

LETTER

Climate warming amplifies the frequency of fish mass mortality events across north temperate lakes

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Scientific Significance Statement

Many animal populations are declining amidst global change. These declines have been exacerbated by mass mortality events linked to extreme temperatures. Although sustained temperature increases are expected over the 21st century, few approaches have examined if climate change will predictably accelerate occurrences of ecological catastrophes. We modeled the relationship between fish mortality events across north temperate lakes with concurrent water and air temperature profiles. Both water and air temperature were reliable predictors of fish mortality events. Based on water and air temperature climate projections, the models predict ~ 6- to 34-fold increases, respectively, in the frequency of fish mortality events by 2100. Our modeling approach reveals strong associations between rising temperatures and frequencies of ecological catastrophes unfolding in real time.

Abstract

Recent increases of animal mass mortality events have coincided with substantial changes in global climate. Yet, tractable approaches that predict how climate change will accentuate occurrences of these ecological catastrophes remain nascent. We compiled one of the most comprehensive datasets of lentic fish mortality events, thermal tolerances of affected families, and 1.2 million air and water temperature profiles across 8891 north temperate lakes in North America. Temperature extremes within and across lakes were strongly associated with the three most frequent cause types (infectious agents, summerkills, winterkills). Thermal tolerances mediated the lethality of direct thermal stress, but mortalities of warm- and cold-water fishes occurred at similar temperature deviations. Water and air temperature-based models accurately predicted contemporary summerkills and suggested ~ 6- to 34-fold increases, respectively, in their frequency by 2100. These models forecast and contextualize impending ecosystem changes in an increasingly volatile world.

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Data Availability Statement: Data are available in a public GitHub repository at https://github.com/simontye/2020_MME_Temp

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

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Animal mass mortality events—sudden die-offs that affect many demographic classes within populations—have increased in frequency and magnitude since the mid-20th century (Fey et al. 2015) concomitant with global change (Garrahou et al. 2019). These extreme demographic events impact ecosystem function (McDowell et al. 2017), imperil population persistence (Mangel and Tier 1994; Anderson et al. 2017), restructure ecological communities (Hansen et al. 2017; Fey et al. 2019), and reduce global food supply (Soon and Ransangan 2019). Documented animal mortality events have disproportionately affected freshwater fishes (Fey et al. 2015), which are already experiencing global declines (He et al. 2010). Freshwater fish mortality events often coincide with environmental conditions related to warm temperature, such as thermal and oxygen stress (Barica 1975; Till et al. 2019), infectious disease outbreaks (Marcos-López et al. 2010), and anthropogenic activities (Thronson and Quigg 2008). Expanding and refining approaches to accurately predict extreme ecological events across broader scales (Denny et al. 2009; Sinervo et al. 2010; Bailey and van de Pol 2016; Shen et al. 2018) remains imperative to understanding how climate warming will restructure ecosystems.

Most global freshwater lakes are in north temperate regions of North America (Verpoorter et al. 2014), and these lakes have recently experienced substantial increases in surface water temperature (Woolway et al. 2020), lake heatwaves (Woolway et al. 2021), widespread deoxygenation events (Jane et al. 2021), rapid thermal regime shifts (Kraemer et al. 2021), and intensified thermal stratification (Woolway et al. 2021). These conditions are major contributing factors to increased frequencies of fish mortality events (Thronson and Quigg 2008; Fey et al. 2015), and strong positive relationships exist between the occurrence of fish mortality events and either air (Phelps et al. 2019) or waterbody-specific water temperature (Till et al. 2019) in adjacent regions of North American north temperate lakes.

Although regional air temperature variability is generally reduced by thermal inertia of the Laurentian Great Lakes (Notaro et al. 2013), the relationship between regional air and water temperature is dynamic across time (Kraemer et al. 2015) and space, partially due to lake geomorphology (e.g., lake surface area and depth; Kraemer et al. 2015) and dynamic environmental conditions such as productivity (O'Reilly et al. 2015). For example, regional lake geomorphology has strong effects on water temperature (Kraemer et al. 2015), and high productivity lakes frequently experience harmful algal blooms that rapidly reduce dissolved oxygen concentration (Barica 1975). However, climate models that couple air and water temperature have predicted unanticipated temperature increases in terrestrial regions near large waterbodies (Gröger et al. 2021). Therefore, assessing the feasibility of using widely available air temperature estimates, vs. less available depth-specific water temperature estimates, to predict future occurrences of fish mortality events is critical for understanding how future freshwater ecosystems may be restructured.

