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Increasing maximum lake surface temperature under climate change

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Abstract

Annual maximum lake surface temperature influences ecosystem structure and function and, in particular, the rates of metabolic activities, species survival and biogeography. Here, we evaluated 50 years of observational data, from 1966 to 2015, for ten European lakes to quantify changes in the annual maximum surface temperature and the duration above a potentially critical temperature of 20 °C. Our results show that annual maximum lake surface temperature has increased at an average rate of +0.58 °C decade^{-1} (95% confidence interval 0.18), which is similar to the observed increase in annual maximum air temperature of +0.42 °C decade^{-1} (95% confidence interval 0.28) over the same period. Increments in lake maximum temperature among the ten lakes range from +0.1 in the west to +1.9 °C decade^{-1} in the east. Absolute maximum lake surface water temperatures were reached in Wörthersee, 27.5 °C, and Neusiedler See, 31.7 °C. Periods exceeding a critical temperature of 20 °C each year became two to six times longer than the respective average (6 to 93). The depth at which water temperature exceeded 20 °C increased from less than 1 to more than 6 m in Mondsee, Austria, over the 50 years studied. As a consequence, the habitable environment became increasingly restricted for many organisms that are adapted to historic conditions.

Keywords Warming · Critical temperatures · Extremes · Trends · Europe

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1 Introduction

Climate change is an essential feature of the Anthropocene (Steffen et al. 2011; Keys et al. 2019). Ecosystems worldwide are being affected by global warming faster than expected (Carey 2012), particularly aquatic ecosystems such as lakes (O'Reilly et al. 2015; Sharma et al. 2015). In fact, in some regions, lake surface water temperatures (LSWT) are rising faster than the overlying air during summer (Schneider and Hook 2010; O'Reilly et al. 2015) in response to, among other things, an earlier onset of thermal stratification (Austin and Colman 2007), a decrease in over-lake wind speed (Woolway et al. 2019a), changes in water clarity (Rose et al. 2016) and/or an increase of incoming solar radiation (Schmid and Köster 2016). Warming of LSWT affects the water quality of lakes in many ways (Whitehead et al. 2009; Bhateria and Jain 2016) with prominent biological implications (Elliott 2012).

The majority of the numerous articles published on the effects of global warming on temperature over the last 30 years are based on annual or seasonal mean temperatures (O'Reilly et al. 2015; Woolway and Merchant 2017, 2018). Among others, long-term changes in mean LSWT summarized for 19 European lakes by Arvola et al. (2010) and globally by O'Reilly et al. (2015) suggested an average summer increase of 0.34 °C decade^{-1} over recent decades. In an analysis of LSWT for 23 Austrian lakes, Dokulil (2013) found considerable monthly and seasonal differences in the interannual range of the minimum to maximum anomaly, with the greatest variability in spring and the largest mean anomaly (1.3 °C) in summer. Similar observations were reported from a suite of lakes in Poland (Skowron 2012). In general, greater attention has been focused on changes in summer SWT (Dokulil 2014; O'Reilly et al. 2015; Woolway and Merchant 2017; Gray et al. 2018). Average summer water temperatures are not entirely representative of possible climatic effects (Winslow et al. 2017). A specific analysis showed that climatic effects on lake minimum ($LSWT_{min}$) or maximum surface water temperature ($LSWT_{max}$) have, as single extreme values, much greater variability than average lake temperature, need a higher temporal resolution and hence are less often reported. The minimum temperature increased coherently in several European lakes (Woolway et al. 2019b) while changes in $LSWT_{max}$ were reported for Austria and Poland (Dokulil 2018; Ptak et al. 2019). In this study, we analyse the changes and temporal development of $LSWT_{max}$ from long-term in situ observations (50 years) in a suite of European lakes.

Lake maximum temperature increase can have serious biological impacts when potential thermal limits are reached or exceeded for prolonged periods. The increment in the duration and exceedance of potentially critical temperature limits, and their changes with depth, are ecologically important but poorly studied. Many lacustrine species are constrained by their physiological or developmental thermal tolerance during episodic high-temperature events (Butcher et al. 2017). Comparison of the thermal tolerance of aquatic organisms with a potentially critical temperature can provide indicators that define the impacts of global warming on biodiversity (Bates et al. 2013; Bennett et al. 2018). Prolonged periods higher than a critical temperature can affect traits such as heat tolerance, embryonic development, or growth in different organisms (Sharma et al. 2007; Daufresne et al. 2009; Vadadi-Fülöp et al. 2012). Maximum growth parameters for many freshwater and marine species centre around 20 to 25 °C under ambient conditions (Thomas et al. 2017; Margesin 2009; Chen 2015). Poikilotherms, such as fish, are sensitive to even moderate changes in thermal conditions. Roubeix et al. (2017) identified maximum annual water temperatures of 18, 20 and 22 °C as crucial for structuring fish assemblages, and Winslow et al. (2017) used 20 °C to declinate a threshold temperature in spring and fall for the timing of fish spawning.

