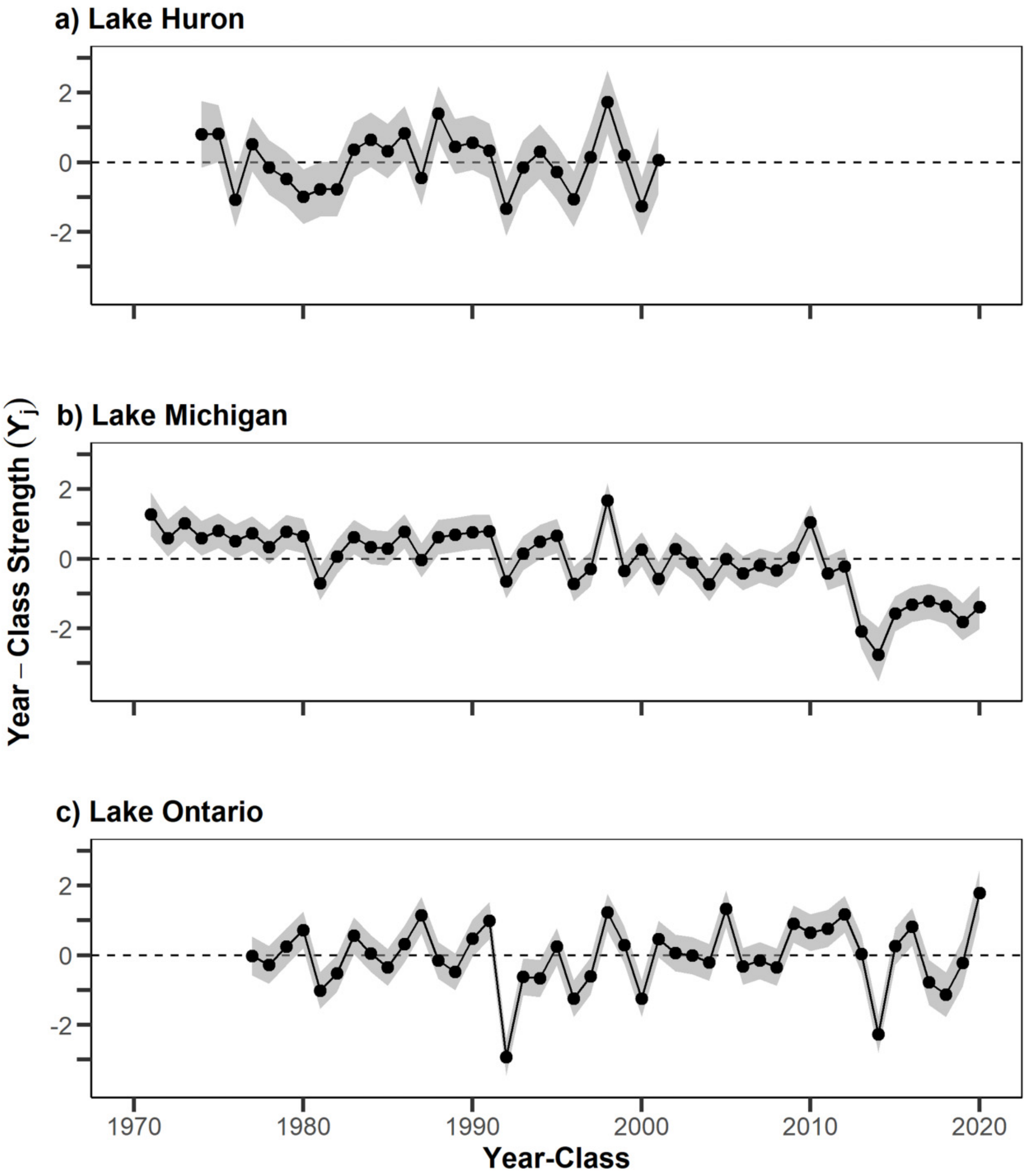
Regional average year-class strength was significantly positively correlated with spring-summer degree-days when including all lakes (1977–2001; $r = 0.61$) and when only including lakes Michigan and Ontario (1977–2020; $r = 0.30$; Fig. 6). Regional average year-class strength was significantly negatively correlated with spring precipitation when including lakes Michigan and Ontario (1977–2020; $r = -0.32$) but not across all lakes (1977–2001; Table 2). Neither winter severity pre-hatch nor winter severity post-hatch were significantly correlated with regional average year-class strength (Table 2).