Here, we develop predictive air and water temperature-based models to examine how climate change has accelerated the frequency of fish mortality events across north temperate lakes. We assembled 526 lentic fish mortality events, thermal tolerances of affected fish taxa, and ~1.2 million air and water temperature profiles, productivity estimates (Secchi depth), and lake surface area across 8891 north temperate lakes of North America (PRISM Climate Group, Oregon State University 2014; Winslow et al. 2017). We compared air and water temperatures within and across lakes with the three most frequent cause types of regional fish mortality events: infectious agents, summerkills (mortalities associated with warm temperature; Barica 1975), and winterkills (mortalities associated with cold temperature; Hurst 2007). We then used air and water temperature-based models to predict frequencies of summerkills across ~3.9 million air and water temperature profiles of regional lakes during the mid- and late-21st century (2041–2059; 2081–2099; Maurer et al. 2007; Winslow et al. 2017) under Representative Concentration Pathway 8.5 (RCP 8.5), the only climate scenario with available regional water temperature estimates (Winslow et al. 2017). Our models predict substantial increases in the frequency of summerkills over coming decades and suggest complex air-water temperature dynamics strongly influence the maximum extent of anticipated mortality increases. This approach demonstrates the feasibility of tractably forecasting thermally driven ecological catastrophes across broad spatiotemporal scales.

Materials and methods

We compiled 526 documented lentic fish mortality events across Minnesota and Wisconsin lakes from 2003 to 2013, then used descriptions of observations to assign maximally general cause categories to each observation: anthropogenic, infectious disease, summerkill, winterkill, or unknown (Fig. 1; Supporting Information Table S1). Summerkills and winterkills are mortalities caused by seasonal environmental conditions associated with extreme temperatures (Greenbank 1945; Barica 1975) and, therefore, were differentiated by meteorological season. To compare thermal tolerances of affected taxa, we classified mortalities by taxonomic family, thermal category, and mean critical thermal maximum (CT_{max}) based on a regional assessment of freshwater fish thermal preferences (Lyons et al. 2009). We used waterbody identifier conversion tables provided by Minnesota IT Services and Wisconsin Department of Natural Resources to associate waterbodies with unique identifiers in the National Hydrological Dataset.

Because our focus was the relationship between summerkills and local temperature, we developed models to predict frequencies of summerkills in relation to concurrent local air (PRISM Climate Group, Oregon State University 2014) and waterbody-specific water temperature profiles (Winslow et al. 2017) across north temperate lakes of North America.

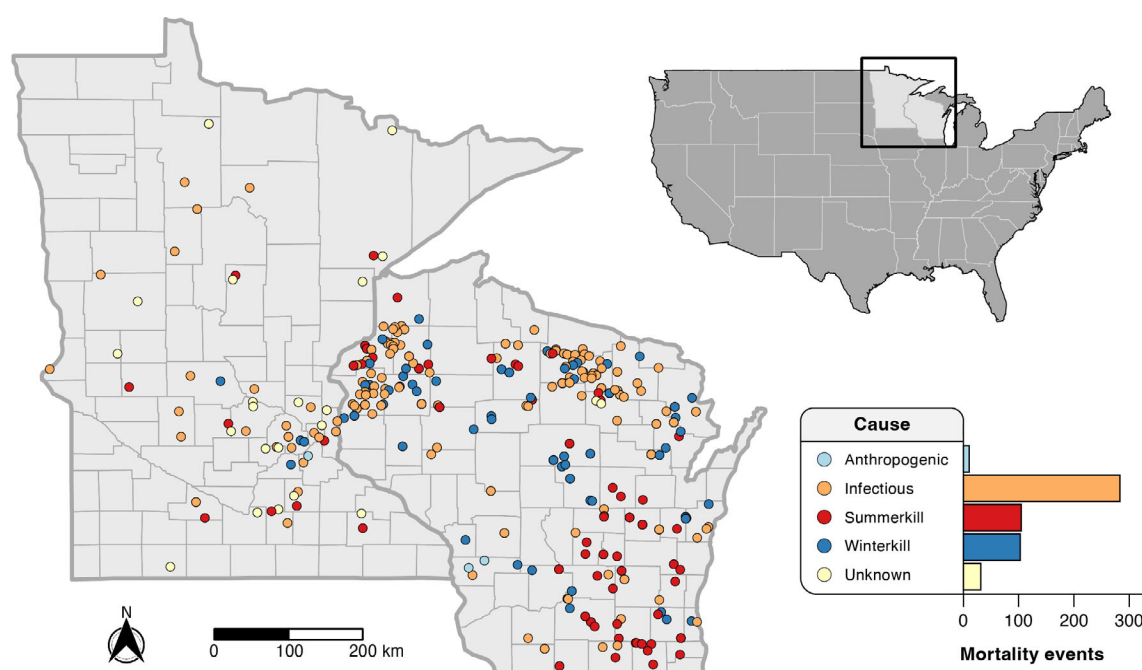


Fig. 1. Locations and frequency of fish mortality events by cause across lakes of Minnesota and Wisconsin ($n = 526$; 2003–2013). Summerkills and winterkills describe elevated mortalities caused by seasonal, thermal-related environmental conditions, such as hypoxia and thermal stress. States and counties are separated by thick and thin dark gray lines, respectively.