Changes in $LSWT_{max}$ have not been identified via modelling studies. Indirect observations from air temperature produced contradictory results, either indicating a positive effect (Torbick et al. 2016) or no trend (Tao et al. 2014) on daily maximum temperature. A long-term study on changes and regime shifts for Central European lakes identified a significant increase in annual lake temperature across all seasons as well as a rise in annual minimum and maximum LSWT in several European lakes (Woolway et al. 2017). Trends in global annual and seasonal warming revealed variable tendencies for different climatic zones (Piccolroaz et al. 2020; Maberly et al. (2020).

We hypothesise, therefore, that we will find similar patterns when we investigate changes, trends and duration of $LSWT_{max}$ in lakes from different regions of Europe. We further hypothesise that $LSWT_{max}$ has increased substantially over longer periods due to warming. Consequently, potentially critical temperatures such as 20 °C may be exceeded for a significantly longer time, which has the potential to affect ecosystems in many ways.

2 Methods

2.1 Lake sites and data selection

Lakes were selected based on the length of investigations of LSWT during all seasons. The maximum annual temperature was extracted from these observations. Data were analysed for trends in maximum temperature and increment per decade. Days exceeding a potential critical temperature of 20 °C were estimated for the sites with daily LSWT information (Lough Feeagh, Vättern, Mondsee and Neusiedler See).

Data assembled here originate from ten European lakes, located in Ireland (1), the UK (5), Sweden (1) and Austria (3); they comprise some of the longest data sequences available (Fig. 2). The lakes range in altitude from 20 to 481 m above sea level, in surface area between 0.1 and 1890 km^2 and in mean depth from 1 m and 41 m. More information on lake names, abbreviations, locations, morphometry and the first year of observation are provided in Table 1. The year 1966 was chosen as a start because of the Loch Leven data and 2015 as the end of the data analysis for consistency and to cover exactly 50 years,

Details of data collection and equipment have been summarized for most of these lakes by Woolway et al. (2019b). Information for the additional lakes included here (Vättern, Mondsee and Neusiedler See) follow. Temperature near the drinking water intake at 5-m depth is considered surface water at Lake Vättern since the lake has a mean depth of 41 m and a maximum depth of 128 m. Information on LSWT for Mondsee, Austria, originates from the gauging station located near the lakeshore (479 m above sea level). The temperature was read manually with a thermometer enclosed in a sampler three times per day until the year 1984. Thereafter, LSWT was documented on a chart recorder until 1998 and then changed to digital data collection. Monthly mean water temperature data based on daily observations can be downloaded from https://ehyd.gv.at/ (search code 205286) starting in 1976. To ensure that littoral data do not significantly deviate from pelagic estimates, measurements from the years 1983 to 1998 were systematically combined (15 years, 331 entities, $r^2 = 0.95$). the mean deviation between the two estimates was 0.37 ± 1.6 °C. Pelagic data were also compared to all available satellite-derived LSWT data (Riffler et al. 2015) between March 1989 and September 2013 (25 years, 528 data, $r^2 = 0.91$). Temperatures estimated via satellite data deviated on average by 2.52 ± 2.05 °C from those assessed in situ. Data for Neusiedler See,

Table 1 Characteristics of the lakes investigated in this study. Indicated are the names of each lake with country and abbreviation used, their latitude, longitude, elevation, surface area maximum and mean depth, as well as retention time, the first year of observation and source of information. NB, north basin; SB, south basin

Lake name [country]	Abbr	Latitude north	Longitude east	Elevation (m)	Area(km^2)	Max depth (m)	Mean depth (m)	Retention time (y)	1st year of obs	Source
Lough Feeagh [IE]	FE	53.945°	−9.576°	20	3.92	45	14.5	0.47	1960	Marine Institute
Loch Leven [UK]	LL	56.197°	−3.378°	107	13.3	25.5	3.9	0.42	1964	NERC, UK
Blelham Tarn [UK]	BT	54.396°	−2.977°	47	0.11	14.5	6.8	0.12	1947	NERC, UK
Esthwaite Water [UK]	EW	54.363°	−2.987°	65	1.13	15.5	6.4	0.27	1947	NERC, UK
Windermere NB [UK]	WNB	54.379°	−2.934°	39	8.1	64	25	0.49	1947	NERC, UK
Windermere SB [UK]	WSB	54.316°	−2.951°	39	6.7	42	17	0.27	1947	NERC, UK
Lake Vättern [SE]	LV	58.340°	14.520°	88	1890	128	40	58	1955	Soc. Water Cons.
Mondsee [AT]	MO	47.825°	13.378°	481	13.8	68	36	1.7	1909	BMNT-HZB
Wörthersee [AT]	WÖS	46.628°	14.127°	440	19.39	85	42.1	10.5	1910	BMNT-HZB
Neusiedler See [AT]	NS	47.867°	16.777°	115	320	1.8	1	1	1953	BMNT-HZB

Austria, were measured at the Illmitz gauging station (114 m above sea level) manually until 1999 and then digitally thereafter. Data can be downloaded as monthly averages based on daily observations from https://ehyd.gv.at/ (search code 210179) beginning in 1991 or may be obtained from https://wasser.bgld.gv.at/(go to 'Seen', find 'Illmitz-Biologische-Station'). Data estimated from satellite measurements (25 years, 2579 data, $r^2 = 0.95$) deviated by 0.69 ± 0.31 °C on average from in situ measurements.

