

Surface Water Temperature and Ice Cover of Tatra Mountains Lakes Depend on Altitude, Topographic Shading, and Bathymetry

Milan Novikmec*#

Marek Svitok*

Dušan Kočický†

Ferdinand Šporka‡ and

Peter Bitušík§

*Department of Biology and General Ecology, Faculty of Ecology and Environmental Sciences, Technical University in Zvolen, T. G. Masaryka 24, SK–960 53 Zvolen, Slovakia

†ESPRIT, Ltd., Pletiariska 2, PO Box 27, SK–969 27 Banská Štiavnica, Slovakia

‡Institute of Zoology, Slovak Academy of Sciences, Dúbravská cesta 9, SK–845 06 Bratislava, Slovakia

§Faculty of Science, Matthias Belius University, Tajovského 40, SK–974 01 Banská Bystrica, Slovakia

#Corresponding author:
novikmec@tuzvo.sk

Abstract

This study reflects the growing demand for better understanding the response of alpine lake ecosystems to climate forcing. We combined continuous monitoring of water temperature with GIS-derived data, and modeled the lake surface water temperature (LSWT) and ice-cover characteristics of 18 Tatra Mountains lakes against altitude, lake morphometry, and local topography. The general trend in LSWTs was similar across all studied lakes and showed a high degree of coherence over the whole study period. The daily LSWTs were governed primarily by altitude and topographic shading represented by lake-specific total duration of direct solar radiation (TDDSR). Day-to-day variability of LSWTs was controlled mainly by the maximum depth of the lakes. The surface temperature of deeper lakes was more stable than the temperature of shallow ones. Topographic shading appeared to play an important role in the development and duration of ice-cover. Lakes with low TDDSR retained ice-cover longer than well insulated ones.

This is the first time that the effect of topographic shading was explicitly considered in relation to the surface temperature and ice-cover timing of remote lakes. Including direct solar radiation as a model parameter would considerably improve predictions of temperature characteristics of high-altitude lakes. This may have potentially important implications for climate change studies as it could allow for site-specific modifications of temperatures in high-altitude lakes.

DOI: <http://dx.doi.org/10.1657/1938-4246-45.1.77>

Introduction

Lake water temperature is one of the crucial factors affecting the function of lakes. Temperature controls the lake ecosystems directly, as well as indirectly influencing the physical and chemical parameters of water, nutrient concentrations, and the distribution of aquatic organisms (e.g., Regier et al., 1990; Winder and Hunter, 2008; de Mendoza and Catalan, 2010; Gudas et al., 2010). The critical importance of lake temperature is particularly obvious in alpine lakes. Water temperature in these lakes is usually low, and even slight changes of annual temperature cycles may modify important features and processes of remote lake systems (e.g., Sommaruga-Wöger et al., 1997; Thompson et al., 2009), making the mountain lakes very susceptible to climate forcing. Since a significant warming of air temperature was observed in European mountain lake districts during the 20th century (Beniston et al., 1997; Agustí-Panareda and Thompson, 2002), it is presumed that future changes of air temperature might lead to major changes in water temperature and the duration of ice-cover in mountain lakes (Thompson et al., 2005, 2009).

Detailed knowledge of the duration of ice cover and the thermal regime of mountain lakes is an essential precondition for any prediction of their future changes. Over the past decades, few studies have focused on investigating lake surface water temperatures (LSWT) of high-altitude lakes (e.g., Livingstone and Lotter, 1998; Thompson et al., 2005). LSWT well represents the temperature of the epilimnion (Livingstone et al., 1999), an environmental variable strongly influencing the ecosystem processes and function of lakes.

Although many factors affecting the LSWT are quite well known, there are still some specific questions regarding the importance of individual variables. Due to the close relation between air and lake water temperature, the temperature of mountain lakes is generally related to altitude; lakes at higher elevation are likely to be cooler than lakes at lower elevations; and the relationship between LSWT and altitude has been described as being approximately linear (Livingstone et al., 1999). However, the temperature response of individual lakes may vary considerably in relation to specific characteristics, such as the lake size and depth, intensity of inflow and outflow, valley orientation, meltwater inflows, topographic shading, and wind sheltering (Blenckner, 2005; Thompson et al., 2005). Gregor and Pacl (2005) and Šporka et al. (2006) have indicated that although altitude (which directly affects the air temperature) is probably the key factor determining the LSWT and ice cover timing of Tatra Mountains lakes, the lake morphometry and geomorphic setting may play an important role as well. Such factors should be taken into account in order to understand the responses of alpine lake ecosystems to past and future climatic changes.

In the Tatra Mountains, measurements of lake water temperature have a relatively long tradition starting at the beginning of the 19th century. All temperature data available up to the early 1970s have been summarized by Pacl and Wit-Joźwikowa (1974). The data set consists, however, mainly of spot measurements carried out manually. Recently, quasi-continuous monitoring of lake water temperature has been performed (Šporka et al., 2006).

In this paper, we firstly describe the temporal LSWT pattern of 18 Tatra Mountains lakes and compare their coherence. Sec-

only, we rigorously assess the relative importance of altitude, lake morphometry, and local topography to lake surface temperature. More specifically, we built several models to quantify the relationships between LSWT, ice cover characteristics, and physical features of the lakes.

Methods

STUDY AREA

The Tatra Mountains are situated at the border between Slovakia and Poland (the West Carpathians; 49°10'N, 20°10'E) and experience rapid changes in temperature and precipitation along an altitudinal gradient typical of an alpine environment. The average annual air temperature decreases with elevation by 0.6 °C per 100 m (Konček and Orlicz, 1974). The amount of precipitation varies from ~1000 to ~1600 mm a⁻¹ but can reach >2000 mm a⁻¹ in certain valleys (Chomitz and Šamaj, 1974). Snow cover usually lasts from October to June at elevations above 2000 m.

For the purposes of this study, 18 lakes were selected (Fig. 1), encompassing a gradient of climate and catchment characteristics. The lakes were selected randomly with the restriction that lakes of various morphometry and contrasting local topographic shading (shaded vs. unshaded) were included within each altitudinal belt of ~150 m in order to minimize correlations among independent variables.

All of the surveyed lakes are of glacial origin and are situated above the present-day timberline. In the study area, the bedrock is mainly granitic. The most common soils are undeveloped podsols, leptosols, and regosols. The lakes are soft-water and oligotrophic. The dominant vegetation of the catchment areas is formed mainly by dwarf pine (*Pinus mugo*) shrubs (between 1550 and 1800 m a.s.l.) and in the alpine zone (above 1800 m a.s.l.) by alpine grasslands, rush-heaths, or scree vegetation. Lakes are fishless, without any direct anthropogenic influence. Basic characteristics of the studied lakes are presented in Table 1.