4. Discussion

We indexed alewife year-class strength for lakes Huron, Michigan, and Ontario from 1977 to 2020 and provide evidence that alewife recruitment is regionally synchronized. Our results suggest that alewife recruitment is set by age 1. Moreover, our study suggests that annual regional climate conditions contribute to alewife recruitment success and regional synchrony, as spring-summer degree-days were positively related to year-class strength.

An advantage of the mixed-modeling approach was the ability to account for changes in the sampling-year effect. These datasets span a large number of years throughout which there were likely changes in catchability due to interannual variability in food web composition, changes in the timing of the survey, or lake-wide ecosystem changes. For example, increased water clarity could plausibly affect capture

Fig. 3. Year-class strength estimates for alewife *Alosa pseudoharengus* from (*a*) Lake Huron, (*b*) Lake Michigan, and (*c*) Lake Ontario. Zero represents the mean year-class strength value across the time series. The gray shaded area represents 95% confidence intervals.



efficiency of sampling gear (Bunnell et al. 2021). The Lake Michigan ecosystem has undergone substantial changes that could decrease catchability in a daytime bottom trawl, including increased water clarity (Binding et al. 2015; Yousef et al. 2017; Bunnell et al. 2021), high salmonid predation (Madenjian et al. 2002), decreased prey availability (Barbiero et al. 2012; Bunnell et al. 2018), and declining adult alewife abundance (Madenjian et al. 2002; Madenjian 2022). Adult alewife abundance may have reached a sufficiently low level by 2014 such that catchability in the bottom trawl survey generally decreased. The findings of Swain et al. (1994) provide support for this hypothesis, as these researchers estimated that catchability of older Atlantic cod (*Gadus morhua*) in the bottom trawl survey of the southern Gulf of St. Lawrence was relatively low when older Atlantic cod abundance was low.

This study provides evidence that alewife year-class strength is generally set by age-1 in the study lakes and may be set earlier in Lake Michigan. Previous studies have modeled recruitment based on relative abundances of age-3 alewife due to incomplete recruitment to the sampling gear before this age (Eck and Brown 1985; Krause 1999; Madenjian et al. 2005). We chose to use age-1 as the earliest age to include because (1) age-1 abundances were strong predictors of subsequent age-3 abundances of cohorts, (2) previous studies have shown a potential effect of winter severity on the survival of age-0 individuals to age-1 (e.g., O'Gorman et al. 2004; Höök et al. 2007), (3) the dataset for Lake Ontario does

Fig. 4. Sampling-year effect estimate for trawl surveys from (*a*) Lake Huron, (*b*) Lake Michigan, and (*c*) Lake Ontario. A minimal effect of sampling-year is indicated by a value of zero. The gray shaded area represents 95% confidence intervals.