We compared 24 models that included major environmental covariates and either air or water temperature estimates (Supporting Information Tables S2, S3). We used logloss, a measure for evaluating fits of models with binary outcomes (e.g., presence or absence of mortality events), for model selection. The best fit air and water temperature-based models included environmental covariates (latitude, longitude, lake surface area, mean annual Secchi depth, ice duration, precipitation, human population density) and either (1) maximum, mean, and minimum air temperature and z-scores (logloss = 2.44) or (2) mean surface water temperature and z-score (logloss = 2.48; Supporting Information Fig. S1).

We then used best fit air and water models to predict frequencies of summerkills based on modeled air and water temperature estimates for the mid- and late-21st century (2041–2059; 2081–2099) under Representative Concentration Pathway 8.5—the worst-case climate scenario and only scenario with water temperature projections across our study region (Winslow et al. 2017). We acquired modeled air temperature estimates (monthly maximum, mean, and minimum) from the World Climate Research Program's Coupled Model Intercomparison Project phase 3 multi-model dataset (CMIP3; Maurer et al. 2007), and associated waterbody centroids with the nearest temperature estimates ($1/8^\circ$ resolution). We used these slightly outdated air temperature projections because they were part of the model ensemble used to create regional water temperature estimates (Winslow et al. 2017). We

acquired modeled monthly water temperature variables from the same extensive assessment used in historical models ($1/8^\circ$ resolution; Winslow et al. 2017).

Several model adjustments were necessary for future predictions. First, we removed ice duration because future estimates are unavailable across most of the study region. Second, because we wanted to account for variation in productivity across lakes but are unable to predict future productivity, we considered annual mean Secchi depth by lake as a constant over time, as in the historical models. Third, we performed predictive models without down-sampling and lambda regularization, which train models on data subsets and reduce model overfitting, because they alter intercept terms. To visualize probabilities of best fit models over time, we performed thin plate spline regressions via the *fields* package (Nychka et al. 2017) and interpolated these data across the study region via the *raster* package (Hijmans 2021). Details about data compilation, model selection, and statistical analyses are in the Supporting Information.

Results and discussion

Strong relationships exist between local air and water temperatures and the three most frequent drivers of mortality events across the study region: infectious disease ($n = 281$), summerkills ($n = 103$), and winterkills ($n = 101$; Fig. 1). Summerkills had the strongest, positive relationships with local