WATER TEMPERATURE DATA

Lake surface water temperature (LSWT) was measured at hourly intervals in each lake from July 2010 to September 2011, using miniature thermistors with integrated data loggers (8-TR Minilog, Vemco Ltd., Shad Bay, Nova Scotia, Canada). The thermistors were inserted into the underside of a float consisting of rectangular Styrofoam blocks (13 cm × 13 cm × 5 cm) in such a way that the thermistor's sensors were approximately 5 cm under the lake surface and the Styrofoam blocks shaded the temperature sensors from direct solar radiation. The thermistors were anchored either near the lake outflow—to ensure a continual flow of epilimnetic water around them—or in the deeper central region of lakes without outflow, far enough from the shore to avoid any local littoral effects and minimize any disturbance.

The average LSWT for each month was calculated and used as a temperature characteristic for each lake. However, only data from May to October were considered in the analyses because most of the lakes were frozen during the rest of the year. In a similar way, the standard deviation of LSWT (SD LSWT) was calculated for each month and lake. This measure provides a quantification of temporal variability (stability) of the LSWT.

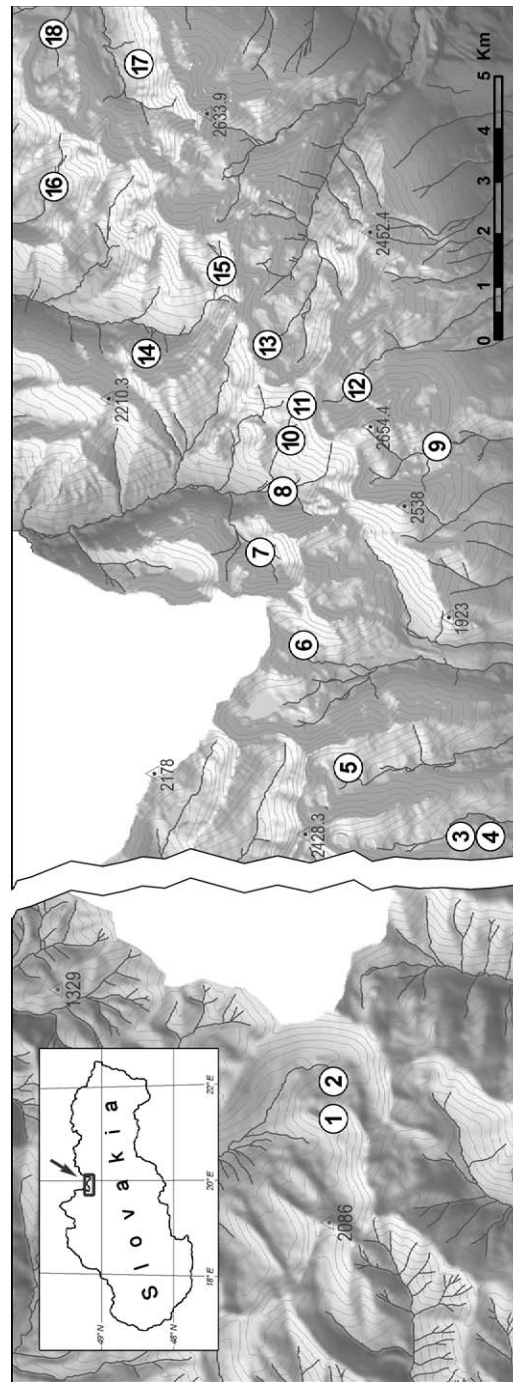


FIGURE 1. Topographic map showing location of studied lakes (numbered circles). Lakes are numbered as follows: 1—Štvrté Roháčske pleso, 2—Prvé Roháčske pleso, 3—Vysné Furkotské pleso, 4—Nižné Furkotské pleso, 5—Nižné Kozie pleso, 6—Malé Žabie (Mengusovské) pleso, 7—Zmrzlé pleso, 8—Zelené Kačacie pleso, 9—Batizovské pleso, 10—Litvorové pleso, 11—Zamrznuté pleso, 12—Dlhé Velické pleso, 13—Pusté pleso, 14—Malé Žabie Javorové pleso, 15—Žabie Javorové pleso, 16—Kolové pleso, 17—Čierne Kežmarské pleso, and 18—Veľké Biele pleso. Triangles depict important elevation points. Width of the cut in the middle of figure accounts for approximately 20 km.

TABLE 1

Basic characteristics of 18 studied lakes (TDDSR = total duration of direct solar radiation; GR = annual global radiation).

Lake	Location	Altitude (m)	Lake area (m ²)	Volume (m ³)	Max. depth (m)	Ave. depth (m)	TDDSR (h a ⁻¹)	GR (Wh m ⁻² a ⁻¹)
Batizovské pleso	49°09'09"N, 20°07'57"E	1884	34,775	232,089	10.5	6.7	3167	1,246,706
Čierne Kežmarské pleso	49°12'29"N, 20°13'36"E	1579	2910	5128	4.0	1.8	1788	968,374
Dlhé Velické pleso	49°09'58"N, 20°08'45"E	1939	6255	14,408	5.6	2.3	1974	978,589
Prvé Roháčske pleso	49°12'24"N, 19°44'39"E	1562	22,250	77,063	7.7	3.5	2155	1,107,544
Štvrté Roháčske pleso	49°12'21"N, 19°44'10"E	1719	14,400	46,067	8.2	3.2	2318	1,144,853
Kolové pleso	49°13'15"N, 20°11'36"E	1565	18,280	10,846	1.2	0.6	1769	1,014,462
Litvorové pleso	49°10'40"N, 20°07'53"E	1860	18,645	135,000	19.1	7.2	1546	960,089
Malé Žabie Javorové pleso	49°10'26"N, 20°04'38"E	1704	1800	2049	3.1	1.1	2170	1,028,589
Malé Žabie (Mengusovské) pleso	49°12'10"N, 20°09'05"E	1920	12,060	45,696	12.6	3.8	2741	1,190,564
Nížné Furkotské pleso	49°08'26"N, 20°01'53"E	1626	1645	682	1.2	0.4	3418	1,317,771
Nížné Kozie pleso	49°09'51"N, 20°02'42"E	1942	7800	4650	2.3	0.6	2426	1,143,309
Pusté pleso	49°10'58"N, 20°09'20"E	2056	11,890	32,079	6.6	2.7	2817	1,239,678
Veľké Biele pleso	49°13'20"N, 20°13'54"E	1615	9670	4278	0.8	0.4	3409	1,289,441
Vyšné Furkotské pleso	49°08'38"N, 20°01'54"E	1698	4080	3306	2.4	0.8	3281	1,252,167
Žabie Javorové pleso	49°10'35"N, 20°08'24"E	1878	11,320	60,453	15.3	5.3	1436	905,648
Zamrznuté pleso	49°10'40"N, 20°07'07"E	2040	11,395	43,388	10.8	3.8	1667	1,034,014
Zelené Kačacie pleso	49°10'51"N, 20°06'05"E	1575	25,335	28,236	2.7	1.1	1495	943,702
Zmrzlé pleso	49°11'31"N, 20°10'12"E	1762	22,015	86,269	12.5	3.9	1525	936,859