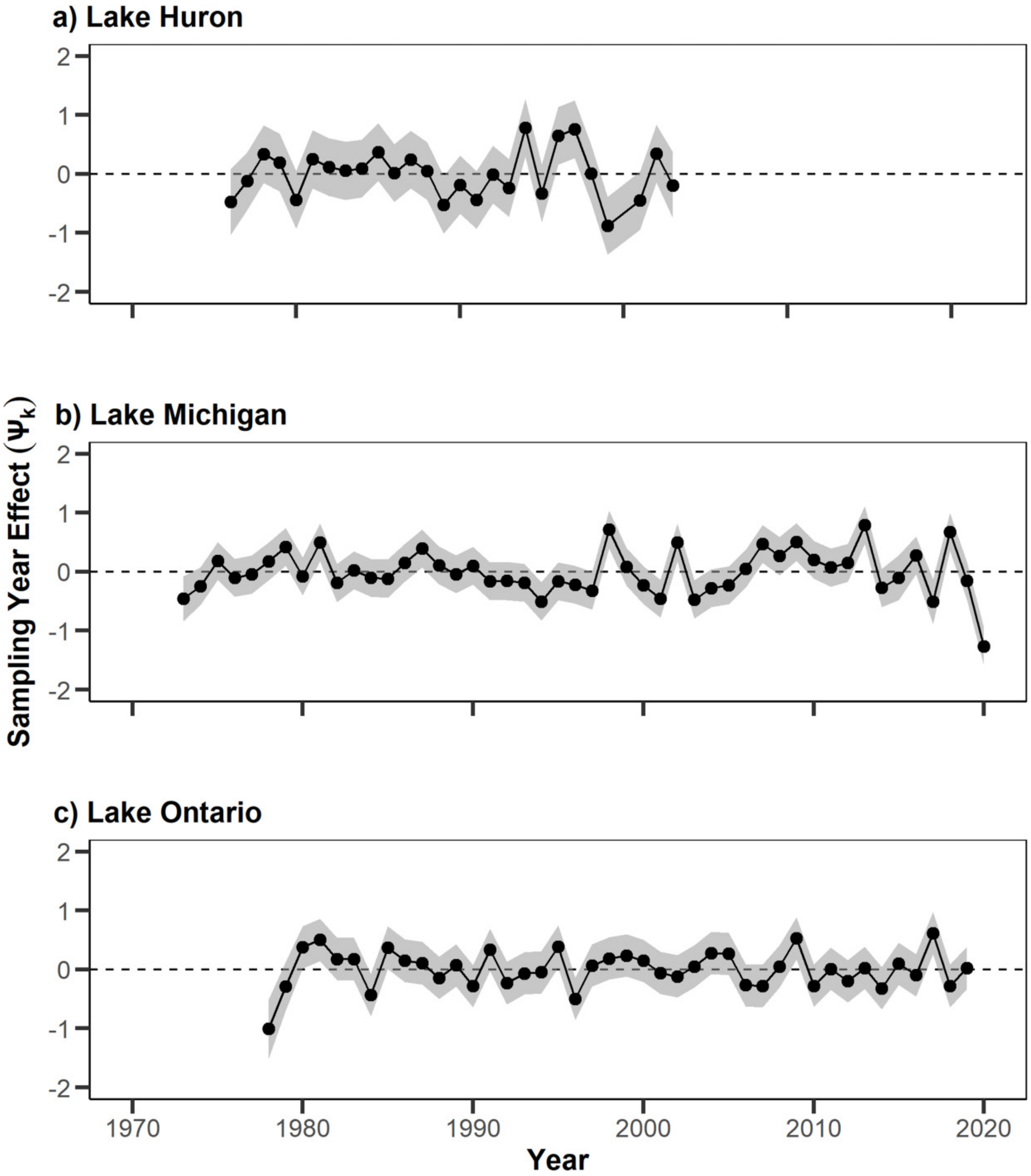
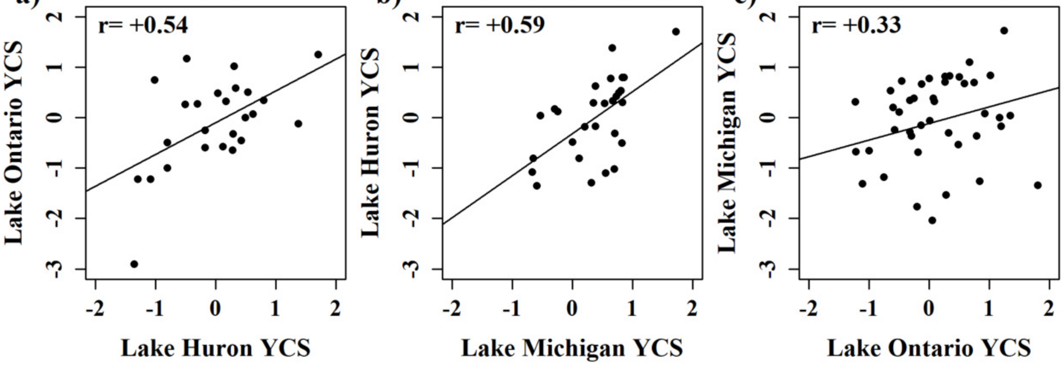