LSWT measurements were usually made at the same time of day in each lake to avoid bias being introduced by the strong diel variability in surface water temperature (Woolway et al. 2015). Nevertheless, maximum temperatures may be missed on certain days.

Surface air temperatures are from the European Centre for Medium-Range Weather Forecasts (ECMWF) ERA5 re-analyses product, available on a 0.25°-by-0.25° latitude-longitude grid resolution (Hersbach et al. 2020). Daily air temperature data were extracted for each lake from the grid in which the lake centre was located (https://cds.climate.copernicus.eu/). the annual sequence of $\mathrm{LSWT}_{\mathrm{max}}$ and the relationship between $\mathrm{AT}_{\mathrm{max}}$ and $\mathrm{LSWT}_{\mathrm{max}}$ for all lakes in the study are included in Appendix 1.

2.2 Defining a critical temperature

Given the enormous number of aquatic species and their wide thermal tolerances, critical temperatures or thresholds are not easy to define. However, many species of pelagic organisms such as rotifers, copepods and, particularly, fish reach constraints at or above 20 °C (Herzig 1983a, 1983b; Herzig and Winkler 1986; Roubeix et al. 2017). In accordance with Winslow et al. (2017), we chose 20 °C as a potential critical temperature to analyse changes in periods that exceeded 20 °C each year. To compensate for the large interannual variability, we used the sum of the days over every 5-year period, called a pentad. Pentads revealed a clearer picture than 5-year averages of exceedance days. Details of exceedance days per year can be found in Appendix 2, as well as results for other temperatures. The annual average increase of the epilimnetic water layer with temperatures greater than 20 °C was calculated from fortnightly sampled temperature profiles in Mondsee and averaged for each pentad.

2.3 Statistical methods

Trends in the time series were estimated using the non-parametric Mann-Kendall Test using software PAST version 4.03 (Hammer et al. 2001, https://palaeo-electronica.org/2001_1/past/main.htm). The magnitude of the trend was assessed by Sen's method with Makesens 2.0 application provided by the Finnish Meteorological Institute (https://en.ilmatieteenlaitos.fi/makesens). Randomness of the data was verified by runs test.

3 Results

3.1 Annual maximum temperature observations

Based on Sen's slope, the change of maximum air temperature ($\mathrm{AT}_{\mathrm{max}}$) per decade was 0.1 to 0.7 °C (average + 0.42, c.i. 0.28). The lowest increments were observed in Lough Feeagh and Lake Vättern and the highest in Neusiedler See (Table 2). $\mathrm{AT}_{\mathrm{max}}$ is significantly linear correlated with $\mathrm{LSWT}_{\mathrm{max}}$ in all lakes except Loch Leven and Lake Vättern, which show no

Table 2 Maximum air temperature (AT_{max}) increment per decade from Sen's slope plus lower and upper 95% c.l. AT_{max} versus maximum lake surface water temperature ($LSWT_{max}$) as linear regression. b = slope of regression, r^2 = coefficient of determination, p = significance (*italics* = non-significant)

		AT_{max} vs time		AT_{max} vs $LSWT_{max}$			
Lake	°C dec^{-1}	Lower	Upper	b	r^2	p	
Lough Feeagh	0.1	−0.1	0.6	1.05	0.60	<0.001	LSWT > AT
Loch Leven	0.3	−0.05	0.6	0.12	0.01	*0.592*	–
Blelhalm Tarn	0.5	0.5	0.9	0.95	0.45	<0.001	LSWT < AT
Esthwaite Water	0.5	0.09	0.9	1.03	0.55	<0.001	LSWT > AT
Windermere NB	0.5	0.05	0.9	1.06	0.69	<0.001	LSWT > AT
Windermere SB	0.5	0.09	0.9	1.09	0.64	<0.001	LSWT > AT
Lake Vättern	0.1	−0.3	0.6	0.38	0.04	*0.232*	–
Mondsee	0.5	0.2	0.9	0.76	0.51	<0.001	LSWT < AT
Wörthersee	0.5	0.2	0.8	0.72	0.50	<0.001	LSWT < AT
Neusiedler See	0.7	0–2	1.0	1.08	0.38	<0.001	LSWT > AT

correlation with $LSWT_{max}$ (Table 2 and Appendix 1). The rate of increase of $LSWT_{max}$ is statistically greater than that of AT_{max} in five lakes, equal to it in one lake and smaller than it in two lakes.

The individual time series indicate considerable regional differences in the trend of maximum LSWT (Fig. 2). Lough Feeagh and Loch Leven do not show a trend in their time sequence. As indicated by the notch-box whiskers in Fig. 3, the median and interquartile range of $LSWT_{max}$ are not statistically different. Frequencies are large below 20 °C in Lough Feeagh, while almost equal frequencies below and above 20 °C occurred in Loch Leven.