Because ice cover may develop multiple times before a continuous cover is formed, the date of ice-in was defined as the calendar date after which a lake was completely and continuously covered by ice. It was indicated by a decrease of LSWT to 0 °C and subsequent stable low diurnal temperature variability. Similarly, the ice-out date was defined as the date when a lake was largely free of ice, indicated by an LSWT increase above 0 °C and greater diurnal temperature fluctuations (within-day standard deviation of LSWT > 0.1 °C), though some lakes might retain small floating ice blocks (personal observation). The duration of ice cover was defined as the time interval between ice-in and ice-out dates.

LAKE PARAMETERS

Variables representing altitudinal gradient (altitude) and lake morphometry (lake area, volume, average and maximum depth) were obtained from Gregor and Pacl (2005). Total duration of direct solar radiation (TDDSR) and global radiation (GR) that represent topographic shading of lakes were calculated from an insolation model. The ArcGIS Spatial Analyst extension (ESRI, 2009) was used to prepare spatial data and create models. This application enables mapping and analyzing the effects of the sun over a geographic area for specific time periods. It accounts for atmospheric effects, site latitude and elevation, steepness (slope) and compass direction (aspect), daily and seasonal shifts of the sun angle, and effects of shadows cast by surrounding topography. The model inputs were 20 × 20 m digital elevation models (Malík et al., 2007), derived from contour maps and digital maps of the river networks and lakes vectorized from base 1:10,000 topographic maps of the Slovak Republic. The resultant outputs were global radiation (direct radiation + diffuse radiation) in Wh m⁻² and the duration of direct solar radiation in hours for each lake for the selected time interval. The calculation of insolation was based on

the methods derived from the hemispherical view shed algorithm (Rich et al., 1994; Fu and Rich, 2000, 2002; Rich and Fu, 2000).

DATA ANALYSIS

Multiple regression analysis was used to examine the effect of altitudinal gradient, lake morphometry, and topographic settings on lake temperatures (LSWT, SD LSWT) and ice cover characteristics (ice duration, ice-in and ice-out date). Distribution of the variables was examined prior to the analyses. Strongly skewed data on lake volume and maximum depth were logarithmically transformed to make their distribution more symmetric.

At the next stage, collinear independent variables were identified to avoid unstable estimates of regression coefficients and inflation of standard errors (Quinn and Keough, 2002). Strongly correlated variables were deleted sequentially until all of the remaining variables had product moment correlation coefficients less than 0.75. In total, three variables were deleted: lake volume (positively correlated with lake area and average depth), average depth (positively correlated with maximum depth and volume), and GR (positively correlated with TDDSR).

The most adequate regression models were identified using the best-subset regression approach. However, this approach is often criticized for providing unstable selections of variables, biased estimates of regression coefficients and their standard errors (c.f. Breiman, 1995; Miller, 2002). To deal with these drawbacks, we employed cross-validation and bootstrap techniques that provided more robust model building. The final regression models were chosen from all possible combinations of predictors, as those with the smallest residual sum of squares based on the delete-*d* cross-validation method with 1000 validation sets (Shao, 1993). The optimal size of the validation sets (*d*) was chosen according to Shao (1997). Subsequently, the confidence intervals for the regression coefficients were computed by non-parametric bootstrap method

(9999 replicates). Confidence limits were obtained using a bias-corrected accelerated percentile method (Efron and Tibshirani, 1986).

The fit of the final models was evaluated using root mean square errors (RMSE) and a variation partitioning procedure (Borcard et al., 1992). The quality of each model was carefully checked using residual diagnostic plots, and the models performed reasonably well. The values of variation inflation factors (VIF) were examined to ensure the absence of complex collinearity among predictors. All VIF values were far below the value at which multicollinearity is of concern (cf. Quinn and Keough, 2002).

All statistical analyses were performed in R language (R Development Core Team, 2011).

Results

COHERENCE OF LSWT

The general temporal trend of LSWT was similar in all studied lakes (Fig. 2). Despite the differences in altitude, lake morphology and local topography, the LSWT time series pattern was coherent, as indicated by strong pairwise correlations (Fisher weighted mean R^2 [95% Confidence Interval] = 0.74 [0.72; 0.76]). The proportion of shared variance was highest in nearby situated lake pairs with comparable physical features (e.g., Nižné Furkotské pleso and Vyšné Furkotské pleso: $R^2 = 0.95$, [0.91; 0.96]; Štvrté Roháčske pleso and Prvé Roháčske pleso: $R^2 = 0.94$, [0.92; 0.96]). The lowest amount of shared variance ($R^2 = 0.26$, [0.13; 0.40]) was found between the LSWTs of the higher altitude, deeper, and shaded Zamrznuté pleso and lower altitude, shallow, and well insolated Vyšné Furkotské pleso.

DRIVERS OF LSWT

The mean LSWTs varied considerably among lakes (4.2–10.6 °C). The LSWT of most of the lakes reached their maximum in August, with the highest recorded mean daily temperature (21.4 °C; Nižné Furkotské pleso) and the difference between the maximum measured daily mean LSWT of this warmest and the coldest lake (Dlhé Velické pleso) being as much as 11.4 °C. Multiple regression analysis revealed that this variability is governed primarily by altitude and direct solar radiation (Table 2). During all but one month (October), the mean LSWT was significantly negatively related to

altitude. Mean monthly LSWT decreased linearly at rates of 0.6 to 1.8 °C per 100 m, holding other variables constant. The rate of decreasing temperature with altitude was steeper during May, June, and July (mean rate = -1.3 °C per 100 m) than in the rest of the open water season (-0.8 °C per 100 m). In contrast to altitude, TDDSR showed a significant positive relationship with the mean monthly LSWT during all months. Topographically shaded lakes showed consistently lower temperatures than unshaded but otherwise similar lakes across different altitudinal belts (Fig. 3). Mean monthly LSWT increased linearly with direct insolation from 0.9 to 2.6 °C $1000 \text{ h}^{-1} \text{ a}^{-1}$, holding other variables constant. Again, as was seen for altitude, the effect of TDDSR on LSWT was stronger from May to July (2.3 °C $1000 \text{ h}^{-1} \text{ a}^{-1}$) than in the rest of year (1.5 °C $1000 \text{ h}^{-1} \text{ a}^{-1}$). The results of regression analysis showed only a minor effect of maximum depth on LSWT, and no significant effect from lake area.