Fig. 5. Scatterplots of alewife *Alosa pseudoharengus* year-class strength estimates between (*a*) lakes Huron and Ontario, (*b*) lakes Michigan and Huron, and (*c*) lakes Ontario and Michigan. Trend lines are presented to visualize the direction of the correlation.



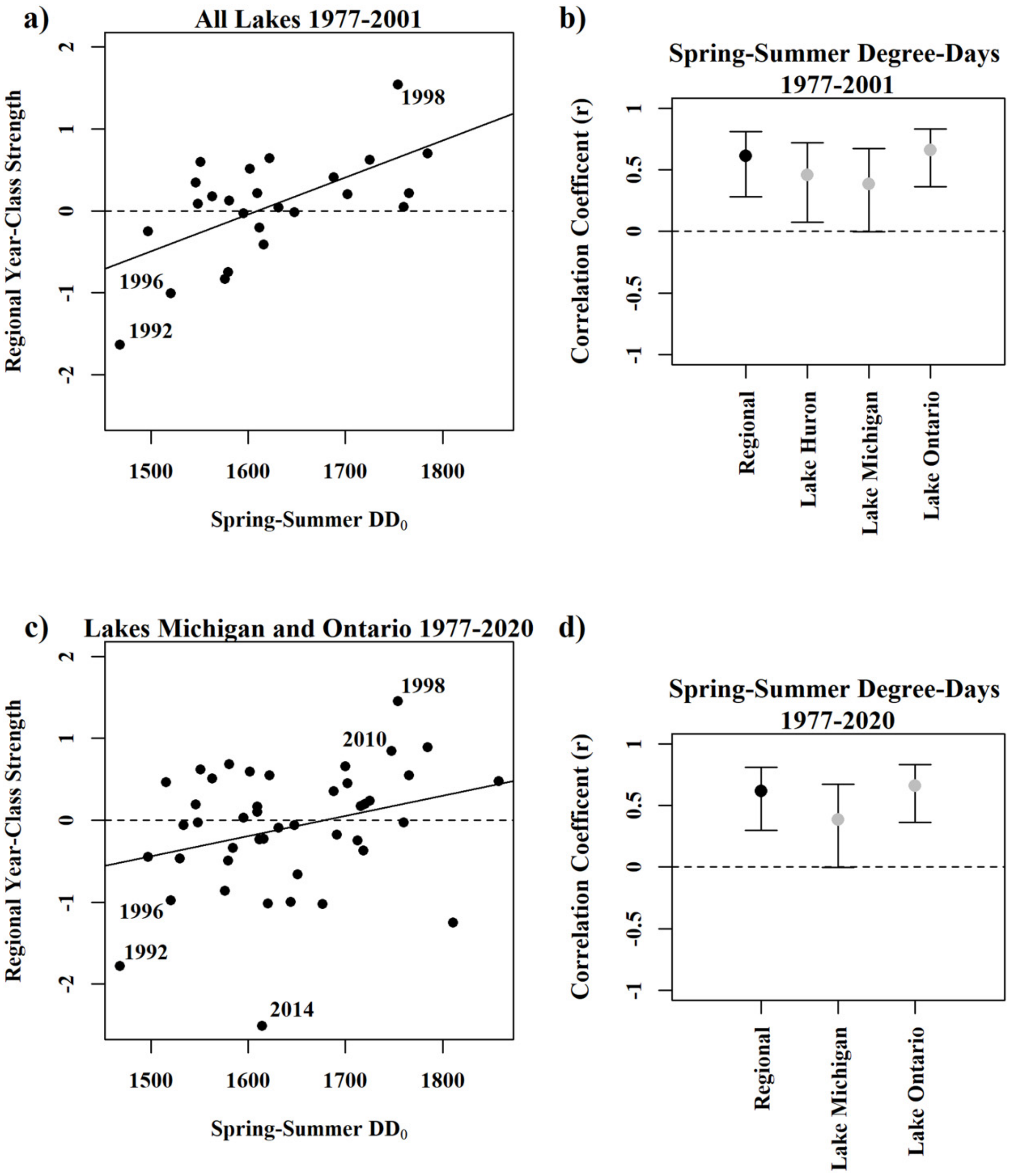


Fig. 6. Scatterplots of spring-summer degree-days versus regional alewife *Alosa pseudoharengus* year-class strength for (*a*) 1977–2001 and (*c*) 1977–2020. Trend lines are presented to visualize the direction of the correlation. Pairwise Pearson correlation coefficients (r +/−95% confidence intervals) of spring-summer degree days versus regional year-class strength and year-class strength for each respective lake for (*b*) 1977–2001 and (*d*) 1977–2020.

Table 2. Pairwise Pearson correlation coefficients (r) relating alewife *Alosa pseudoharengus* regional year-class strength and the regional climatic indices for all three lakes from 1977–2001 and Lakes Michigan and Ontario from 1977–2020. Significant correlations at $p < 0.01$ are reported in bold.

	All Lakes (1977–2001)		Lakes Michigan and Ontario (1977–2020)	
	r	*p*-value	*r*	*p*-value
Winter severity pre-spawn	−0.30	0.15	−0.25	0.10
Spring precipitation	−0.13	0.54	−0.32	0.03
Spring-summer degree-days	**0.61**	**<0.01**	**0.61**	**<0.01**
Winter severity post-spawn	−0.29	0.15	−0.17	0.26

not include age-0 abundances, and (4) the mixed-modeling approach allows for the inclusion of ages before full vulnerability to sampling gear. Abundances at younger ages (i.e., age 0, age (1) have also been found to be strong predictors of abundances at older ages for other species in the Great Lakes, including yellow perch in Saginaw Bay (Ivan et al. 2011) and Lake Erie (Farmer et al. 2015) and bloater in Lake Michigan (Bunnell et al. 2010). In recent years, the age structure of the alewife population in Lake Michigan has become truncated (Vidal et al. 2019), and it has become difficult to use traditional stock-recruitment models without indices for older individuals. The fact that Lake Michigan