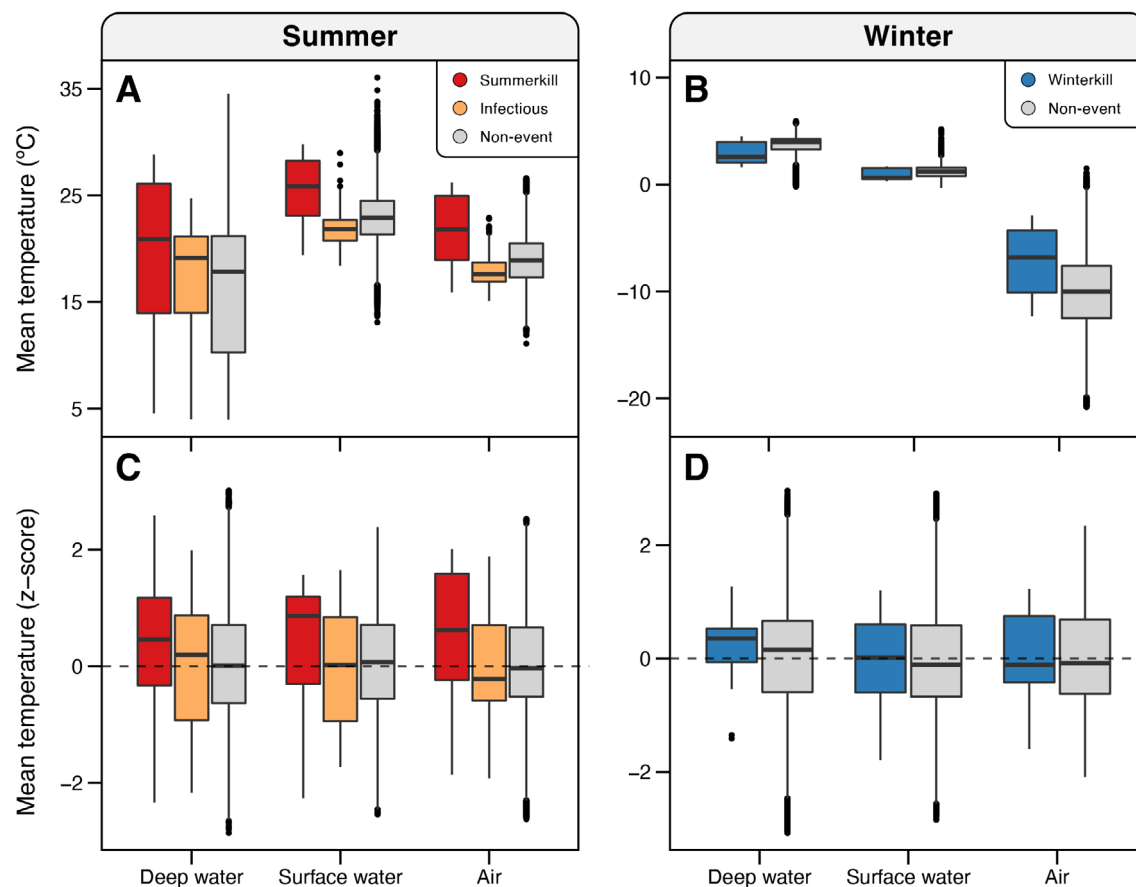


Fig. 2. Monthly mean deep water, surface water, and air temperature estimates and z-scores when the most frequent causes of fish mortality events (infectious, summerkill, winterkill) were (colored boxes) and were not (gray boxes) documented across Wisconsin and Minnesota (2003–2013). Left column shows temperature estimates (A) and z-scores (C) when summerkills (red) and infectious events (orange) were documented compared to summer non-events (gray); right column shows temperature estimates (B) and z-scores (D) when winterkills (dark blue) were documented compared to winter non-events (gray). The z-scores represent standardized deviations from mean temperatures within lakes over the study period. Boxplots show medians (thick line) bounded by upper and lower quartiles (thin lines) with outliers (black circles).

temperatures and occurred when monthly mean air, surface water, and deep-water temperature were $\sim 15\%$, $\sim 13\%$, and $\sim 17\%$ above median summertime temperatures, respectively (Fig. 2; Dunnett test difference air = 2.71, $p < 0.001$; t -test, $t = -8.08$, $df = 94.03$, $p < 0.001$; Dunnett test difference surface water = 2.47, $p < 0.001$; t -test, $t = -7.84$, $df = 94.04$, $p < 0.001$; Dunnett test difference deep water = 4.12, $p < 0.001$; t -test, $t = -5.79$, $df = 94.05$, $p < 0.001$). These air and surface water temperature patterns corroborate findings from geographically reduced datasets (Phelps et al. 2019; Till et al. 2019), while the previously undocumented relationship with deep-water temperature likely emerged due to the broadened spatial extent that incorporated colder lakes (Notaro et al. 2013). Summerkills were also strongly affected by lake geomorphology and local environmental conditions (Supporting Information Fig. S1). However, although small lakes are disproportionately susceptible to harmful algal blooms that can rapidly reduce dissolved oxygen concentration (Barica 1975), summerkills were primarily

documented in lakes with $\sim 82\%$ higher mean surface area (t -test, $t = -0.75$, $df = 67.73$, $p < 0.45$) and $\sim 29\%$ higher annual mean Secchi depth (m), a common proxy for productivity (t -test, $t = 9.99$, $df = 73.77$, $p < 0.001$)—consistent with potential observation bias toward documenting summerkills in larger, more frequently visited lakes.

Most summerkills affected warm-water fishes (Supporting Information Table S1), and there was a negative relationship between CT_{max} of fish families affected by summerkills and its difference with concurrent maximum surface water temperature (Fig. 3A; $r^2 = 0.40$, $F_{1,59} = 39.7$, $\beta = -0.41$, $SE = 0.07$, $t = -6.30$, $p < 0.001$). While cold-water fishes clearly experience high direct thermal stress from warming temperatures (Fig. 3A; Notaro et al. 2013), there was no statistically significant relationship between CT_{max} and the z-score of maximum surface water temperature (Fig. 3B; $r^2 = 0.03$, $F_{1,59} = 1.55$, $\beta = -0.64$, $SE = 0.52$, $t = -1.25$, $p = 0.22$). These findings imply similar deviations in surface water temperature have