In order to compare the relative effect of important variables on LSWT directly, the regression models consisting of altitude, TDDSR, and maximum depth were fitted to LSWT data for each month. The variance partitioning procedure showed that the fraction of variance uniquely attributable to TDDSR (32%; average across months) was almost as high as the variance explained by altitude (38%). The relative effect of maximum depth was low (5%). The seasonal pattern of the partial determination coefficients is shown in Figure 4. The variance explained by altitude and TDDSR showed weak opposite trends. The variance attributable to TDDSR was higher at the beginning and at the end of the open water season, while the altitudinal effect dominated during summer months. The overall performance of these models was quite good, as indicated by a root mean square error (RMSE) of 1.5 °C (average across months). If topographic shading and lake bathymetry are not taken into account, as is usually the case, the RMSE then increases to 3.1 °C.

Daily fluctuations of LSWT were the greatest at the beginning of the open water season (SD LSWT = 2.4 °C, average across lakes in May) and consistently decreased until the lakes were frozen (SD LSWT = 1.0 °C, average across lakes in October). The temporal stability of temperatures was governed mainly by lake depth as indicated by a high partial R^2 in the final regression models. Deeper lakes showed less variation in daily temperatures than shallow lakes (Table 3). Altitude and TDDSR were also included in some models, but their effect was weaker.

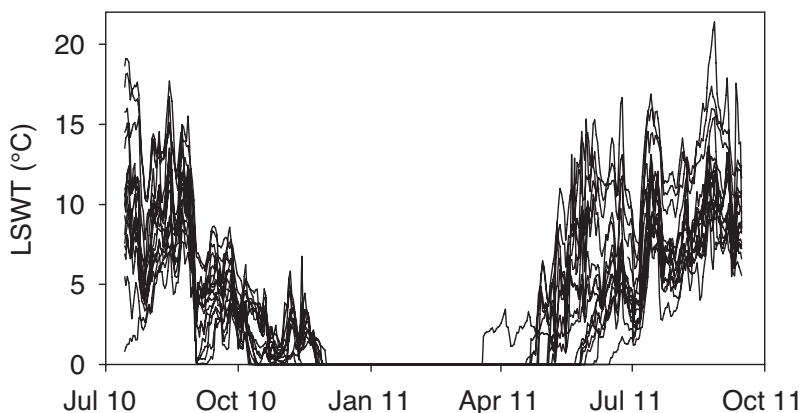


FIGURE 2. Daily mean lake surface water temperatures (at 5 cm depth) of 18 Tatra Mountains lakes measured from July 2010 to September 2011.

TABLE 2

Final regression models predicting mean monthly lake surface water temperature (LSWT) from altitude, direct solar radiation (TDDSR), and maximum lake depth. Regression coefficients (b), bootstrapped confidence limits [95% CL], variance explained uniquely by the particular variable (partial R²), the performance of the whole models (F, R², p) and sample size (n) are displayed.

Date (mm.yy)	Altitude		TDDSR		log Maximum depth		Whole model			
	b [95% CL]	partial R ²	b [95% CL]	partial R ²	b [95% CL]	partial R ²	F	R ²	p	n
07.10	-0.0117 [-0.0200; -0.0047]	0.31	0.0026 [0.0009; 0.0050]	0.23			7.25	0.51	0.0069	17
08.10	-0.0071 [-0.0126; -0.0031]	0.27	0.0016 [0.0005; 0.0027]	0.22			7.82	0.51	0.0047	18
09.10	-0.0096 [-0.0122; -0.0066]	0.66	0.0013 [0.0007; 0.0021]	0.21	0.8595 [0.1552; 1.4762]	0.12	22.14	0.84	< 0.0001	17
10.10			0.0009 [0.0003; 0.0015]	0.42			6.46	0.42	0.0316	11
05.11	-0.0177 [-0.0255; -0.0013]	0.54	0.0024 [0.0007; 0.0038]	0.55			9.77	0.74	0.0094	10
06.11	-0.0157 [-0.0217; -0.0110]	0.59	0.0026 [0.0014; 0.0039]	0.24			22.80	0.79	< 0.0001	15
07.11	-0.0085 [-0.0143; -0.0040]	0.38	0.0016 [0.0002; 0.0029]	0.20			7.19	0.53	0.0079	16
08.11	-0.0078 [-0.0142; -0.0019]	0.28	0.0019 [0.0003; 0.0033]	0.25			5.92	0.48	0.0148	16
09.11	-0.0061 [-0.0115; -0.0020]	0.26	0.0017 [0.0005; 0.0029]	0.30			6.50	0.50	0.0111	16

DRIVERS OF ICE COVER

The temperature time series showed that all of the studied lakes freeze during the winter (Fig. 2). The LSWT of some lakes decreased to 0 °C as early as in the beginning of September. However, their LSWTs rose again and declined repeatedly toward zero. The stable formation of ice cover on the studied lakes occurred from early October (Žabie Javorové pleso) to mid-December 2010 (Nižné Furkotské pleso). The timing of freezing was independent of altitude, lake area, and depth, since the best regression model included TDDSR as the only predictor of the ice-in dates (Table 4). Solar radiation was positively related to the ice-in date and explained 48% of the variability in the data set.

Thawing of the studied lakes spanned more than 80 days, from late March (Kolové pleso) to mid-June (Zamrznuté pleso). The best regression model explaining the variability in ice-out dates encompasses altitude and maximum depth (Table 4). Deeper lakes and lakes at higher altitudes thawed slower than shallow lakes and lakes situated at lower altitudes, respectively. These two variables accounted for 77% of the variability in breakup dates.

The duration of ice cover varied from 113 days (Kolové pleso) to 247 days (Zamrznuté pleso) and exhibited a linear dependence on altitude and TDDSR, respectively (Table 4). Indeed, lakes at higher altitudes were frozen for a longer time than those at lower elevations, and topographically shaded lakes retained their ice cover longer than well insulated ones. The model explained 64% of the variability in the length of ice cover.