The lakes in the English Lake District are all characterized by decreasing maximum LSWTs in the 1950s and no obvious trend between 1966 and 2015, probably as a result of lower temporal data resolution (every 1 or 2 weeks; Fig. 2) although Mann-Kendall analysis indicates weak significance (Table 3). The interquartile range and median of the two shallow lakes, Blelham Tarn and Esthwaite Water, differ significantly from the nearby basins of Windermere as well as Lough Feeagh in Ireland and Loch Leven in Scotland. Frequencies for Blelham Tarn and Esthwaite Water are

Table 3 Statistical summary of time series 1966–2015 for the lake surface temperature time series from 1966 to 2015 for each studied lake (lake names are abbreviated as in Table 1. Mann-Kendall trend statistics and temperature increment per decade from Sen's slope with lower and upper 95% c.l.

	Mann-Kendall trend				Sen's slope as °C dec^{-1}		
Lake	**S**	**Z**	p	Signif.	Slope	Lower	Upper
FE	162	1.4334	0.15176	no	0.19	−0.18	0.51
LL	76	0.6277	0.53016	no	0.10	−0.17	0.44
BT	180	1.4987	0.13396	no	0.27	−0.07	0.64
EW	227	1.8912	0.05860	no	0.33	0	0.67
WNB	280	2.3357	0.01950	*	0.40	0.07	0.69
WSB	230	1.9152	0.05534	no	0.35	0	0.72
LV	411	3.4322	0.00060	***	0.69	0.36	1.08
MO	634	5.2967	1.18E-07	****	1.18	0.79	1.51
WöS	478	3.9926	6.54E-05	***	0.40	0.22	0.57
NS	860	7.1900	6.48E-13	*****	1.90	1.57	2.19

centred around 20 °C with peaks of over 25 °C in both cases (Fig. 3). The two basins of Windermere had a similar frequency distribution (Fig. 2).

Maximum LSWT increased substantially between 1966 and 2015 in the largest and deepest lake of this ensemble, Lake Vättern (Fig. 1 and Table 3). The median of the Vättern data is 20 °C, like in Blelham Tarn and Esthwaite Water, but the interquartile range is slightly greater and maximum LSWT reaches 30 °C (Fig. 3).

The three Austrian lakes differ significantly from all others and from each other (Figs. 2 and 3). Frequencies centred around the median $\mathrm{LSWT}_{\max}$ of 24 °C, 25.2 °C and 26.1 °C for Mondsee, Wörthersee and Neusiedler See, respectively. Absolute maxima were 28.4 °C in MO, 27.5 °C in WöS and 31.7 °C in NS (Fig. 3). The lowest maximum temperatures in these three lakes were well above those of all other lakes.

Temperature increments of $\mathrm{LSWT}_{\max}$ per decade ranged from 0.1 to 1.9 °C (Table 3). The average increase for all lakes was +0.58 °C per decade (95% confidence interval, 0.18).

The influence of sampling frequency on interannual variability and the rate of change in $\mathrm{LSWT}_{\max}$ were analysed for two lakes (Wörthersee and Neusiedler See). Down-sampling to a 21-day frequency did not affect the calculated rate of change in maximum lake surface temperature (Appendix 3).

3.2 Periods with temperatures ≥20 °C

The maximum surface temperature did not reach 20 °C every year in Lough Feeagh (Appendix 2). Cumulative days ≥20 °C per 5 years remained in general low, peaking at 19 days in the

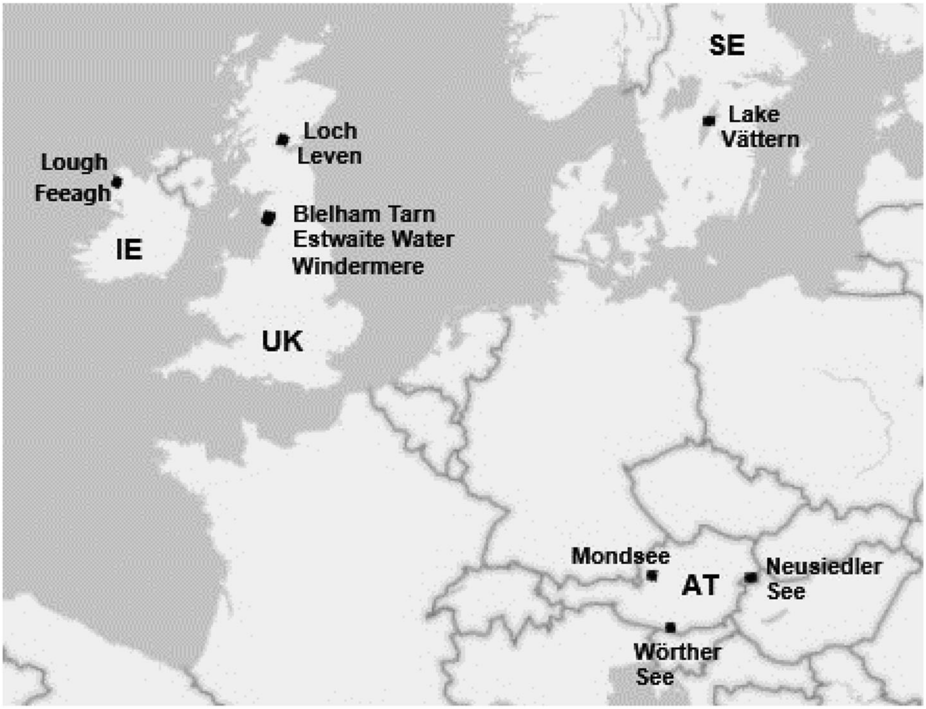

Fig. 1 Map of Europe indicating the geographical position of the lakes in this study. For details, refer to Table 1