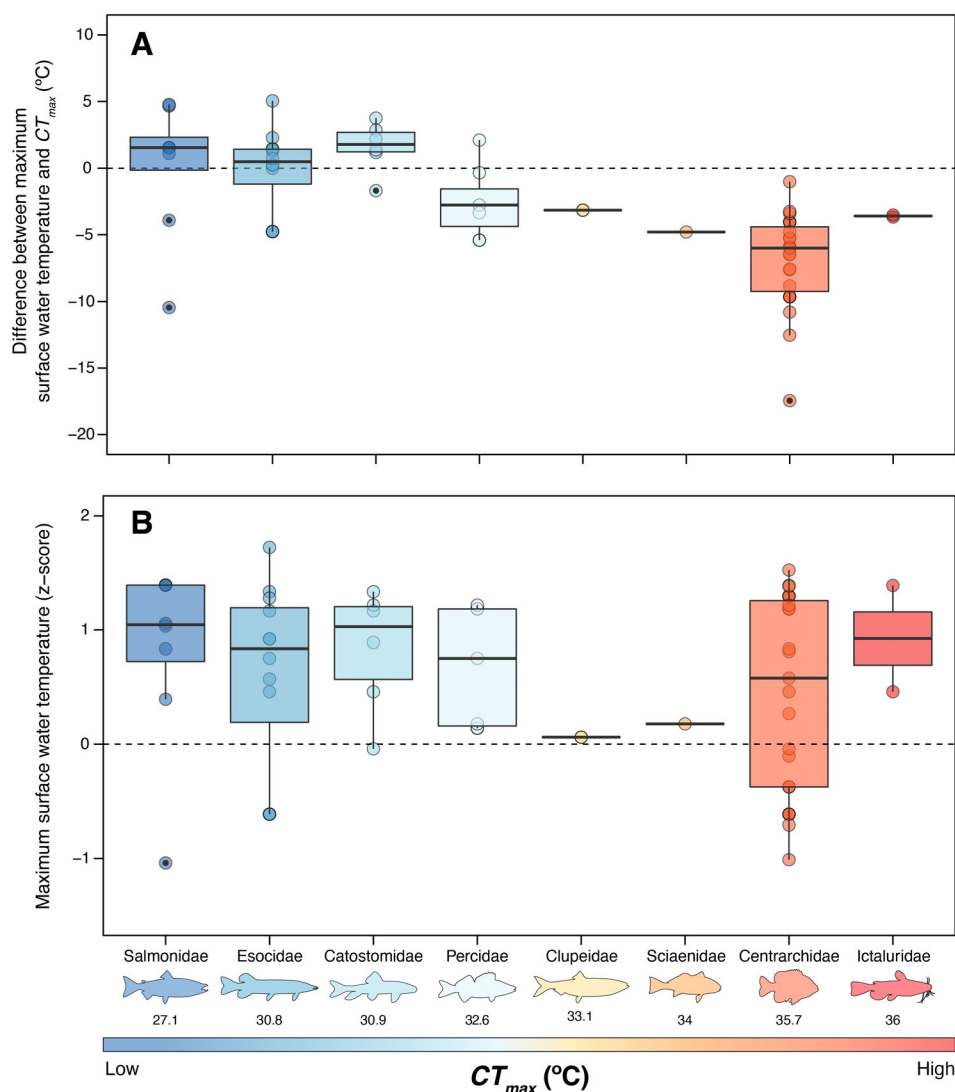


Fig. 3. Critical thermal maximum (CT_{max}) of fish families (Supporting Information Table S2) that were affected by summerkills across Minnesota and Wisconsin (2003–2013) compared to concurrent raw (A) and z-scores of (B) monthly maximum surface water temperature estimates. The z-scores represent deviations from standardized maximum surface water temperature within lakes over the study period. Colors represent relatively low (blue) and high (red) CT_{max} of each affected family. Black circles indicate outliers and dashed lines indicate whether temperatures were above or below CT_{max} (A) and standardized maximum surface water temperature (B), respectively.

equally strong impacts on survival of both warm- and cold-water fishes; yet, concerns about effects of climate change on freshwater fish have prioritized cold-water over warm-water fishes (Myers et al. 2017), as well the effects of increased mean temperature over increased temperature variation (Vasseur et al. 2014). Consequently, expectations for warm-water fishes to increasingly contribute to global food supply (e.g., Ictaluridae; Dunham and Elasmad 2017) and regional fisheries (e.g., Centrarchidae; Hansen et al. 2017) in light of continued overfishing of regional cold-water species (Embke et al. 2019) may be overly optimistic. On the other hand, temperate fish have high intraspecific variation in thermal tolerance (Nati et al. 2021) and mechanisms underlying ecological

shifts and thermal-related mortalities may differ, potentially providing opportunities for populations to evolve adaptations that enhance thermal tolerance (Chen et al. 2018).