Discussion

COHERENCE OF LSWT

Surface water temperature of the studied lakes fluctuated coherently over the whole study period, as indicated by strong correlations between time series. Lakes in the same geographic region frequently show synchronous patterns of inter-annual variability, mainly of the physical lake variables such as the water temperature (Blenckner, 2005). The temperature of spatially close lakes responds coherently to regional climate forcing (Magnuson et al., 1990; Livingstone et al., 1999; Thompson et al., 2005). Moreover, it has been shown that the surface temperature of lakes can fluctuate with a high degree of coherence over a span of several hundred kilometers (Livingstone and Dokulil, 2001) and not only at large temporal scales, but also from day to day (Livingstone and Padisak, 2007). Temperatures of the uppermost parts of the water column of individual lakes act regionally in coherence mainly due to the strong relation to regional air temperature, which is reflected extremely well in the surface temperature of lakes (Livingstone and Lotter, 1998). As has been shown in previous work (Šporka et al., 2006), the synchronous pattern of LSWT in Tatra Mountains lakes reflects changes in ambient air temperature.

Nevertheless, the degree of coherence in LSWT changes with the geographical and physical similarity of the Tatra Mountains lakes. Lakes in close proximity, with comparable physical features, showed substantially higher coherence than lakes with different properties and/or at different elevations. In mountain areas, altitude (as a proxy for air temperature) and factors related to lake location (Livingstone et al., 2010) are expected to be key variables disrupting synchronous lake temperature fluctuations. The different trends

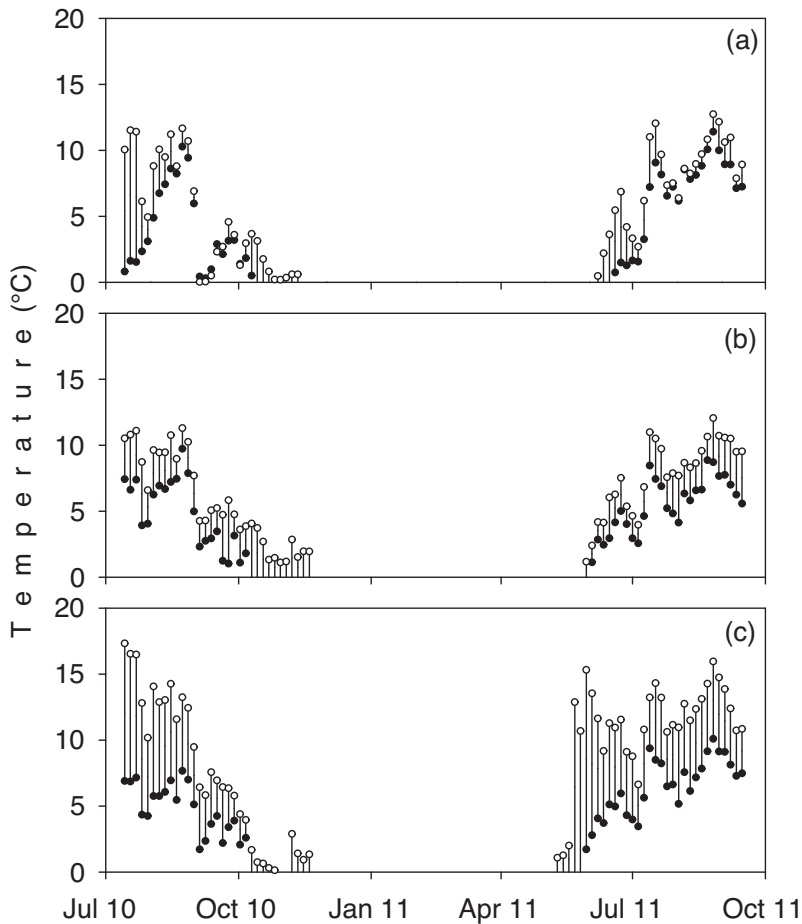


FIGURE 3. Differences in daily mean lake surface water temperatures of morphologically similar lakes with contrasting amounts of direct solar radiation: (a) Zamrznuté pleso (shaded lake—black circle) vs. Pusté pleso (unshaded lake—white circle), altitude \approx 2050 m; (b) Žabie Javorové pleso (shaded) vs. Malé Žabie (Mengusovské) pleso (unshaded), altitude \approx 1900 m; and (c) Zmrzlé pleso (shaded) vs. Štvrté Roháčske pleso (unshaded), altitude \approx 1740 m. Data are on time scale of 5 days. For lakes characteristics see Table 1.

in LSWT are especially apparent considering the broad altitudinal gradient (e.g. Livingstone et al., 2005b). Lake depth, residence time, or other physical features control how long the climatic signal of ambient temperature is stored in the lake system (Blenckner, 2005), and these variables consequently introduce dissimilar lake responses.

DRIVERS OF LSWT

As indicated by our data, the surface temperature of the studied lakes was primarily altitude-dependent and decreased linearly with

increasing elevation. In mountain areas, air temperature is strongly related to altitude and decreases as altitude increases. Because of the strong relationship between air and lake surface water temperatures, the LSWT of mountain lakes is generally related to altitude (Livingstone et al., 1999; Thompson et al., 2009). Lakes of higher elevation are likely to be cooler than lower elevation lakes, and the relationship between LSWT and altitude has been described as being approximately linear (Livingstone and Lotter, 1998; Livingstone et al., 1999, 2005b). The effect of altitude varies seasonally, as can be seen in the range of monthly temperature lapse rates (from -1.8 to -0.6 $^{\circ}\text{C } 100 \text{ m}^{-1}$). The most likely cause is the

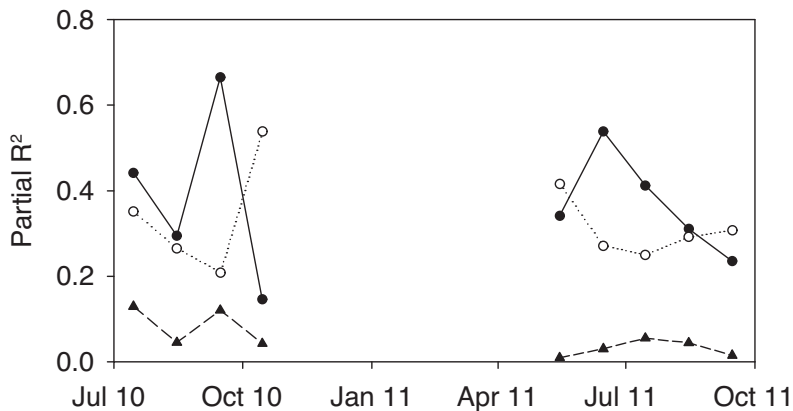


FIGURE 4. Temporal trends in relative effect size (partial R^2) of altitude (black circle), total duration of direct solar radiation (TDDSR) (white circle), and maximum depth (triangle) on daily lake surface water temperatures.

