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The extent and variability of storm-induced temperature changes in lakes measured with long-term and high-frequency data

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The intensity and frequency of storms are projected to increase in many regions of the world because of climate change. Storms can alter environmental conditions in many ecosystems. In lakes and reservoirs, storms can reduce epilimnetic temperatures from wind-induced mixing with colder hypolimnetic waters, direct precipitation to the lake's surface, and watershed runoff. We analyzed 18 long-term and high-frequency lake datasets from 11 countries to assess the magnitude of wind- vs. rainstorm-induced changes in epilimnetic temperature. We found small day-to-day epilimnetic temperature decreases in response to strong wind and heavy rain during stratified conditions. Day-to-day epilimnetic temperature decreased, on average, by 0.28°C during the strongest windstorms (storm mean daily wind speed among lakes: 6.7 ± 2.7 m s^{-1}, 1 SD) and by 0.15°C after the heaviest rainstorms (storm mean daily rainfall: 21.3 ± 9.0 mm). The largest decreases in epilimnetic temperature were observed ≥2 d after sustained strong wind or heavy rain (top 5^{th} percentile of wind and rain events for each lake) in shallow and medium-depth lakes. The smallest decreases occurred in deep lakes. Epilimnetic temperature change from windstorms, but not rainstorms, was negatively correlated with maximum lake depth. However, even the largest storm-induced mean epilimnetic temperature decreases were typically <2°C. Day-to-day temperature change, in the absence of storms, often exceeded storm-induced temperature changes. Because storm-induced temperature changes to lake surface waters were minimal, changes in other limnological variables (e.g., nutrient concentrations or light) from storms may have larger impacts on biological communities than temperature changes.

Climate change is increasing the frequency of extreme weather events such as droughts, heat waves, and storms in many regions of the world (Coumou and Rahmstorf 2012; Seneviratne et al. 2012; Nielsen and Ball 2015). Storms, in particular, are changing in frequency and intensity in wind speed (Knutson et al. 2015; Kang and Elsner 2018) and precipitation (Easterling et al. 2000; Thiery et al. 2016). Storms often alter environmental conditions which can influence the composition and structure of biotic communities in terrestrial and aquatic ecosystems (Jentsch et al. 2007; Lawson et al. 2015). Therefore, assessment of how extreme weather events impact environmental conditions and the resulting consequences for biotic interactions and ecosystem functions and services is critically important (e.g., Cardinale et al. 2012).

Storms can affect lake ecosystem conditions in many ways. For example, storms can alter thermal stratification during the thermally stratified period (Jennings et al. 2012; de Eyto et al. 2016; Kasprzak et al. 2017) and deepen the thermocline, sometimes resulting in complete mixing of the water column (Yount 1961; Klug et al. 2012; Abell and Hamilton 2015). In stratified lakes, epilimnetic temperatures may decrease because of colder water from the hypolimnion mixing into the epilimnion (Znachor et al. 2008; Umaña-Villalobos 2014), upwelling, internal waves breaking at the shore, or heat flux at the lake surface altered by wind, rain, or changes in air temperature (e.g., Andreas et al. 1995; Kasprzak et al. 2017; Rooney et al. 2018). However, the extent of temperature change from storm events also depends on a variety of environmental and lake characteristics (Padisák et al. 1988; Kuha et al. 2016; Andersen et al. 2020), such as the frequency of storm events (Smits et al. 2020), internal seiche dynamics (Woolway et al., 2018), lake mixing regime (Jennings et al. 2012; Kuha et al. 2016), and the ratio of the watershed area to the lake surface area (WA:SA) (Jennings et al. 2012; Klug et al. 2012). Therefore, what constitutes a storm and how storms may affect lake processes are highly variable, making comparisons across waterbodies difficult (Stockwell et al. 2020).

Most studies, typically conducted in shallow to medium-depth lakes, have found that epilimnetic temperature does not change (Robarts et al. 1998; Jennings et al. 2012; Ji et al. 2018) or decreases slightly (<1–3°C; Klug et al. 2012; Abell and Hamilton 2015; de Eyto et al. 2016) after a storm. A few lakes exhibited more substantial decreases in epilimnetic temperatures (by 3–6°C; Znachor et al. 2008; Klug et al. 2012; Kuha et al. 2016), but these cases were often a result of severe storms associated with tropical cyclones. Temperature decreases can also occur in deep lakes when wind-driven circulation drives upwelling of hypolimnetic waters (Rinke et al. 2009; Soulignac et al. 2018). We are unaware of any study that has documented a statistically or ecologically significant increase in epilimnetic water temperatures following a storm.

The impacts of storms on water temperature, however, have largely been limited to studies of a single lake or region (Robarts et al. 1998; Kuha et al. 2016; Kasprzak et al. 2017), or constrained to one or a few storm events (Havens et al. 2011; de Eyto et al. 2016; Jung et al. 2016). Jennings et al. (2012) conducted a global study of the impacts of storms on lakes but did not perform a specific standardized assessment of storm-induced temperature changes. Here, we address this gap by conducting a quantitative, comparative, and standardized analysis of wind vs. rainstorm-induced temperature change in lakes across the globe. We used 18 long-term and high-frequency lake and meteorological datasets to assess day-to-day changes in lake water temperatures in response to storms, and how such temperature responses may be mediated by environmental and lake characteristics.

Materials and methods

Study sites

High-frequency meteorological and lake temperature data were compiled from 18 lakes across 11 countries (Table 1). The period of data collection across the lakes ranged from 2 to 18 yr (Supporting Information Table S1) and the measurement frequency ranged from every minute to once per day. Lakes spanned five orders of magnitude in surface area, from 0.03 (Emerald) to 2700 km^2 (Kivu), and two orders of magnitude in maximum depth, from 3.1 (La Salada) to 594 m (Crater). We followed the precedent of prior study by characterizing lakes into depth classifications (e.g., Beaulieu et al. 2013; Edlund et al. 2017; Stockwell et al. 2020) to test storm-induced temperature responses across lakes with diverse morphometric characteristics. Based on natural breaks in the distribution of maximum depths (Z_{max}), lakes were characterized as shallow ($Z_{max} < 20$ m; $n = 5$), medium (20 m $\leq Z_{max} <$ 70 m; $n = 10$) and deep ($Z_{max} \geq 70$ m; $n = 3$) (Table 1). The lakes also encompassed a range of trophic states (from oligotrophic to eutrophic), mixing regimes (mono-, di-, and polymictic), meteorological and thermal profile characteristics (Table 2), and comprised both reservoirs and naturally formed lakes. The diverse range of systems render our analyses representative of lakes globally.