Although summerkills were our main focus due to existing links with regional temperature increases (Phelps et al. 2019; Till et al. 2019), most mortality events were caused by infectious diseases (Fig. 1)—the dynamics, transmission, and virulence of which are often partially mediated by climate (Marcos-López et al. 2010). Importantly, mortality diagnoses were based on visual surveys, not pathological analyses, and speculations about temporal dynamics of infectious outbreaks in a warming climate are unwarranted with these data. Observationally, however, summertime infectious events occurred

when monthly mean air and surface water temperature were $\sim 7\%$ and $\sim 5\%$ below median summertime temperatures, respectively (Fig. 2A; Dunnett test difference air = -0.88 , $p < 0.001$; t -test, $t = 8.59$, $df = 234.78$, $p < 0.001$; Dunnett test difference surface = -1.14 , $p < 0.001$; t -test, $t = 10.18$, $df = 234.7$, $p < 0.001$), and monthly mean deep-water temperature was $\sim 7\%$ above median summertime deep-water temperature (Dunnett test difference = 1.32 , $p < 0.008$; t -test, $t = -3.85$, $df = 234.54$, $p < 0.001$). In addition, there were no differences in temperature variation within lakes when summertime infectious events were and were not documented (Fig. 2B).

Most summertime infectious events were attributed to *Flavobacterium columnare* (81%, $n = 227$), an opportunistic pathogen that can cause increased mortality at higher temperature (Holt et al. 1975) but experiences trade-offs between increased thermal tolerance and lower virulence (Ashrafi et al. 2018). However, we cannot distinguish between infectious outbreaks due to community dynamics and temperature increases, and refrain from making inferences about how the frequency of infectious outbreaks may change over time. Better understanding infectious disease dynamics in the wild is an ongoing concern (Marcos-López et al. 2010), and broader considerations for other common infectious agents of regional fish, such as congener bacteria (*Flavobacterium branchiophilum*, *Flavobacterium psychrophilum*) that cause gill and coldwater disease, respectively, and prefer slightly cooler temperatures (Starliper 2011) are also warranted as seasonal temperature dynamics change across regional lakes (Woolway et al. 2020; Kraemer et al. 2021).

We anticipated winterkills to exhibit a negative relationship with temperature because sustained ice cover and weak thermal stratification can generate hypoxic conditions (Hurst 2007). However, winterkills occurred when monthly mean surface water ($F_{1,299907} = 3.95$, $p < 0.05$) and deep-water temperatures ($F_{1,299907} = 20.53$, $p < 0.001$) were $\sim 32\%$ and $\sim 50\%$ below median wintertime temperatures, respectively (Fig. 2C). Moreover, winterkills were negatively associated with ice duration (Supporting Information Fig. S2; $F_{1,97799} = 24.58$, $p < 0.001$), but not snow accumulation ($F_{1,272643} = 2.29$, $p < 0.13$), and occurred when mean air temperature was $\sim 35\%$ above median wintertime temperatures ($F_{1,299907} = 9.74$, $p < 0.002$). While these results vaguely suggest low water temperatures (Greenbank 1945; Hurst 2007) or earlier thermal stratification (e.g., reduced ice duration and increased air temperature, Woolway et al. 2021) may have affected thermal-oxygen dynamics and led to hypoxic conditions, accurate dates of winterkills are difficult to obtain because of wintertime visibility constraints. Lastly, winterkills are strongly mediated by local processes of geomorphology, wind speed, and lake respiration (Greenbank 1945), but are generally predicted to decrease in frequency across north temperate lakes because declines in snow and ice coverage are expected to increase wintertime dissolved oxygen concentrations (Woolway

et al. 2020). While not explored here due to paucities of future estimates of ice duration and other key environmental variables, reductions in winterkills may partially offset mortality increases due to other causes.

Spatiotemporal trends of summerkill predictions

The best fit water and air temperature-based models for summerkills performed similarly well (Supporting Information Table S2) and included down-sampled ridge regressions with maximum, mean, and minimum air temperature and z-scores (Supporting Information Fig. S1; logloss = 2.44) and mean surface temperature and z-score (logloss = 2.48). Compared to the median of five documented summerkills per year across the historical time period and study region, both air and water temperature models generated slightly higher predictions of eight summerkills per year ($n = 19$ years, mean = 9.36, SE = 1.90, range = 3–26; $n = 19$ years, mean = 9.36, SE = 1.38, range = 3–19), respectively (Fig. 4A, left). These models suggested air and water temperatures, as well as lake surface area, had similar positive effects (Supporting Information Fig. S1) and major environmental conditions including ice duration and Secchi depth, had appreciable effects. In addition, there was a latitudinal effect that was evident in existing spatial variation of summerkills (Fig. 1) and contributed to significant spatial autocorrelation among summerkill probabilities from best fit air (Moran $I > 0.23$; $p < 0.001$) and water temperature-based models (Moran $I > 0.06$; $p < 0.001$; Supporting Information Table S4). Therefore, because recent regional air and water temperatures are more decoupled due to the proximity of the Laurentian Great Lakes (Notaro et al. 2013), recent air temperature estimates may be a reasonable predictor of fish mortality events for north temperature regions without depth-specific water temperature profiles, though not necessarily when predicting over future decades (Fig. 4C; Supporting Information Fig. S3).