TABLE 3

Final regression models predicting monthly SD of LSWT from altitude, direct solar radiation (TDDSR), and maximum lake depth. Regression coefficients (b), bootstrapped confidence limits [95% CL], variance explained uniquely by the particular variable (partial R²), the performance of the whole models (F, R², p) and sample size (n) are displayed.

Date (mm.yy)	Altitude		TDDSR		log Maximum depth		Whole model			
	b [95% CL]	partial R ²	b [95% CL]	partial R ²	b [95% CL]	partial R ²	F	R ²	p	n
07.10	-0.0025 [-0.0043; -0.0005]	0.31	0.0006 [0.0003; 0.0012]	0.28	-0.4147 [-0.5705; -0.1665]	0.54	8.44	0.55	0.0039	17
08.10					-0.4089 [-0.5594; -0.2460]	0.65	18.74	0.54	0.0005	18
09.10	0.0018 [0.0009; 0.0028]	0.38					15.57	0.69	0.0003	17
10.10										11
05.11										10
06.11										15
07.11										16
08.11	-0.0012 [-0.0029; -0.0002]	0.14	0.0006 [0.0002; 0.0010]	0.49			9.05	0.58	0.0035	16
09.11					-0.5810 [-1.2306; -0.1223]	0.38	8.40	0.38	0.0117	16

TABLE 4

Final regression models predicting ice cover characteristics from altitude, direct solar radiation (TDDSR), and maximum lake depth. Regression coefficients (b), bootstrapped confidence limits [95% CL], variance explained uniquely by the particular variable (partial R²), the performance of the whole models (F, R², p) and sample size (n) are displayed.

Ice cover characteristic	Altitude		TDDSR		log Maximum depth		Whole model			
	b [95% CL]	partial R ²	b [95% CL]	partial R ²	b [95% CL]	partial R ²	F	R ²	p	n
Ice-in date			0.021 [0.009; 0.031]	0.48			14.81	0.48	0.0014	18
Ice-out date	0.075 [0.043; 0.113]	0.24			9.344 [2.471; 18.634]	0.11	23.87	0.77	< 0.0001	17
Ice duration	0.141 [0.073; 0.221]	0.40	-0.027 [-0.043; -0.008]	0.24			12.37	0.64	0.0008	17

rapid warming of earlier thawing lakes at lower altitudes, which increases the temperature differences between elevations and consequently moves up the lapse rate during early summer. Later in the summer, when the LSWT of the lower lakes has already reached their maximum but the temperature of higher situated lakes still rises, the LSWT lapse rate declines considerably. This seasonal pattern is similar to that observed in a previous study of Tatra Mountains lakes (Šporka et al., 2006). The lack of a relationship between LSWT and altitude in October may be either the artifact of the low number of lakes ($n = 11$) on which the regression was based or, more likely, the consequence of a substantial, rapid decrease of the LSWT at lower altitude lakes potentially due to the occurrence of air temperature inversions and resulting equalization of temperatures among the lakes. Nevertheless, 95% confidence limits of the monthly regression coefficients for altitude were wider than $0.6\text{ }^{\circ}\text{C } 100\text{ m}^{-1}$, and thus the patterns of seasonal differences should be considered with a certain amount of caution.

Besides the altitudinal gradient, many other variables have considerable effect on lake temperature regulation, including within-lake characteristics (e.g., lake size and depth, lake inflow, or outflow) as well as local factors related to geomorphological settings (e.g., lake valley orientation, meltwater inflow, topographic shading, or wind sheltering) (Livingstone et al., 2005a; Thompson et al., 2005). In the Tatra Mountains, Šporka et al. (2006) suggested the importance of lake morphometry and geographical setting to lake surface water temperature. Besides altitude, we explicitly tested the effect of lake morphometry and local topography on LSWT. The amount of solar radiation and, to some extent, maximum depth were significantly related to the surface water temperature of the studied lakes. Moreover, the relative effect of TDDSR on LSWT was almost as great as the effect of altitude. Although not directly evaluated, the important role of topographic shading was clearly demonstrated in Lake Hagelseewli by Livingstone et al. (1999). They concluded that topographic shading results in a depression of LSWT because of the blocking of incident solar radiation, as well as the extension of the period of partial ice cover due to spatially heterogeneous thawing. Other within-catchment processes related to topographic shading (e.g. the longer persistence of snow in catchment and continual meltwater inflows) may also be of considerable importance (Thompson et al., 2005).

The effect of TDDSR varied seasonally in a similar manner as the effect of altitude. This same pattern is attributable to the above-mentioned processes. The stronger effect of TDDSR during early summer is presumably caused by the rapid snowmelt in fully insolated catchments. On the other hand, snowfields remaining in the catchments of topographically shaded lakes might lower the LSWTs, though slightly, and thus contribute to the temperature differences between shaded and unshaded lakes (see also Thompson et al., 2005). For example, Dlhé Velické pleso is affected by the flow-through of cool water from snowmelt. A snowfield extending to the lake surface was observed to persist on the steep NW slope of the basin almost throughout the year. Consequently, this lake had the lowest LSWTs among all of the studied lakes, despite the fact that the lake is situated neither at the highest altitude nor has the lowest amount of solar radiation. Similarly, the high relative importance of TDDSR in regression models at the beginning and at the end of the open water season is probably caused by the

influence of long-lasting snowfields and the persistence of new snow, respectively, in topographically shaded catchments. In general, a low amount of incident solar radiation in the lake basin accounts for higher snow accumulation (Barry, 2008).

In contrast to monthly temperatures, day-to-day variability of LSWT was driven mainly by the maximum depth of the lakes. The lake surface water temperature of deeper lakes was more stable than that for shallow ones. This is not surprising, since lake depth is an important parameter in lake thermodynamics (Dutra et al., 2010). When exposed to the same ambient temperature, deeper lakes have a higher heat capacity leading to reduced short-term fluctuations and higher temperature stability. Nevertheless, when considering the temperature stability, significant relationships were found in only 5 out of 9 studied months and thus the generality of these models is questionable.