alewife recruitment appears to be largely set by age-1 (if not earlier) could allow fisheries scientists and managers to use relative abundance data from younger ages to proactively assess the strength of alewife year-classes. Thereby, managers may be able to determine alewife year class strength before an alewife cohort reaches age 3. This could allow for proactive management of salmonine stocking or harvest in anticipation of available forage availability.

The observation of recruitment synchrony among the three study lakes adds to the growing body of evidence that the spatial scale of fish recruitment synchrony in freshwater systems can be much broader than an earlier estimate of 50 km (Myers et al. 1997; see, for example, Bunnell et al. 2010; Collingsworth et al. 2014; Myers et al. 2015; Honsey et al. 2016; Bunnell et al. 2017). With the development of modeling methods and the availability of larger datasets, spatial synchrony of freshwater fish population dynamics for the Great Lakes is now observed to be up to 400 km for short term and 800 km for long-term trends (Bunnell et al. 2010); although, it is important to note that these various studies have used different methods for calculating scales of synchrony. This broad-scale recruitment synchrony may be common among Great Lakes fish populations, as the Great Lakes have similarities with marine systems in terms of physical and biological properties (Ludsin et al. 2014) and marine fishes typically exhibit much broader scales of recruitment synchrony (Myers et al. 1997). In addition, many Great Lakes fishes (e.g., percids, clupeids, coregonines) have similar life-history strategies to those of many marine fishes, including broadcast spawning, high fecundity, and pelagic larval stages (Ludsin et al. 2014). As such, alewife recruitment may be synchronized in the Great Lakes because survival of individuals in early life stages can be strongly influenced by climatic conditions (e.g., seasonal temperatures) and other physical processes that are correlated at broad scales, much like marine systems.