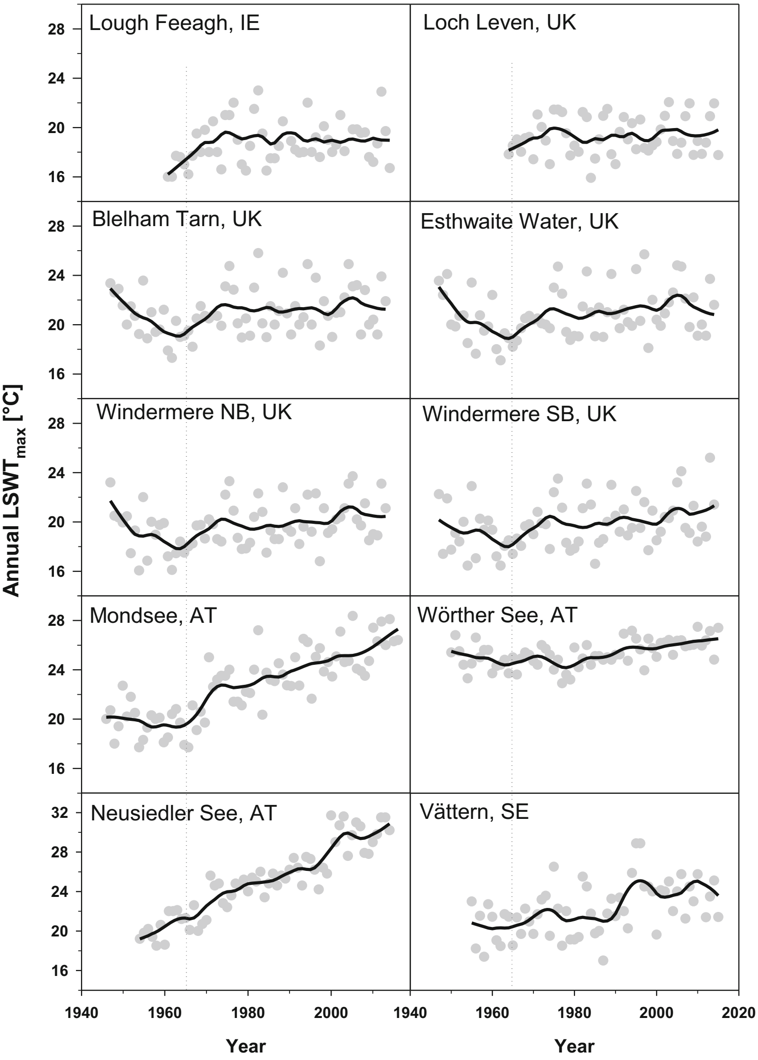

Fig. 2 Annual maximum lake surface water temperature (LSWT$_{max}$) for each lake and all available years. LSWT$_{max}$ shown as grey points and the LOWESS smoother (11-year length) as a solid black line. The dotted line indicates the year 1966, which was used as the common starting point for trend analysis (see text). The name and country of each lake are indicated in the panels

pentad 1981–1985 (Fig. 4a). Other pentads remained below the annual average of 7 days for all years between 1966 and 2015. In Lake Vättern, cumulative day periods reaching or exceeding 20 °C showed an increasing tendency (Fig. 4b). The aggregated number of days remained largely below the annual average of 13 days in the pentads until 1990. During the following five pentads from 1991 to 2015, days equal or greater than 20 °C first increased to 60 and then to 91 and varied thereafter between 72 and 53 days.

All pentad periods exceeded 20 °C and were higher than the long-term mean of 51 days in Mondsee (Fig. 5a). The 5-year sum of the number of days surpassing 20 °C systematically increased from 80 (1976–1980) to 362 days in the 2001–2005 period. The two following