DRIVERS OF ICE COVER

The timing of ice-in is considered to be influenced by the synergistic effect of local weather conditions and to depend on declining air temperatures throughout autumn (Williams et al., 2004). Moreover, lake freezing processes (along with air temperature) are believed to be primarily driven by internal lake properties and processes (Leppäranta, 2010), which are closely related to lake morphological parameters. Freezing also tends to reflect the lake size and/or lake depth (Stewart and Haugen, 1990; Thompson et al., 2005). Deeper lakes thus require a longer period with air temperatures below $0\text{ }^{\circ}\text{C}$ before they freeze over (Jensen et al., 2007). Thus, it might be expected that the development of lake ice cover should be related to altitude and lake size. Surprisingly, the freezing of the studied lakes was independent of both the altitude and lake size (represented by area and depth).

Considering the altitudinal independence of lake freezing, our results are in close agreement with the results of Šporka et al. (2006), who argued that other factors apart from elevation or lake morphometry need to be considered when discussing the ice phenology in mountain areas. The authors pointed out that the lake setting and/or local topographic shading govern wind and radiation exposure, and thereby potentially affect the mixing depth and LSWT in autumn—processes important for ice formation. We explicitly tested one of these hypotheses, and the results showed that ice-in dates were significantly related to the duration of direct solar radiation. The importance of radiation can be illustrated by Pusté pleso, the highest elevation lake (2056 m a.s.l.) in this study. The freezing of this lake was delayed for almost one month after the first lakes froze up. Pusté pleso has a substantially higher yearly amount of TDDSR (2817 h) than Zamrznuté pleso (1667 h of TDDSR), which is situated a bit lower (2040 m a.s.l.), but froze earlier. And this is not a unique case. All the lakes with the earliest dates of ice-in have distinctly lower input of solar radiation than those of comparable altitudes and morphometry but with later dates of freezing. Though of probably minor relevance, the more common occurrence of temperature inversions in autumn must not be neglected when assessing the degree of altitudinal dependence of ice-in timing (Šporka et al., 2006).

At approximately the same time as the first lakes froze over, several other lakes were frozen only temporarily, with a thin ice cover lasting only for a few days. The lakes that froze early included

lakes of various sizes that could, per se, result in a non-significant effect of lake area and/or depth. Moreover, the influence of solar radiation could, at least partially, explain the lack of correlation between the lake size and ice-in date. Some of the repeatedly thawed lakes were very shallow (e.g. Kolové pleso) and/or received considerably higher amount of TDDSR (e.g. Vel'ké Biele pleso). Besides the direct influence of solar radiation, a potentially important factor in heating the water of shallow lakes can be high sediment heat storage (Goloso et al., 2007). Together with the fact that a thin and snow-free ice layer is vulnerable to solar radiation (Leppäranta, 2010; Leppäranta and Wang, 2008), the above-mentioned factors could easily eliminate the temporary ice cover of shallow lakes.

The timing of ice breakup and ice-cover duration appeared to be altitude dependent, with later thawing dates and longer ice-cover periods at higher elevations. Despite the complexity and multiplicity of thawing processes, some degree of altitudinal dependence of ice thawing was expected due to the well known relationship between air temperature and altitude. Generally, air temperature is of primary importance in ice phenology and the timing of lake ice-out (Palecki and Barry, 1986; Livingstone, 1997, 1999, 2000; Williams and Stefan, 2006). Specifically for the Tatra Mountains lakes, Šporka et al. (2006) reported a comparable pattern of altitudinal dependence of ice-cover duration resulting from the altitudinal dependence of the ice-out alone.

Sunlight plays a major role in the physical processes of ice thawing (Leppäranta, 2010), allowing us to expect certain relationships among ice-cover duration, ice-out timing, and TDDSR. Nevertheless, although the ice-cover duration of the studied lakes showed a significant relationship with TDDSR, the ice-out dates did not. We believe that this is an artifact of this particular data set rather than a reflection of a truly non-significant relationship between TDDSR and thawing dates. It should be noted that the regression diagnostics of the latter model revealed a relatively high Cook's distance for Kolové pleso ($D = 0.5$), which indicates a substantial influence of the data collected from this lake on the regression coefficients. When we excluded this shallow and exceptionally early thawing lake from the analysis and reanalyzed the data set, TDDSR was retained as a significant predictor (b [95% confidence interval] = -0.0100 [-0.0150 ; -0.0036]), and the overall performance of the model markedly improved ($\Delta R^2 = 0.07$, $\Delta RMSE = 3$ days). A possible explanation for such an early ice-out date of Kolové pleso might be the combination of geographic position and lake morphometry. This lake was at the lowest altitude within our study and may experience a substantially higher ambient spring air temperature. Moreover, this lake has a relatively large surface area and thus we can speculate about the role of the wind in the timing of ice breakup (Leppäranta and Wang, 2008).

Our findings indicate that the amount of solar radiation plays a substantial role in thawing of the lake ice cover. The susceptibility of ice cover to thawing is governed by its physical properties, especially the ice thickness. The condition of the ice cover depends on many factors, several of which are driven by solar radiation (Livingstone, 1997). However, before sunlight reaches the ice, any overlying snow cover has to be melted and this makes the snow thickness another important factor in thawing processes (Elo, 2006; Jensen et al., 2007; Williams et al., 2004). Again, incident solar

radiation is recognized to be the main control of snowmelt in the spring (Koivusalo and Kokkonen, 2002). In general, local conditions such as topographic shading and lake location control both the lake ice thickness and snow cover depth (Łajczak, 1982; Gregor and Pacl, 2005). To conclude, thawing of the ice cover includes several interconnected processes governed by sunlight.

Conclusions

Predicting the temperature characteristics of mountain lakes is challenging because of the multiplicity of processes involved and complications in obtaining accurate high-resolution data in remote areas. The approach adopted here combines continuous monitoring of lake surface water temperature with GIS-derived data.

We modeled lake surface water temperature and ice-cover characteristics against altitude, lake morphometry, and local topography. To the best of our knowledge, this is the first time that the effect of topographic shading was explicitly considered in relation to temperature characteristics of mountain lakes. The results confirmed the importance of altitude and lake depth on surface water temperatures and ice-cover timing. Interestingly, our study demonstrates that topographic shading is a key factor involved in the modification of temperature characteristics of alpine lakes. Including direct solar radiation as a model parameter would considerably improve predictions of lake temperatures and ice-cover features.

These results offer challenges for further studies of both direct and mediated effects of solar radiation on temperature conditions of high-elevation lakes. Our findings are potentially useful for (i) comprehensible explanations of the responses of high-altitude lake physical properties to ongoing and future climate changes; (ii) interpreting the results of paleolimnological studies aimed at reconstructing past climate history; and finally, but not of minor importance, (iii) better understanding the factors affecting the composition and distribution of high-altitude lake communities. These all have implications for the present conservation and management of vulnerable high-altitude aquatic ecosystems, as well as for predicting their future development related to a changing climate.