Meteorological and lake temperature data

We focused on wind speed (m s^{-1}) and daily rain (mm d^{-1}) as meteorological factors that can impact lake temperatures by physically mixing the lake (wind) or through delivery of water (directly by rain or indirectly by runoff) with a different temperature than the lake. Meteorological data were recorded across a range of frequencies, from every minute to once per day, depending on the lake and variable. Rain data were typically collected at daily intervals. To standardize the frequency of measurements among lakes, we calculated mean daily wind speed and daily rain (each day being defined from 0:00 to 23:59) for each lake using the package *openair* in R v3.6.0 (Carslaw and Ropkins 2012). We did not use maximum daily wind speed because these observations were not available for all lakes and mean and maximum wind speeds were strongly correlated when data were available for both ($r = 0.89$, $n = 6$ lakes). We did not apply elevational corrections for air temperature or wind speed because sensors were located at different heights above the surface for different lakes and not all lakes had sensor height recorded. A location correction was also not applied because some stations were located on land whereas some were on water. Ultimately, unadjusted sensor height did not affect our results because we standardized storm events within each lake (*see* below). Snow and hail were not included in rain measurements. Information on the location of the weather stations are provided in Supporting Information Table S2.

High-frequency water temperature data were recorded near the deepest location or the center of each lake (Table 1). Therefore, the effects of internal seiches and upwelling on temperature variability was expected to be low (*see* Rinke et al. 2009). As with the meteorological data, we averaged sub-daily temperature measurements for each depth of data collection to daily values using *openair* to standardize the frequency of data collection across lakes and to match that frequency with the meteorological data.

We calculated epilimnetic, metalimnetic, and hypolimnetic temperatures using *rLakeAnalyzer* in R v3.6.0 (Read et al. 2011), which calculates the volumetric mean of temperatures from depths located within each respective stratum. If the lake was not stratified, and no thermocline depth was calculated (as 1°C change in temperature over a 1-m change in depth), the epilimnetic temperature was the volumetric mean of the full water column profile (and metalimnetic and hypolimnetic temperatures were subsequently not calculated in these cases). Profiles were excluded if >50% of the temperature data from the water column measurement depths were not available or recorded. Four lakes (La Salada, Emerald, Cheney, and Taupo) only had high-frequency lake temperature data from one depth in the epilimnion (Supporting Information Table S1), which we assumed to represent the epilimnion for each of these four lakes. One lake (Harp) only had temperature measurements up to one-third of the station depth from the surface, which were used to calculate epilimnetic temperature. However, Harp had a thermocline depth calculated for 97% of the daily records during the stratified period, thus epilimnetic temperature was still calculated for most daily profiles in the series based on the thermocline depth. We were not able to calculate metalimnetic or hypolimnetic temperature for these five lakes. While subsurface temperature (i.e., temperature at 0.1 m depth) may differ from the bulk epilimnion temperature, intensive surface mixing during storms should homogenize the epilimnion. Further, sensor depths varied lake by lake (i.e., not all lakes had measurements at 0.1 m depth). Therefore, we chose to focus on the entire epilimnion.

Other ways to calculate thermocline depth exist (e.g., absolute temperature difference from the surface and temperature gradient from the surface methods); however, each method also has limitations depending on a mosaic of lake and environmental characteristics (Wilson et al. 2020). Therefore, we chose to calculate epilimnetic temperatures and other water column stability metrics using *rLakeAnalyzer* from

Table 1. Location and characteristics of lakes in our study, arranged in order of shallowest to deepest maximum depth.

Lake	Country codes	Lat	Lon	Elevation (m)	Area (km^2)	Z_{max} (m)	Z_{mean} (m)	Residence time (years)	Catchment area (km^2)	Mixing regime	Trophic state
La Salada	AR	−39.457	−62.707	14	3.5	3.1	2.5	NA	16.5	Poly	Eu
Muggelsee	DE	52.446	13.650	34	7.3	8.0	4.9	0.1	7000.0	Poly	Eu
Emerald	US	36.597	−118.676	2800	0.03	10.0	6.0	0.2	1.2	Di	Oligo
Cheney	US	37.726	−97.794	433	40.1	12.5	5.1	1.2	2416.0	Poly	Eu
Oneida	US	43.181	−75.926	112	207.0	16.8	6.8	0.5	3579.0	Poly	Meso-eu
Annie	US	27.208	−81.352	34	0.3	20.7	9.1	2.5	14.0	Mono	Oligo-meso
Erken	SE	59.845	18.624	10	27.0	21.0	9.0	7.0	140.0	Di	Meso
Sammamish	US	47.616	−122.089	9	19.8	32.0	18.0	2.4	250.0	Di	Meso
Harp	CA	45.370	−79.130	327	0.7	37.5	13.3	3.2	5.42	Di	Oligo
Windermere	GB	54.311	−2.954	39	14.8	41.0	21.3	0.2–1	248.8	Mono	Meso
Kinneret	IL	32.833	35.583	−210	168.7	41.7	25.6	7–10	2730.0	Mono	Meso-eu
Rimov	CZ	48.849	14.491	470	2.0	42.0	15.6	0.2	488.0	Di	Eu
Feeagh	IE	53.949	−9.577	20	3.9	45.0	14.5	0.5	84.1	Mono	Oligo
Washington	US	47.610	−122.256	5	87.6	65.2	32.9	2.4	1270.0	Di	Oligo
Stechlinsee	DE	53.152	13.029	60	4.3	66.0	22.8	34.4	12.4	Di	Oligo
Taupo	NZ	−38.780	175.974	356	616.0	186.0	95.5	11.0	3487.0	Mono	Oligo
Kivu	RW/CD	−1.725	29.238	1463	2700.0	485.0	240.0	100.0	5100.0	Mero	Oligo
Crater	US	42.953	−122.086	1882	53.2	594.0	350.0	150.0	14.4	Di	Oligo

For trophic state: eu, eutrophic; meso, mesotrophic; oligo, oligotrophic. For mixing regime: di, dimictic; mero, meromictic; mono, monomictic; poly, polymictic. For country codes: AR, Argentina; CA, Canada; CD, Democratic Republic of the Congo; CZ, Czech Republic; DE, Germany; GB, United Kingdom; IE, Ireland; IL, Israel; NZ, New Zealand; SE, Sweden; RW, Rwanda; US, United States. NA, no data available.

the precedence of other studies (e.g., Klug et al. 2012; Hansen et al. 2017; Woolway et al. 2018).

Statistical analyses

Analysis 1: Daily changes in water temperature

We first assessed day-to-day changes in water temperature under all conditions of wind and rain across lakes and seasons. Storms were not explicitly considered in this analysis (*see* Analysis 2). Specifically, we compared daily rain (day t) and changes in mean daily wind speed (day $[t+1]$ – day t) with daily changes in epilimnetic, metalimnetic, and hypolimnetic temperature (day $[t+1]$ – day t). We expected epilimnetic temperature to decrease following high rainfall on the previous day or from an increase in mean daily wind speed. Epilimnetic temperature change was compared to previous-day rain (day t) because rain effects on epilimnetic temperature could be delayed from runoff into a lake, depending on antecedent lake conditions and watershed attributes such as WA: SA (Stockwell et al. 2020).