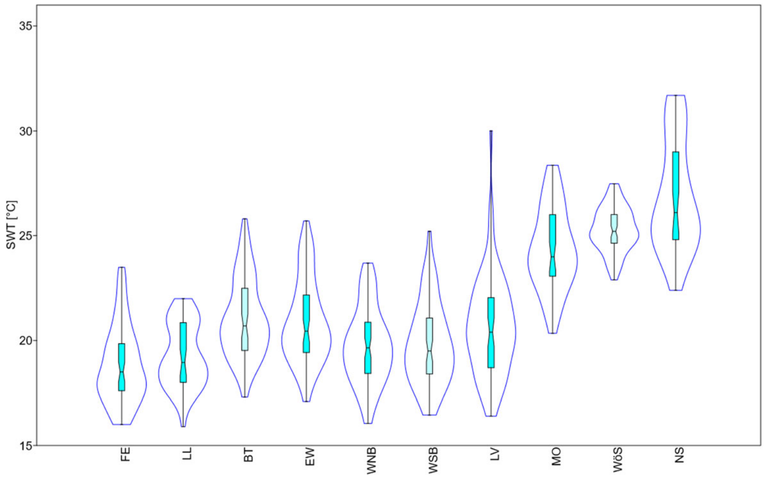

Fig. 3 Notch-box whisker plot plus violin plot of annual maximum lake surface temperatures ($LSWT_{max}$) for each studied lake. Abbreviations for lakes analysed are given in Table 1. Box limits are the 25 and 75 percentiles, the horizontal line is the median, and the notch indicates the 95% confidence limits. Whiskers reach the maximum and minimum values. The violin plot indicates the distribution of the maximum $LSWT_{max}$ values

periods decreased from 331 to 289 days. All periods from 1991 to 2015 had day-totals greater than five times the daily average across all pentads indicating long phases of temperatures at or above 20 °C. Periods in each individual year between 1985 and 2015 lasted at least 30 days (1 month), many for 2 months and more than 3 months in 2003. Correspondingly, the water layer with temperatures ≥20 °C deepened from an average of 0.5 m during the 1976–1980 period to 6.4 m in the 2006–2010 pentad (Fig. 5b).

Wörthersee, south of the Alpine range and closer to the Mediterranean climate, is generally warmer than the lakes analysed above. Periods of LSWT temperatures greater than 20 °C occurred each year since 1951 and, in most years, were more than five times the long-term average of 93 days (Fig. 6a). Within the 65-year period from 1950 to 2015, all years were warmer than 20 °C for at least 2 months except 1968 and 1980. In several years, 20 °C was exceeded for more than 3 months and in 2011 even for 4 months. The daily average across all pentads for Wörthersee is 13 times greater than that for Lough Feeagh and almost twice the value for Mondsee (Fig. 6a).

With a mean depth of only 1 m, Neusiedler See is the shallowest of the lakes studied here. Due to the warm Pannonian climate in the region, the lake exceeded 20 °C in all 5-year periods usually during June to September but sometimes in May or October (Fig. 6B). Total days per period increased continuously from 243 (3 times the daily mean across all pentads of 84) to 519 days in the 1996–2000 pentad (6 times the mean of 84). Thereafter, the cumulative number of days declined to 475 days in 2011–2015 but was still 5.5 times higher than the long-term mean across all pentads.

4 Discussion

4.1 Changes in lake maximum temperature

This analysis of changes in the annual maximum surface temperatures in ten lakes from 1966 and 2015 is the first such comparison for a suite of European lakes. Our analysis revealed a 19-fold variation in the rate of increase of annual maximum surface temperature, which ranged

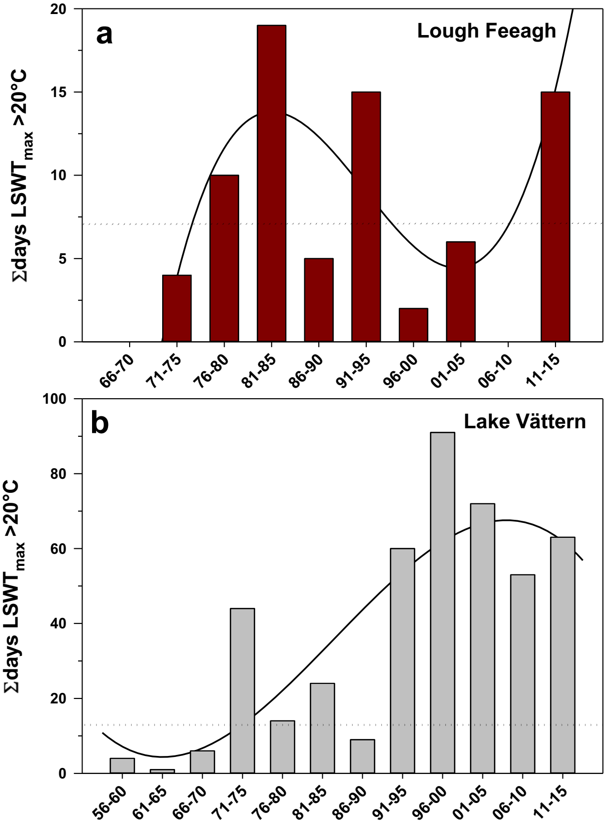

Fig. 4 Aggregated number of days for 5-year periods (pentads) when temperatures exceeded 20 °C. **a** Lough Feeagh 1966 to 2015. **b** Lake Vättern 1956 to 2015. The dotted line is the average of days for all years (6 and 13, respectively). The solid line is a 3rd-order polynomial simply to visualize the development over time

from 0.10 in the west to 1.9 °C decade^{-1} in the east. The average increase in maximum temperature over time, +0.58 °C decade^{-1} (95% confidence interval 0.18), is greater than the global average increase of +0.34 °C decade^{-1} reported during the summer for lakes globally (O'Reilly et al. 2015), +0.42 °C decade^{-1} (95% confidence interval 0.28, range 0.10 to 1.2 °C decade^{-1}) for 22 lakes in Austria (Dokulil 2018) and + 0.39 °C decade^{-1} (range 0.25 to 0.56 °C decade^{-1}) for nine lowland lakes in Poland (Ptak et al. 2019).