During the mid-21st century, water and air temperature model predictions began to diverge and estimated 21 ($n = 19$ years, mean = 25.32, SE = 2.68, range = 14–63) and 41 summerkills per year ($n = 19$ years, mean = 72.25, SE = 14.87, range = 9–252), respectively (Fig. 4A, middle). Model predictions increasingly diverged over the late 21st century, with the water and air temperature model predicting 41 ($n = 19$ years, mean = 38.44, SE = 1.76, range = 25–56) and 182 summerkills per year ($n = 19$ years, mean = 223.03, SE = 27.23, range = 67–449), respectively, by 2100 (Fig. 4A, right). These projections, based on the worst-case climate scenario, are ~ 6 - to 34-fold increases compared to the median of historical summerkills frequencies across north temperate lakes. Importantly, though, these predictions do not consider uncertainty in the underlying models that estimated future air or water temperatures.

Spatiotemporal differences between water and air model probabilities largely occurred across the mid- and late-21st century because (1) the water temperature-based model generated higher probabilities across lower latitudes, where most

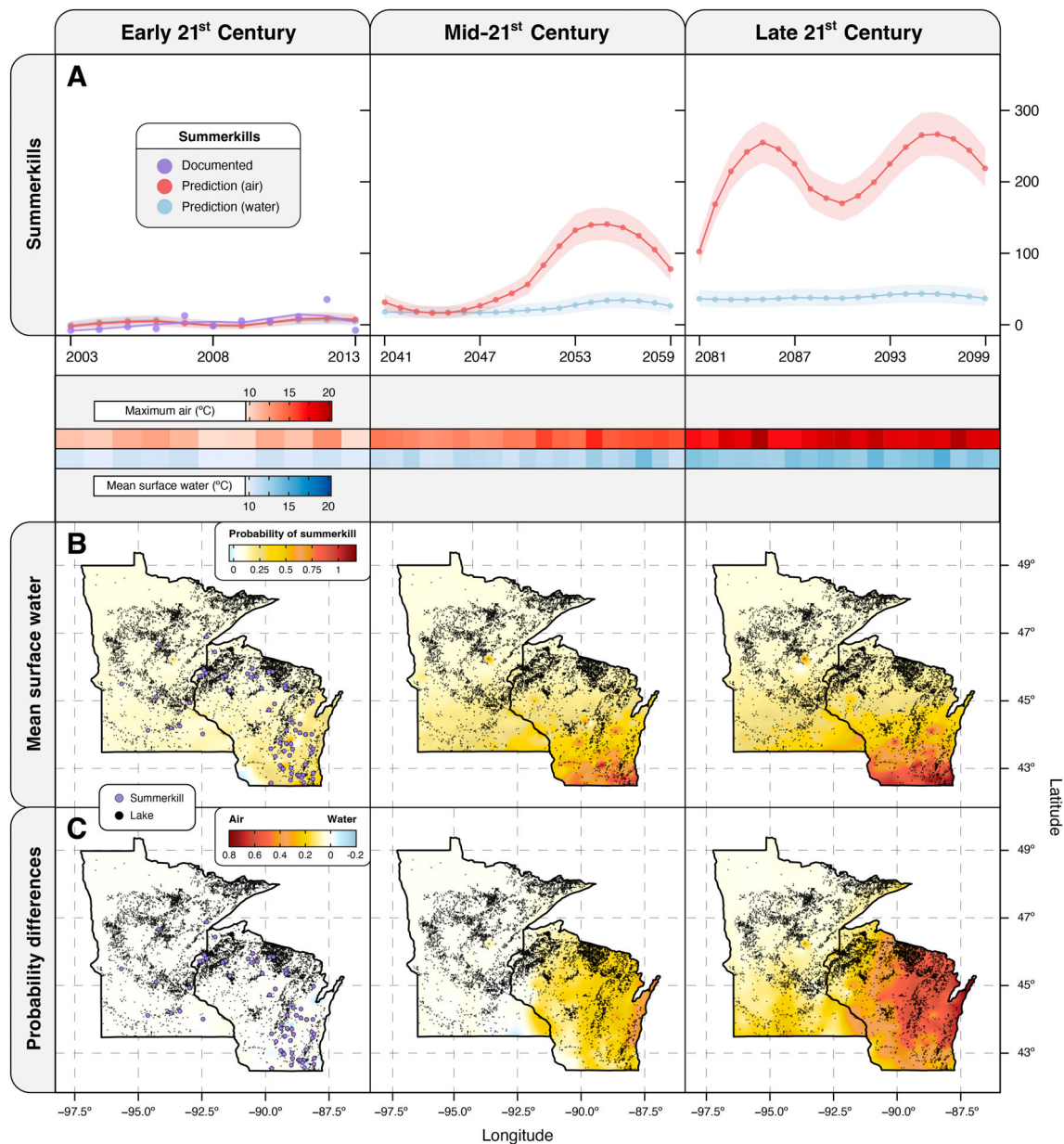


Fig. 4. Documented and estimated future frequencies of summerkills over time (A), probabilities of summerkills based on the water temperature model (B), and differences between probabilities of summerkills from air and water temperature models (C). For (A), documented (purple circles) and predicted annual frequencies of summerkills based on maximum air or water temperature models (red or blue circles, respectively) with 95% confidence intervals (shaded areas) across each time period; the temperature panel (bottom) shows annual mean air and surface water temperature across the study region. For (B,C), locations of documented summerkills (early 21st century) and regional lakes are shown via purple and black circles, respectively.

historical summerkills have been documented and few lakes occur, and (2) the air temperature-based model generated higher probabilities across eastern Wisconsin that borders the Laurentian Great Lakes, where fewer historical summerkills have been documented but many lakes occur (Fig. 4C). Spatial autocorrelation among summerkill predictions from the water temperature model, but not the air temperature model, deteriorated over the mid- and late-21st century, respectively

(Moran $I = 0.005$, $p = 0.16$; Moran $I = 0.003$, $p = 0.30$; Supporting Information Table S4). This finding, in conjunction with divergent predicted future frequencies of summerkills, clearly demonstrates the efficacy of our air temperature model depends upon the reliability of underlying temperature projections (Shen et al. 2018) and regional air–water temperature dynamics (Notaro et al. 2013; Winslow et al. 2017). While North American temperate lakes have recently