Analysis 2: Storms and temperature in stratified period

We next evaluated the effects of storms on epilimnetic temperature by comparing the temperature changes between the top 5th percentile (top 5%) of observed wind and rain events to the bottom 95th percentile (bottom 95%) observed wind and rain events, on a lake-by-lake basis. Because the impacts of a storm on a lake depends on a myriad of factors such as lake morphology, antecedent conditions, and atmospheric conditions, we defined a storm as the top 5% of wind and rain events of each lake as a way to standardize across-lake differences (Perga et al. 2018; Stockwell et al. 2020).

Epilimnetic temperature may also change in response to storms that last more than 1 d. To evaluate this possibility, we assessed the cumulative effects of mean daily wind speed and daily rain on epilimnetic temperature changes over 2- to 7-d time intervals (hereafter, referred to as storm intervals), in addition to the 1-d interval in Analysis 1. Storms were defined as the top 5% cumulative mean wind speed or cumulative previous-day rain amounts over each respective storm interval. We assumed that storms of <1 d in duration were captured with the 1-d interval. The effects of storms vs. other possible factors on epilimnetic temperature change (e.g., seasonality in lake temperature) is likely more difficult to disentangle with each subsequent day interval, so we did not analyze storm intervals >7 d.

We limited the data for Analysis 2 to the thermally stratified period for each lake to standardize the time period across our diverse and globally distributed set of lakes. The thermally stratified period for each lake was determined by seasonal epilimnetic temperature, thermocline depth, and Schmidt stability calculations from *rLakeAnalyzer* (Read et al. 2011). For the four lakes with water temperature measurements at only a single, near-surface depth, we determined the thermally stratified period by seasonal epilimnetic temperatures and consultation with the local researchers. All subsequent analyses were based

Table 2. Mean (±1 SD) meteorological and lake physics metrics during the thermally stratified period across lakes from daily observations. Schmidt stability was not calculated for five lakes that did not have full water column temperature profiles (La Salada, Emerald, Cheney, Harp, and Taupo).

Lake	Atmospheric temperature (°C)	Solar radiation (W m^{-2})	Rain (mm)	Wind speed (m s^{-1})	Epilimnetic temperature (°C)	Hypolimnetic temperature (°C)	Schmidt stability (J m^{-2})
La Salada	17.4 ± 5.2	NA	1.5 ± 5.3	6.6 ± 2.6	18.7 ± 4.3	NA	NA
Muggelsee	16.3 ± 4.5	181.6 ± 84.9	1.7 ± 4.2	3.0 ± 1.4	18.2 ± 4.3	17.9 ± 3.5	7.1 ± 10.0
Emerald	9.2 ± 5.9	206 ± 88.2	0.6 ± 4.4	1.4 ± 0.5	9.7 ± 6.2	NA	NA
Cheney	18.8 ± 8.3	NA	3.0 ± 10.3	5.0 ± 2.0	18.6 ± 6.9	NA	NA
Oneida	17.9 ± 5.1	166.6 ± 82.7	2.2 ± 5.0	2.9 ± 1.7	20.0 ± 4.3	18.4 ± 4.2	25.5 ± 32.0
Annie	22.7 ± 4.9	222 ± 64.4	3.3 ± 9.5	1.7 ± 0.8	25.5 ± 4.3	16.7 ± 1.3	317 ± 171
Erken	15.2 ± 3.6	193 ± 79.2	1.9 ± 4.8	3.6 ± 1.5	16.9 ± 3.3	13.5 ± 2.3	60.4 ± 58.9
Sammamish	14.9 ± 4.8	159 ± 90.2	2.0 ± 5.0	2.3 ± 1.0	17.1 ± 4.7	9.6 ± 0.8	579 ± 396
Harp	14.5 ± 5.4	NA	3.5 ± 7.8	2.0 ± 0.7	18.7 ± 5.0	NA	NA
Windermere	12.7 ± 3.3	150 ± 82.1	5.1 ± 9.0	3.1 ± 1.5	14.1 ± 3.7	8.9 ± 1.0	451 ± 291
Kinneret	25.1 ± 4.6	249 ± 73.8	0.4 ± 2.4	2.8 ± 1.1	25.5 ± 3.9	16.2 ± 0.8	1910 ± 847
Rimov	13.0 ± 6.0	170 ± 98.2	2.1 ± 5.5	1.7 ± 0.9	15.1 ± 4.9	7.1 ± 1.9	510 ± 355
Feeagh	12.5 ± 2.8	NA	3.8 ± 6.0	4.7 ± 1.8	13.5 ± 2.8	11.9 ± 1.8	170 ± 162
Washington	14.7 ± 4.5	161 ± 88.7	2.2 ± 5.2	3.2 ± 1.4	16.0 ± 4.3	9.2 ± 0.8	1770 ± 1170
Stechlinsee	13.5 ± 5.2	152 ± 87.1	1.0 ± 2.1	2.4 ± 1.0	16.1 ± 4.9	5.7 ± 0.4	1190 ± 723
Taupo	14.8 ± 3.5	NA	1.9 ± 4.8	3.5 ± 1.9	16.7 ± 3.2	NA	NA
Kivu	21.6 ± 0.8	210 ± 54.7	3.2 ± 7.2	3.0 ± 0.6	24.4 ± 0.4	23.4 ± 0.1	12,400 ± 2800
Crater	6.5 ± 7.2	NA	1.4 ± 5.1	4.3 ± 2.6	9.9 ± 4.0	4.3 ± 0.3	13,600 ± 11,000

NA, non-available data.

solely on data during the thermally stratified period in each lake.

To quantify the effects of storms on water temperature, we compared the cumulative changes in water temperature (as the sum of the day-to-day water temperature changes) during the top 5% of cumulative (summed) mean daily wind speed and cumulative (summed) previous-day total rain amounts with the bottom 95% observations, over 1- to 7-d intervals. For example, if the cumulative mean daily wind speed over days 10–14 was in the top 5% of windstorms for the 4-d interval, then the corresponding cumulative change in epilimnetic temperature (*ET*) would be:

$$\sum_{t=10}^{13}(ET_{t+1}-ET_t)$$

Likewise, if cumulative rain over the same 4-d interval was in the top 5% of rain events, then the corresponding cumulative change in epilimnetic temperature, accounting for a 1-d lag (*see* Analysis 1), would be:

$$\sum_{t=11}^{14}(ET_{t+1}-ET_t)$$

The analyses were performed only with epilimnetic temperature changes because metalimnetic or hypolimnetic temperature data were not available for all lakes (Supporting Information Table S1). We calculated the mean epilimnetic temperature difference between the top 5% and bottom 95% groups (hereafter, referred to as mean $ETD_{5\text{-}95}$) by subtracting the mean epilimnetic temperature difference for the bottom 95% group (ETD_{95}) from the top 5% group (ETD_5) for each storm type, each storm interval, and each lake. Mean $ETD_{5\text{-}95}$ was tested for significant differences by storm type (wind or rain), storm window (1- to 7-d intervals), and lake depth (shallow, medium, and deep) using a full-factorial three-way ANOVA with post-hoc Tukey pairwise comparisons.