At the basin level, the best climatic index predictor of regional year-class strength was spring-summer degree-days, which was positively correlated with regional average year-class strength (i.e., warmer spring-summer temperatures led to relatively strong year-classes, and vice versa). Spring-summer temperatures were also found to positively influence alewife recruitment in previous studies (Madenjian et al. 2005; Höök et al. 2008; Bunnell et al. 2017). Warmer temperatures lead to higher metabolic rates and may contribute to higher growth rates so long as sufficient prey are available (Venturelli et al. 2010; Honsey et al. 2019). The growth of an individual during early life stages is critical as larger young fish are less likely to starve and potentially better able to avoid predation (Miller et al. 1988). In addition, overwinter survival of alewife has been related to individual size (Post and Evans 1989; Höök et al. 2007) with a suggested approximate size threshold of 60 mm required to survive the first winter (Brown 1972; O'Gorman and Schneider 1986). In several other fish species, years with warmer spring temperatures have led to earlier hatching, faster growth, and a longer growing season, thus increasing survival rates and positively influencing year-class strength (Johnson and Evans 1990; Cargnelli and Gross 1996; Post et al. 1998).

Winter temperature was not strongly associated with regional year-class strength. However, the directions of correlation coefficients relating to regional year-class strength were negative for both pre-spawn and post-spawn winter severity indices. Cold winters can contribute to relatively cold spring conditions immediately following the cold winter. Thus, cold winters pre-spawn may partially reflect cooler spring-summer temperatures that leads to a relatively weaker year-class strength. In fact, pre-spawn winter severity was correlated with subsequent spring-summer degree-days (Table S3). Previous studies have found a lack of a significant effect of post-spawn winter severity on year-class strength for alewife in both Lake Michigan (Madenjian et al. 2005; Collingsworth et al. 2014) and Lake Huron (Collingsworth et al. 2014). An exception to these previous studies is O'Gorman et al. (2004), who concluded that, in Lake Ontario, winter severity during the first year of life had a significant negative effect on alewife recruitment.

Although this study investigated the potential for climate conditions to drive alewife recruitment synchrony, there are certainly other abiotic and biotic factors that contribute to recruitment variation, especially when recruitment is indexed at older ages (i.e., age 3 and older). Previous studies have concluded that high rates of salmonid predation were a significant driver of alewife recruitment to age-3 in Lake Michigan (Madenjian et al. 2005; Collingsworth et al. 2014) and Lake Huron (He et al. 2015). Similarly, in Lake Ontario, predation of alewife by salmonids was concluded to have a negative effect on adult alewife abundances (Murry et al. 2010). Clearly, food web dynamics have an influence on survival of alewife to older ages and should be considered when predicting abundances.

In conclusion, this study used a mixed-modeling approach to assess year-class strength of alewife in three Great Lakes. Results indicate that alewife year-class strength is generally synchronized across lakes Huron, Michigan, and Ontario. Climatic conditions, in particular spring-summer degree-days, appear to contribute to regional synchrony of these populations. With average temperatures anticipated to increase in the future, it is possible that average alewife recruitment levels could also increase. However, given the breadth of ecosystem-level changes plausible through global changes, we suggest such expectations are far from certain. In total, this study demonstrates (a) the utility of a mixed-modeling approach to generate and analyze informative indices of year-class strength; (b) the value of long-term annual surveys of fish stocks for further understanding and prediction of ecological processes (Franklin 1989; Hughes et al. 2017); and (c) the importance of climatic factors in influencing recruitment in large-freshwater systems and their ability to synchronize recruitment in these systems across broad scales.

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Data availability

The U. S. Geological Survey (USGS) data for Lakes Michigan and Huron are publicly available at https://doi.org/10.5066/P95KVYGG and the data for Lake Ontario are publicly available at https://doi.org/10.5066/P9LFED8G. The data generated in this study including the mixed-model estimates and regional climate indices are available in the supplementary materials.

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Supplementary material

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