undergone substantial water temperature increases (Notaro et al. 2013; Woolway et al. 2020), the Great Laurentian Lakes generally mitigate increases in regional summertime air temperature and variation (Notaro et al. 2013), and lower rates of future water temperature increase are expected partially because of sustained declines in ice and snow coverage (Woolway et al. 2020).

However, despite future predictions for buffered increases in water temperature, regional lakes are still expected to experience some of the largest air and surface water temperature increases across the United States under increased carbon dioxide concentrations (Fang and Stefan 2009). In addition, warming temperatures have already decreased dissolved oxygen—the main underlying cause of documented summerkills (Thronson and Quigg 2008; Fey et al. 2015)—across deep-water habitats of north temperate lakes due to intensified thermal stratification and decreased water clarity (Jane et al. 2021). Moreover, regional eutrophication is expected to increase under a warmer, more precipitous climate (Sinha et al. 2017), which will likely exacerbate increases in water temperature and decreases in dissolved oxygen concentrations (Williamson et al. 2016). These circumstances further suggest expanding approaches that use climate projections to predict frequencies of biological catastrophes in freshwater systems will depend upon understanding multifaceted implications of global change on thermal-oxygen dynamics (Woolway et al. 2020; Kraemer et al. 2021).

The documented relationships between summerkills, winterkills, and infectious disease-induced mortality events suggest water temperature increases will alter the primary causes and frequencies of lentic fish mass mortality events. Indeed, similar approaches have been used to predict increases in extinction risk of lizard (Sinervo et al. 2010) and amphibian populations (Lowe 2012). Because global temperatures will continue to increase over the coming century (Maurer et al. 2007), robust frameworks that provide baseline predictions regarding long-term predictability of ecological catastrophes (Sinervo et al. 2010; Bailey and van de Pol 2016), and highlight consequential uncertainties under future climate projections (Shen et al. 2018), are imperative for effective conservation management (McDowell et al. 2017; Soon and Ransangan 2019). Development of future forecasting approaches should account for additional effects of warming temperatures such as declines in recruitment and production (Cohen et al. 2016; Hansen et al. 2017; Dahlke et al. 2020), as well as factors that could ameliorate the likelihood of future events such as adaptation and evolutionary rescue (Morgan et al. 2020) or management strategies for mitigating eutrophication (Williamson et al. 2016). Collectively, our results suggest sustained local temperature increases will greatly increase the likelihood of ecological catastrophes, especially as global efforts to mitigate climate warming remain nascent.

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