We were also interested in testing whether epilimnetic temperatures responded differently to concurrent windstorms and rainstorms ("wind plus rain") compared to windstorms only and rainstorms only. However, we only descriptively report on epilimnetic temperature changes from wind plus rainstorms (i.e., both wind and rain events that were in the top 5% on the same day) over a 1-d storm interval because wind plus rainstorms were uncommon and became even less common as the day intervals increased. Further, no deep lakes had concurrent wind plus rain observations and so we were not able to test for lake depth (or storm interval), as in the three-way ANOVA above.

Analysis 3: Environmental factors and temperature

We assessed how lake and environmental characteristics may moderate epilimnetic temperature changes induced by storms. We performed multiple linear regression analysis of the mean $ETD_{5\text{-}95}$ calculated for wind and rainstorms (from the seven individual storm intervals) with lake and environmental characteristics that are likely to affect lake thermal dynamics: maximum lake depth, lake surface area, water residence time (WRT), WA:SA, elevation, mean daily wind speed in the top 5% wind events across the 7 d, mean daily rain in the top 5% rain events across the 7 d, and the mean cumulative difference in the changes in mean air temperature between the top 5% and bottom 95% wind and rain events (*see* Supporting Information Table S3 for explanatory variable Pearson-product moment correlations). Maximum and mean lake depth were strongly correlated (r = 0.98), so we only included maximum lake depth. All explanatory variables except air temperature were $\log_{10}$-transformed to meet assumptions of normality and equal variance with respect to the residuals of the statistical models. The best models were determined through the package *MASS* in R using AIC, which identifies the best fit models while penalizing for model complexity (Quinn and Keough 2002; Venables and Ripley 2002).

Analysis 4: Water column stability and temperature

We tested for significant differences in the percent difference in Schmidt stability and Lake Number (calculated by *rLakeAnalyzer*) before and after wind and rainstorms for a 1-d interval. We included both the percent difference in Lake Number raw values and the number of observations of Lake Number that were <1 before and after wind and rainstorms. Lake Number values <1 indicate strong internal seiche and upwelling effects (Robertson and Imberger 1994; Woolway et al. 2018; Andersen et al. 2020). Based on the calculation through *rLakeAnalyzer*, only windstorms, and not rainstorms, should affect Lake Number changes. However, we still included Lake Number and temperature comparisons with rainstorms to account for any observations where wind and rainstorms occurred concurrently. We used percent differences to standardize across lakes because they have inherently different Schmidt stability and Lake Number values. As with changes in epilimnetic temperatures above, we calculated the mean percent difference of the change in Schmidt stability, Lake Number, and number of Lake Number observations <1 during the top 5% and bottom 95% wind and rain groups. We performed a full-factorial two-way ANOVA to test for differences in the percent change in Schmidt stability (hereafter, referred to as mean $PSD_{5\text{-}95}$), Lake Number ($LN_{5\text{-}95}$), and number of Lake Number observations <1 ($LN1_{5\text{-}95}$) where storm type (wind or rain) and lake depth (shallow, medium, and deep) were the main effects. We used post-hoc Tukey tests for pairwise comparisons. Only lakes with complete water column temperature profiles were included in the analysis (n = 13). $PSD_{5\text{-}95}$, $LN_{5\text{-}95}$, and $LN1_{5\text{-}95}$ were analyzed separately from the multiple linear regression analysis because five lakes did not have Schmidt stability and Lake Number calculated, and because our goal was to test $PSD_{5\text{-}95}$, $LN_{5\text{-}95}$, and $LN1_{5\text{-}95}$ independently to examine how water column stability changed from storms.

All statistical analyses were performed in R v 3.6.0 (R Development Core Team 2019). p values were considered significant at $\alpha = 0.05$.

Results

Analysis 1: Daily changes in water temperature

Mean (± 1 SD) daily wind speed across lakes ranged from 1.4 ± 0.5 m s^{-1} (Emerald) to 6.6 ± 2.6 m s^{-1} (La Salada) during the stratified period (Table 2). Daily rain ranged from 0 (all lakes) to 262 mm (Cheney). Kinneret had the lowest mean daily rain at 0.4 ± 2.4 mm. Windermere and Feeagh had the highest mean daily rain with 5.1 ± 9.0 mm and 3.8 ± 6.0 mm, respectively, during the stratified period (Table 2). Mean epilimnetic temperature during the stratified period ranged from 9.7 ± 6.2°C (Emerald) to 25.5 ± 4.3°C (Annie) and 25.5 ± 3.9°C (Kinneret). Crater had the lowest mean hypolimnetic temperature (4.3 ± 0.3°C) and Kivu the highest mean hypolimnetic temperature (23.4 ± 0.1°C) during the stratified period (Table 2). Mean epilimnetic temperature during the thermally stratified period was not related to latitude, longitude, or elevation (simple linear regressions: $p \geq 0.13$).

In general, deep lakes had smaller day-to-day epilimnetic, metalimnetic, and hypolimnetic temperature changes compared to shallow lakes (Fig. 1, Fig. 2; Supporting Information Fig. S1–S4). The maximum day-to-day increases in epilimnetic temperature change across seasons were 6.4°C in Rimov and 5.8°C in Annie and Sammamish. The maximum day-to-day decreases in epilimnetic temperature were similar in magnitude to the maximum increase, −6.4°C in Emerald and −6.2°C in Annie. Maximum day-to-day changes in metalimnetic and hypolimnetic temperature were similar in magnitude to changes in epilimnetic temperature (Supporting Information Fig. S1–S4). Contrary to our expectations, no relationship was apparent between day-to-day changes in mean daily wind speed or previous-day rain and changes in epilimnetic, metalimnetic, or hypolimnetic temperature. Daily temperature changes in the absence of storms was often greater than those changes during strong wind or rain events (Fig. 1, Fig. 2; Supporting Information Fig. S1–S4).

Analysis 2: Storms and temperature in stratified period

Mean daily wind speed and rain amounts across lakes for a 1-d storm interval were 6.7 ± 2.7 m s^{-1} and 21.3 ± 9.0 mm, respectively. La Salada had the greatest mean storm wind speed at 12.4 ± 1.6 m s^{-1} and Emerald had the lowest mean storm wind speed at 2.7 ± 0.7 m s^{-1}. Cheney had the highest mean storm rain amount at 38.6 ± 24.4 mm and Kinneret had the lowest mean storm rain amount of 7.0 ± 7.4 mm (Supporting Information Table S4).