The increasing rates of $LSWT_{max}$ observed from west to east depend, most likely, on regional climatic conditions across Europe. Surface temperatures in lakes in Ireland and Great Britain are moderated by the mild, balanced climate resulting from the Gulf Stream. Southern Sweden and Austria have a more hybrid oceanic/continental climate with higher temperature variability (Beck et al. 2018). Other morphometric parameters were unrelated to $LSWT_{max}$ dec^{-1} in this study, contrary to findings by Ptak et al. (2018), but more investigations are necessary to resolve the difference (Appendix 4). A gradient of increasing average LSWT, 0.2 to 0.8 °C dec^{-1} from south-west to north-east was substantiated also in a dataset of 26 European lakes (Lieberherr and Wunderle 2018).

Air temperature is one of the key drivers of surface water temperature. Since summer lake temperatures are often greater than AT, we expected $LSWT_{max}$ to be greater than AT_{max}. The increment of annual lake maximum surface temperature was in fact higher than AT_{max} in five of the

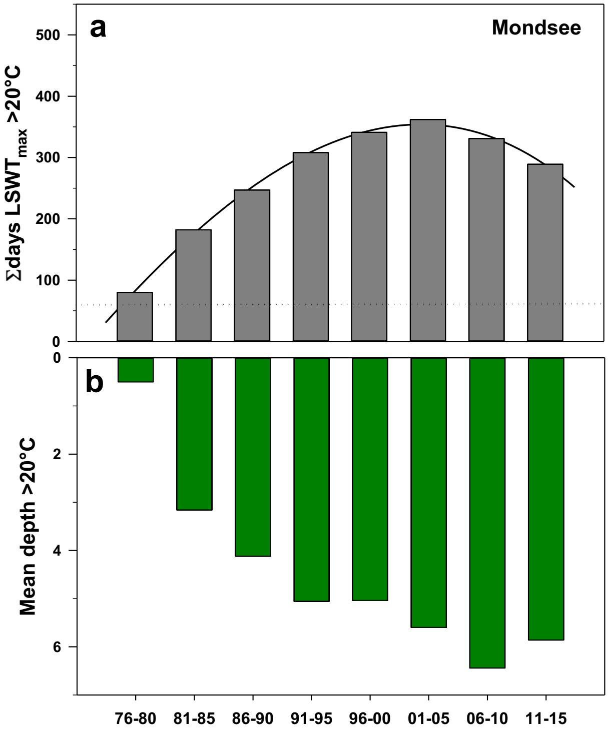

Fig. 5 Aggregated number of days when temperatures exceeded 20 °C in Mondsee for each 5-year period from 1976 to 2015 (**a**). The dotted line is the average of 54 days for all years. The solid line is a 3rd-order polynomial to simply visualize the development over time. **b** Mean depth where the temperature was >20 °C for each 5-year period from 1976 to 2015

10 lakes (see Appendix 1). A 1:1 relation was observed in the smallest lake in the study, Blelham Tarn, UK, while $LSWT_{max}$ was $0.7AT_{max}$ in Mondsee and Wörthersee, the two alpine lakes. No results can be reported for Lake Vättern and Loch Leven since AT_{max} was unrelated to $LSWT_{max}$. The increase in AT in Loch Leven however was greater than LSWT (Carvalho et al. 2012). Winder and Schindler (2004a) reported rates of AT increase by 0.32 °C while volume-weighted mean water column temperature increased by 0.65 °C over four decades in Lake Washington.

4.2 Potential biological impacts

The trend of prolonged periods exceeding the potential critical temperature of 20 °C in recent years and decades in our study (Figs. 4–6) seem to be associated with variations in air temperature and the increasing occurrence of warm extremes (Johnson et al. 2018). Summer temperatures are particularly amplified in cold, deep lakes (Woolway and Merchant 2017). Warming alterations of such lakes in time and space have been characterized by Toffolon et al. (2020) using the difference of maximum LSWT between the five warmest and coldest years as a proxy. Critical water temperatures over extended periods will influence almost all aspects of aquatic ecosystems, particularly the metabolism of the organisms at all levels of the food web (Winder and Schindler 2004b; Kraemer et al. 2017). Increasing duration of periods exceeding a critical temperature, as we have shown here, will affect thermal habitats for the growth of