In general, mean $ETD_{5\text{-}95}$ for wind had the greatest decreases across all storm intervals in shallow and medium-depth lakes (Fig. 3; Supporting Information Table S5, Table S6). The three greatest decreases in mean $ETD_{5\text{-}95}$ for wind were observed in the

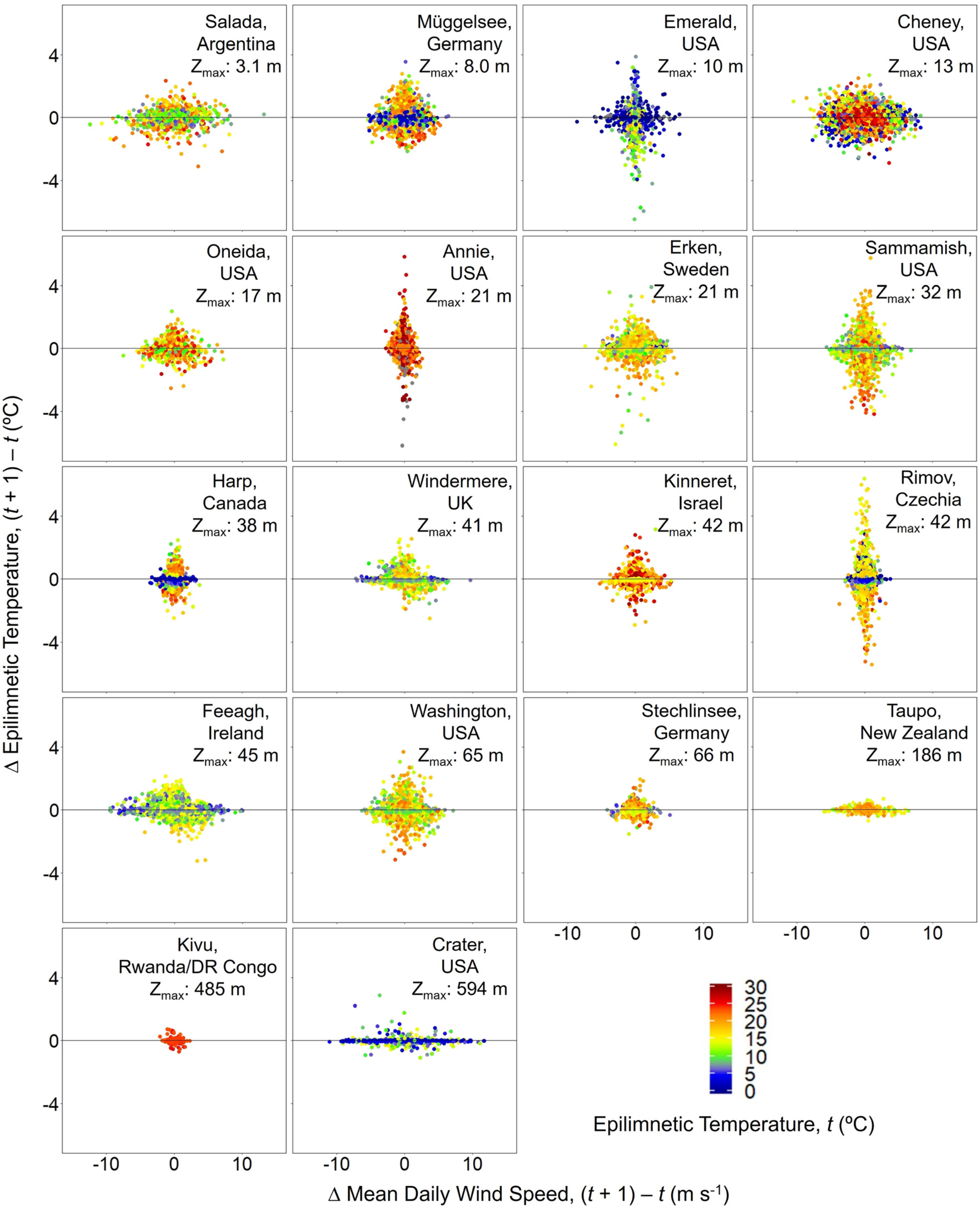

Fig 1. Day-to-day ([t + 1] – t) changes in epilimnetic temperature as a function of day-to-day changes in mean daily wind speed ([t + 1] – t) across all lakes and all sampling dates. Z_{max} is the maximum depth (m) for each lake. Colors refer to the epilimnetic temperature at time t when the data were collected.

shallow polymictic lakes La Salada (–1.5°C), Müggelsee (–1.5°C), and Oneida (–2.5°C). The three deep lakes (Taupo, Kivu, and Crater) exhibited relatively small decreases in mean $ETD_{5\text{-}95}$ for wind (Supporting Information Table S5). Cheney was the only lake to exhibit consistent increases in mean $ETD_{5\text{-}95}$ from wind. The most extreme individual observation of decreased temperature from a storm event was –4.9°C in Oneida, a shallow polymictic lake, and this observation occurred after strong wind.

The effect of storm type on mean $ETD_{5\text{-}95}$ depended on lake depth ($F_{2,210}$ = 4.57, p = 0.01; Table 3). In shallow and medium

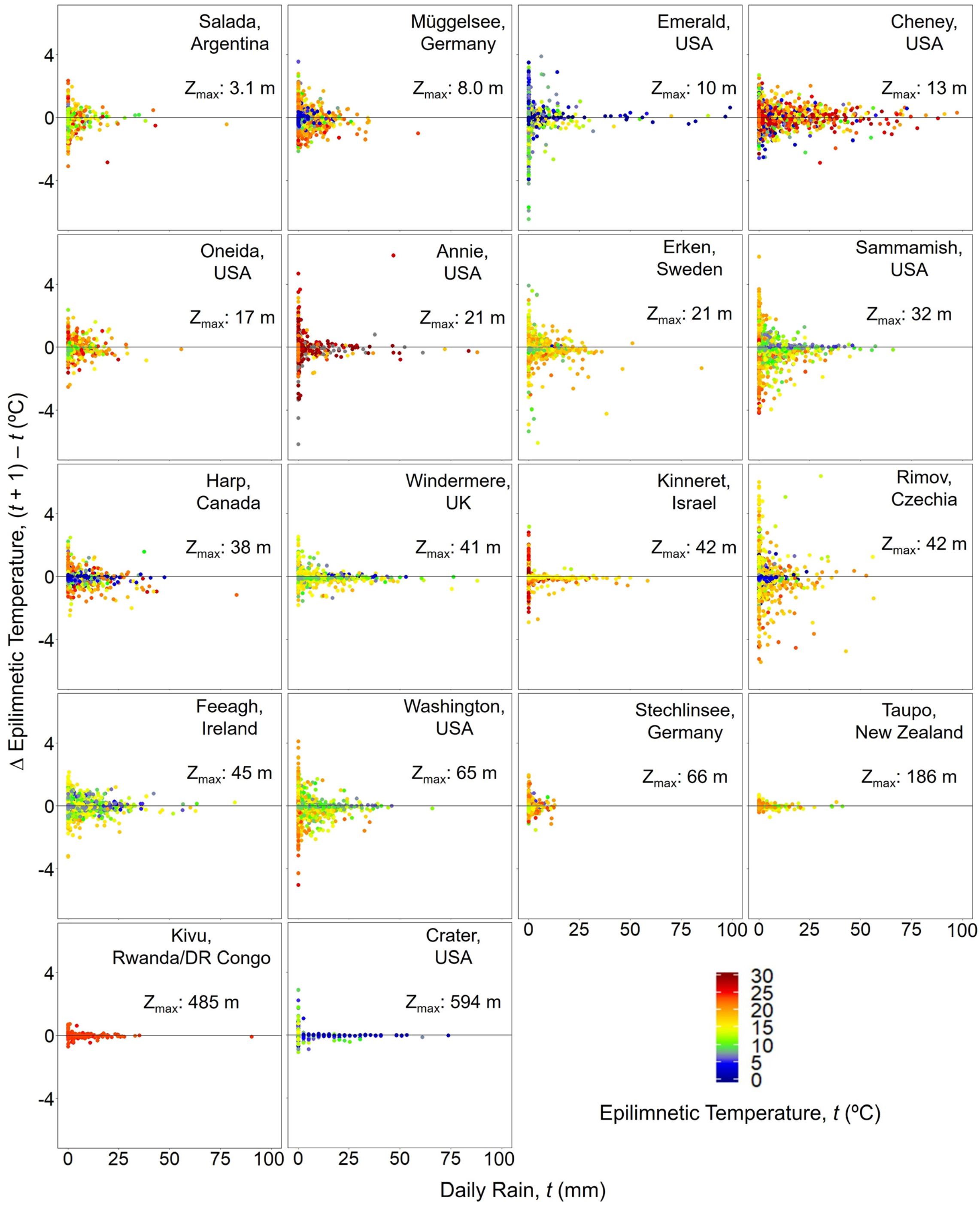

Fig 2. Day-to-day ([t + 1] – t) changes in epilimnetic temperature as a function of daily rain at time t across all lakes and all sampling dates. Z_{max} is the maximum depth (m) for each lake. Colors refer to the epilimnetic temperature at time t when the data were collected. Only a few days had daily rain >100 mm; the x-axis scale ended at 100 mm for presentation purposes.

lakes, but not in deep lakes, windstorms resulted in lower mean $ETD_{5\text{-}95}$ ($p \leq 0.002$) compared to rainstorms ($p \geq 0.10$). Mean $ETD_{5\text{-}95}$ also differed by storm interval ($F_{6,210}$ = 3.43; p = 0.003; Table 3). Mean $ETD_{5\text{-}95}$ had a greater decrease after 5, 6, and 7-d storm intervals compared to a 1-d storm interval ($p \leq 0.03$).

Qualitatively, mean $ETD_{5\text{-}95}$ for wind plus rainstorms (–0.30 ± 0.27°C) was similar to windstorms (–0.28 ± 0.19°C), compared to rainstorms (– 0.15 ± 0.14°C). However, wind plus rainstorm sample sizes were low (mean n of observations = 7.4 per lake; Supporting Information Table S4), with

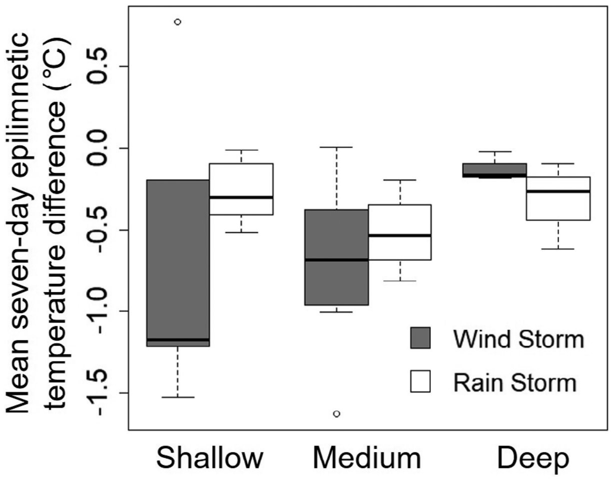

Fig 3. Relationships between the mean cumulative epilimnetic temperature difference between the cumulative top 5% daily mean wind speed and cumulative previous daily rain events and their respective bottom 95% daily mean wind speed or previous daily rain events across the 7-d storm interval during the thermally stratified period.

some lakes (n = 4) having no concurrent wind plus rainstorms. Annually (during the stratified period), lakes experienced 10.6 ± 7.9 windstorms, 10.6 ± 7.8 rainstorms, and 0.7 ± 0.7 concurrent wind plus rainstorms.

Analysis 3: Environmental factors and temperature

Maximum depth and mean $ETD_{5\text{-}95}$ were positively related for windstorms (multiple linear regression: $p = 0.048$; adjusted $R^2 = 0.34$; Fig. 4); however, no significant relationship existed for any explanatory variable and mean $ETD_{5\text{-}95}$ for rainstorms (multiple linear regression: $p = 0.25$).

Analysis 4: Water column stability and temperature

Storm type and lake depth were significant main effects for mean $PSD_{5\text{-}95}$, but not their interaction. Lakes had significantly greater decreases in mean $PSD_{5\text{-}95}$ from windstorms compared to rainstorms (two-way ANOVA: $F_{1,20} = 7.54$; $p = 0.01$; Table 4; Fig. 5). Mean $PSD_{5\text{-}95}$ had about a 4× greater decrease from wind vs. rainstorms (Fig. 5; Supporting Information Table S7). Mean $PSD_{5\text{-}95}$ also differed significantly among lake depths ($F_{2,20} = 5.67$; $p = 0.01$). Shallow lakes had a

Table 3. Three-way ANOVA statistics of the effects of storm type (wind or rainstorm), storm interval (1–7 days), lake depth (shallow, medium, or deep), and their two- and three-way interactions on mean $ETD_{5\text{-}95}$ temperature changes. Significant differences are highlighted in bold.