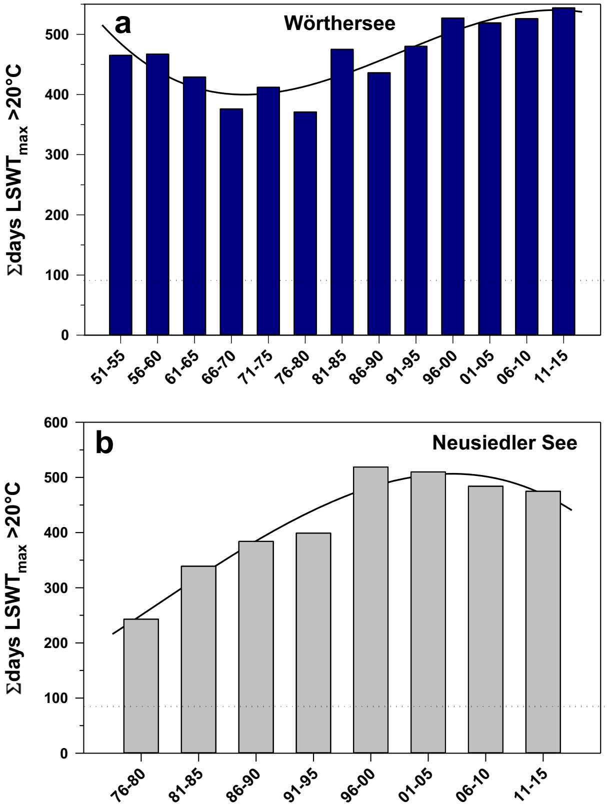

Fig. 6 Aggregated number of days when temperatures exceeded 20 °C. **a** Wörthersee for each 5-year period from 1951 to 2015. **b** Neusiedler See for each 5-year period 1976 to 2015. Dotted lines indicate the average of days for all years (93 and 85, respectively). The solid line is a 3rd-order polynomial simply to visualize the development over time

assemblages from bacteria to fish (Herzig 1983a, 1983b; Herzig and Winkler 1986; Gillooly et al. 2001), via effects on thermal tolerance, competitive ability, and species invasion (Bates et al. 2013). This will alter the geographical distribution of species, but the future velocity of climate change will exceed the ability of many species to migrate to cooler water, especially given the increasingly fragmented nature of inland waters (Woolway and Maberly 2020).

Extended periods of maximum LSWT will also alter lake trophic status, imposing changes on ecosystem functioning. The combined impacts of eutrophication and climate warming are not easy to separate (Jacobson et al. 2017). The exceedance of critical temperatures can modify the physiological functions of individual fish and fish assemblages (Godlewska et al. 2014). Species survival therefore crucially depends on exposure to annual maximum lake water temperature for a critical duration. A review of the physiological basis of effects on fish by climate change is provided by Whitney et al. (2016).

Sharma et al. (2007) predicted an increase of maximum summer temperatures for lakes in Canada until 2100 and Butcher et al. (2017) for lakes in the United States. Many lakes may experience water temperatures as high as 30 °C, with Neusiedler See already exceeding that in several years. Simulated 7-day average maximum water temperatures of more than 30°C are projected to increase from less than 2% to approximately 22% by the end of the twenty-first century (Butcher et al. 2017).

Consequently, thermal habitats will be altered potentially expanding the range of warm water fish species negatively impacting native cold water fish communities. A modelling study of hundreds of lakes worldwide showed a dramatic increase in the intensity and duration of lake heatwaves (Woolway et al. 2021), periods of extreme lake surface temperature, by the end of the twenty-first century even under the lowest greenhouse gas emission scenario (Woolway et al. 2020). This suggests that the extreme summer temperatures reported here will intensify in the coming decades.

Motile organisms such as fish may avoid warmer temperatures by moving to deeper water layers in lakes or move to other ecosystems, but their rate of movement may be exceeded by the velocity of future climate change (Woolway and Maberly 2020). Extended periods of higher temperatures near the surface will ultimately lead to deeper penetration of these temperatures as exemplified for Mondsee. Together with extended periods of thermal stratification (Kraemer et al. 2015), deep water warming (Ambrosetti and Barbanti 1999; Dokulil et al. 2006; Pilla et al. 2020) and reduced oxygen concentration in deeper layers (Foley et al. 2012), the habitable space for fish in the lake becomes limited (Sharma et al. 2007; Jeppesen et al. 2012). Concomitantly, the development and metabolic activity of other organisms are influenced (Winder and Schindler 2004b). Most of these arguments are certainly exacerbated in very shallow, unstratified lakes such as Neusiedler See.

5 Conclusions

Lake surface water temperature data were analysed to show how annual maximum lake surface temperatures responded to climate warming. The results indicate a substantial increase in annual maximum lake surface temperatures in several lakes, especially in the east. The average warming rate was +0.58 °C decade^{-1} (95% confidence interval 0.18) between 1966 and 2015. During the same time, periods with a potential critical temperature of greater than 20 °C have significantly increased, and temperatures greater than 20 °C have expanded deeper into the epilimnion. Changes in annual maximum temperature and prolonged periods exceeding critical temperatures can substantially influence lake ecosystems. Some of the impacted organisms may be able to acclimatize quickly, or even adapt over longer periods, to the changes in temperature; some may even benefit. Motile organisms such as fish may escape to cooler parts of the system, but this may be limited in the future given the forecast high velocity of climate change and ecosystem fragmentation. Temperature changes near the surface and at greater depth are one facet of climate warming potentially restricting the habitable space in lakes. In well-mixed lakes or lakes with anoxic hypolimnia, the lack of refuge areas will distress the whole ecosystem.

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