Model effect	*F*-statistic	*p* value	df
Storm type	5.81	**0.02**	1, 210
Storm interval	3.43	**0.003**	6, 210
Lake depth	9.39	**0.0001**	2, 210
Storm type: Storm interval	0.08	1.00	6, 210
Storm type: Lake depth	4.57	**0.01**	2, 210
Storm interval: Lake depth	0.24	1.00	12, 210
Three-way interaction	0.12	1.00	12, 210

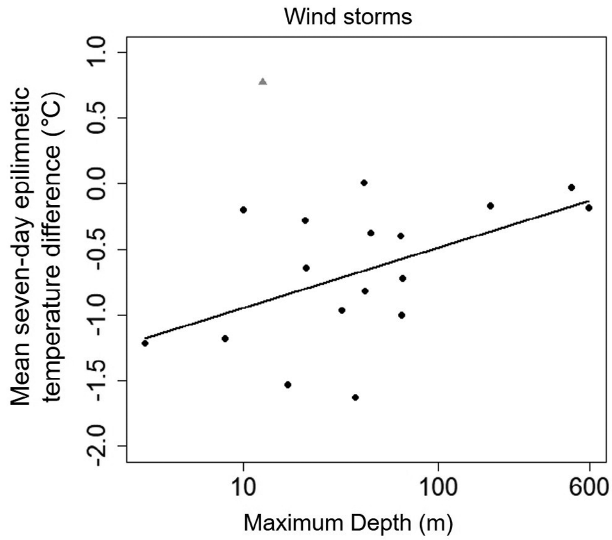

Fig 4. Relationship between maximum depth and mean epilimnetic temperature difference between the top 5% and bottom 95% for daily mean wind speed and across the 1- to 7-d storm intervals during the thermally stratified period. Note that the x-axis is on a $\log_{10}$ scale. Cheney (gray triangle) was not included in the model comparisons because Cheney was the only waterbody to exhibit consistent positive temperature changes from storms.

Table 4. Two-way ANOVA results testing the effects of storm type (wind or rainstorm), lake depth (shallow, medium, or deep), and their interaction on the mean percent difference in Schmidt stability, Lake number, and number of Lake number observations <1 between the top 5% and bottom 95% daily wind speed and previous-day rain observations across lakes during the thermally stratified period. Results are for a 1-d storm interval. Only lakes with complete temperature profiles were included in the model (n = 13). Significant differences are highlighted in bold.

Model effect	*F*-statistic	*p* value	df
Percent difference in Schmidt stability			
Storm type	7.54	**0.01**	1, 20
Lake depth	5.67	**0.01**	2, 20
Two-way interaction	1.94	0.17	2, 20
Percent difference in Lake number			
Storm type	32.1	**<0.0001**	1, 20
Lake depth	2.55	0.10	2, 20
Two-way interaction	0.39	0.69	2, 20
Percent difference in number of Lake number observations <1			
Storm type	10.7	**0.004**	1, 20
Lake depth	0.27	0.76	2, 20
Two-way interaction	0.31	0.73	2, 20

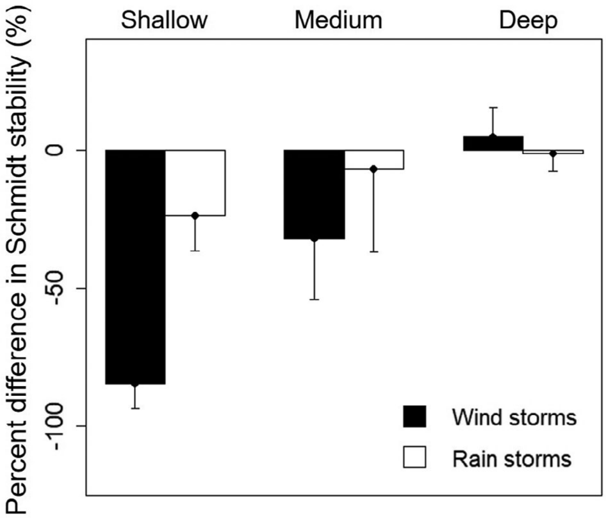

Fig 5. The mean (±1 SD) percent difference in Schmidt stability (J m^{-2}) between the top 5% and bottom 95% mean daily wind speed and previous-day rain observations in shallow, medium, and deep lakes during the thermally stratified period for a 1-d storm interval.

significantly greater decrease in mean $PSD_{5\text{-}95}$ compared to medium and deep lakes ($p \leq 0.04$), but mean $PSD_{5\text{-}95}$ was not different between medium and deep lakes ($p = 0.27$). Shallow lakes had about a ×3 and ×18 greater decrease in mean $PSD_{5\text{-}95}$ from windstorms vs. medium and deep lakes, respectively (Fig. 5; Supporting Information Table S7).

Lakes had significantly lower mean $LN_{5\text{-}95}$ and $LN1_{5\text{-}95}$ from windstorms compared to rainstorms (two-way ANOVA: $F_{1,20} \geq 10.7$; $p \leq 0.004$; Table 4). Mean $LN_{5\text{-}95}$ and $LN1_{5\text{-}95}$ had about a ×7 and ×8 greater decrease, respectively, from wind vs. rainstorms (Supporting Information Table S7). The difference in mean $LN_{5\text{-}95}$ and $LN1_{5\text{-}95}$ did not differ among lake depth or in the interaction between storm type and lake depth ($p \geq 0.10$).

Discussion

Contrary to our expectations, we found that the most extreme changes in epilimnetic temperature often occurred on days without storms. Factors other than storms, such as short time scale variability in meteorological factors that affect lake heat budgets (i.e., air temperature and irradiance changes) and variability in internal lake mixing dynamics (Blanken et al. 2003; Woolway et al. 2018; Yang et al. 2018), may have a much larger effect on day-to-day episodic changes to epilimnetic temperature. Within our observed range of storm-induced epilimnetic temperature changes, decreases were larger in shallow and medium-depth lakes compared to deep lakes, but only for windstorms. The effects of rain on epilimnetic temperatures may be less than wind because of the variability in rainwater and runoff temperature, which depend on the season and climate (Thompson et al. 2008; Doubek et al. 2015; Rooney et al. 2018). Conversely, the potential for wind to affect water temperature more directly scales with lake morphometry and the distribution of heat vertically in lakes (Horn et al. 1986; Stockwell et al. 2020). Overall, however, changes in epilimnetic temperature from storms were small, i.e., mean $ETD_{5\text{-}95}$ for lakes were generally <0.75 and <0.55°C for wind and rainstorms, respectively, even after considering storm intervals of up to 7 d.

Our results suggest that at some depth and lake size, the effects of storms on epilimnetic temperature become minimal because too much energy is needed to effectively mix deep lakes. The effect of wind on mean $ETD_{5\text{-}95}$ was greater for shallow and medium lakes compared to deep lakes (Taupo, Kivu, and Crater), which is likely a result of decreased thermal water column stability from hypolimnetic waters mixing with the epilimnion in shallow and medium-depth lakes (Engle and Melack 2000; Jennings et al. 2012). The amount of energy (from wind) or volume of water (from rain) needed to induce the epilimnion to mix with the meta- and hypolimnion in deep lakes is likely to be large, and infrequent, because deeper lakes tend to have more volume of water on which the atmosphere must act during a storm, compared to shallower lakes (e.g., Eccles 1974). Such reasoning is supported by the greater decrease in $PSD_{5\text{-}95}$ (which is related to temperature changes) in shallower vs. deeper lakes. Similar storm-induced changes in Schmidt stability was found in previous studies conducted on three of the lakes in our dataset (Feeagh: Andersen et al. 2020; Calderó-Pascual et al. 2020; Feeagh, Erken, and Müggelsee: Mesman et al. 2020). Internal seiches, upwelling, and internal waves breaking on the shores can also mix colder hypolimnetic water with the warmer epilimnetic water from storms in deeper lakes (i.e., Kirillin and Shatwell 2016; Kasprzak et al. 2017). However, $LN_{5\text{-}95}$ and $LN1_{5\text{-}95}$ were not statistically different between lakes of different depths. Therefore, any effect of internal mixing dynamics on epilimnetic temperature changes from wind may have been similar across-lake depth.

We found that mean $ETD_{5\text{-}95}$ was statistically similar in shallow and medium lakes for windstorms, whereas mean $PSD_{5\text{-}95}$ was significantly different between shallow and medium lakes. Shallower lakes have inherently lower Schmidt stability values (and tend to be more polymictic such as the ones in our study), and so often have a lower difference between hypolimnetic and epilimnetic temperatures compared to medium-depth lakes (Gerten and Adrian 2001; Woolway et al. 2020). For example, the mean (±1 SD) difference in epilimnetic and hypolimnetic temperatures in our shallow lakes during the thermally stratified period was 0.95 ± 0.92°C. Conversely, medium-depth lakes in our dataset had epilimnetic temperatures about 6.8 ± 2.9°C greater than their hypolimnetic temperatures. Although mixing a shallower lake is energetically easier than a medium-depth lake, more potential exists in medium-depth lakes for larger epilimnetic temperature changes because of colder hypolimnia with more volume of cold water (Zhang et al. 2015; Woolway et al. 2020).

Maximum depth was the only factor significantly related to epilimnetic temperature change during windstorms, but not from rainstorms. A negative association between maximum depth and epilimnetic temperature change was expected (similar mechanism as above). Shallower lakes are more prone to entrainment of metalimnetic and hypolimnetic waters into the epilimnion leading to a decrease in epilimnetic temperature by wind-driven mixing, upwelling, and internal wave breaking at the shore (Kirillin and Shatwell 2016; Kasprzak et al. 2017). No other abiotic or morphometric variables that we tested, including surface area, WA:SA, mean cumulative daily wind speed, or mean cumulative daily rain were correlated with epilimnetic temperature change from wind or rainstorms. Because meteorological factors in the models (e.g., wind speed, rain amount, and air temperature) were not significantly related to epilimnetic temperature changes, our results suggest that storm-induced internal lake dynamics (i.e., mixing during high wind events) mediated by lake characteristics (i.e., depth), affect water temperature more than atmospheric conditions alone.

The daily time step used in our analysis is comparable to that used in other modeling studies that assess the effects of climate change forcing on lakes, such as those in the Inter-Sectoral Impact Model Intercomparison Project (ISIMIP; https://www.isimip.org/). The low sensitivity of surface temperature to daily changes in wind and rain suggest that the cumulative effects of meteorological forcing may be best represented by lake models driven at a daily time step for long-term scenario simulations. Indeed, systematic evaluations of the importance of model time step on simulation accuracy (Ayala et al. 2020) have suggested that daily forcing data simulate seasonal changes in thermal structure nearly as well as hourly data, even though the effects of short-term events may not be explicitly accounted for at daily time steps.

Although we did assess effects of sustained storms over multiple days, we did not assess finer-scale effects of storms, e.g., those lasting just a few hours. Large changes in temperature can occur on sub-daily time scales (Jennings et al. 2012; Woolway et al. 2018), which we were not able to capture in this study. However, the largest changes in mean $ETD_{5\text{-}95}$ were not experienced from just 1-d or (presumably) <1-d storms. Although we did not find a relationship between air and epilimnetic temperature changes from wind and rainstorms, other important drivers of water temperature changes could be the day-to-day change in air vs. water temperature or the diurnal air–water temperature differential (Verburg and Antenucci 2010). Because the depth of temperature measurements differed among lakes (i.e., not all lakes had near-surface measurements at <0.1-m depth), we were not able to effectively assess such differences between changes in air vs. water temperature. We also acknowledge that other mechanisms such as internal seiches may generate changes in water temperature, which we did not specifically analyze. However, the use of mean daily water temperature reduces the short-term effects of seiche movement on water temperature, but would still allow wind-driven mixing associated with seiches to affect daily changes in epilimnion temperature (Saggio and Imberger 1998; Auger et al. 2013). Also, water temperature measurements were made near the center of lakes, which would further reduce the effects of seiches on epilimnetic temperature changes in our study.

Other ways exist to quantify a storm and impacts of a storm on lake conditions. For example, Andersen et al. (2020) defined a storm as conditions 1 d after the storm ($t + 1$) compared to conditions 1 d before a storm ($t - 1$). We tested the robustness of our estimates of mean $ETD_{5\text{-}95}$ from wind and rainstorms using this alternative method. Results were similar whether calculating effects of mean $ETD_{5\text{-}95}$ from our current vs. this alternative approach (paired *t*-tests: $p \geq 0.10$).

Our large-scale study demonstrated that day-to-day changes in lake temperature during non-storm periods were more extreme than storm-induced temperature changes. Moreover, the changes we did see as a result of storms generally were smallest in deep lakes. Given the importance of temperature to phytoplankton growth (e.g., Paerl and Otten 2013), and the interest in how storms may disrupt phytoplankton communities through alterations in mixing, temperature, light, and nutrients (e.g., Vanni et al. 2006; Jung et al. 2016; Stockwell et al. 2020), the relatively small changes in epilimnetic temperatures we observed suggest that storm-induced temperature change may not be the driving factor affecting changes to phytoplankton growth. As storms increase in severity and frequency in many regions globally, an assessment on how storms induce alterations to other environmental conditions such as light and nutrients, and how such changes affect food web dynamics and ecosystem processes, is critically important.

Author contributions

J.P.D., O.A., G.D., A.M.L., V.P.P., J.A.R., N.S., C.T.S., D.S., P.U.-C., P.V., and J.D.S. contributed to the study's conception and data analysis. J.A.R., P.U.-C., R.A., M.B.A., C.L.D., E.D.E., H.F., E.E.G., S.F.G., J.L.G., H.-P.G., J.H., G.K., E.R.N., M.C.P., D.C.P., A.R., L.G.R., S.S., H.M.S., S.J.T., W.T., P.V., and T.Z. provided data. All authors aided in drafting and revising the manuscript and approved the final manuscript version for submission.

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Conflict of interest

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