Acknowledgments

Study was funded by the Scientific Grant Agency of the Ministry of Education of Slovak Republic and the Academy of Sciences, Grant Nos. 1/0464/10 and 1/0180/12. This work was supported by the Slovak Research and Development Agency under the contract No. APVV-0059-11. We are grateful for language correction by David Hardekopf and Ivana Šibíková. Thanks are due to Miro Očadlík for his help during fieldwork and colleagues from Charles University, Prague, and the Institute of Hydrobiology, České Budějovice, for their field assistance. We are grateful to two anonymous reviewers for their comments on the manuscript.

References Cited

Agustí-Panareda, A., and Thompson, R., 2002: Reconstructing air temperature at eleven remote alpine and arctic lakes in Europe from 1781 to 1997. *Journal of Paleolimnology*, 28: 7–23.

- Barry, R., 2008: *Mountain Weather and Climate*. 3rd edition. New York: Cambridge University Press, 506 pp.
- Beniston, M., Diaz, H. F., and Bradley, R. S., 1997: Climatic change at high elevation sites; a review. *Climatic Change*, 36: 233–251.
- Blenckner, T., 2005: A conceptual model of climate-related effects on lake ecosystems. *Hydrobiologia*, 533: 1–14.
- Borcard, D., Legendre, P., and Drapeau, P., 1992: Partialling out the spatial components of ecological variation. *Ecology*, 73: 1045–1055.
- Breiman, L., 1995: Better subset regression using the nonnegative Garrote. *Technometrics*, 37: 373–384.
- de Mendoza, G., and Catalan, J., 2010: Lake macroinvertebrates and the altitudinal environmental gradient in the Pyrenees. *Hydrobiologia*, 648: 51–72.
- Chomitz, K., and Šamaj, F., 1974: Zrážkové pomery. In Konček, M. (ed.), *Klíma Tatier*. Bratislava: Veda, 443–536 (in Slovak).
- Dutra, E., Stepanenko, V. M., Balsamo, G., Viterbo, P., Miranda, P. M. A., Mironov, D., and Schär, Ch., 2010: An offline study of the impact of lakes on the performance of the ECM WF surface scheme. *Boreal Environment Research*, 15: 100–112.
- Efron, B., and Tibshirani, R., 1986: Bootstrap methods for standard errors: confidence intervals and other measures of statistical accuracy. *Statistical Science*, 1: 54–77.
- Elo, A. R., 2006: Long-term modelling of winter ice periods for morphologically different lakes. *Nordic Hydrology*, 37: 107–119.
- ESRI, 2009: ArcGIS version 9.3, Spatial Analyst Extension, Hydrologic Modeling Toolbox. Redlands, California: Environmental Systems Research Institute (ESRI).
- Fu, P., and Rich, P. M., 2000: The Solar Analyst 1.0 Manual. Helios Environmental Modeling Institute (HEMI), U.S.A., <<http://72.10.50.236/pdf/view/34818>>.
- Fu, P., and Rich, P. M., 2002: A geometric solar radiation model with applications in agriculture and forestry. *Computers and Electronics in Agriculture*, 37: 25–35.
- Golosov, S., Maher, O. A., Schipunova, E., Terzhevik, A., Zdorovenova, G., and Kirillin, G., 2007: Physical background of the development of oxygen depletion in ice-covered lakes. *Oecologia*, 151: 331–340.
- Gregor, V., and Pacl, J., 2005: Hydrology of the Tatra mountain lakes. *Acta Hydrologica Slovaca*, 6: 161–187.
- Gudasz, C., Bastviken, D., Steger, K., Premke, K., Sobek, S., and Tranvik, L. J., 2010: Temperature-controlled organic carbon mineralization in lake sediments. *Nature*, 466: 478–481.
- Jensen, O. P., Benson, B. J., Magnuson, J. J., Card, V. M., Futter, M. N., Soranno, P. A., and Stewart, K. M., 2007: Spatial analysis of ice phenology trends across the Laurentian Great Lakes region during a recent warming period. *Limnology and Oceanography*, 52: 2013–2026.
- Koivusalo, H., and Kokkonen, T., 2002: Snow processes in a forest clearing and in a coniferous forest. *Journal of Hydrology*, 262: 145–164.
- Konček, M., and Orlicz, M., 1974: Teplotné pomery. In Konček, M. (ed.), *Klíma Tatier*. Bratislava: Veda, 89–179 (in Slovak).
- Łajczak, A., 1982: Wahania temperatury przypowierzchniowej warianty wody w jeziorach tatrzańskich o różnej ekspozycji. *Czasopismo Geograficzne*, 53: 29–44 (in Polish).
- Leppäranta, M., 2010: Modelling the formation and decay of lake ice. In George, G. (ed.), *The Impact of Climate Change on European Lakes*. Aquatic Ecology Series, Volume 4. Berlin: Springer, 63–83.
- Leppäranta, M., and Wang, K., 2008: The ice cover on small and large lakes: scaling analysis and mathematical modelling. *Hydrobiologia*, 599: 183–189.
- Livingstone, D. M., 1997: Break-up dates of alpine lakes as proxy data for local and regional mean surface air temperatures. *Climatic Change*, 37: 407–439.
- Livingstone, D. M., 1999: Ice break-up on southern Lake Baikal and its relationship to local and regional air temperatures in Siberia and to the North Atlantic Oscillation. *Limnology and Oceanography*, 44: 1486–1497.
- Livingstone, D. M., 2000: Large-scale climatic forcing detected in historical observations of lake ice break-up. *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie*, 27: 2775–2783.
- Livingstone, D. M., and Dokulil, M. T., 2001: Eighty years of spatially coherent Austrian lake surface temperatures and their relationship to regional air temperature and the North Atlantic Oscillation. *Limnology and Oceanography*, 46: 1220–1227.
- Livingstone, D. M., and Lotter, A. E., 1998: The relationship between air and water temperatures in lakes of the Swiss Plateau: a case study with palaeolimnological implications. *Journal of Paleolimnology*, 19: 181–198.
- Livingstone, D. M., and Padisak, J., 2007: Large-scale coherence in the response of lake surface-water temperatures to synoptic-scale climate forcing during summer. *Limnology and Oceanography*, 52: 896–902.
- Livingstone, D. M., Lotter, A. E., and Walker, I. R., 1999: The decrease in summer surface temperature with altitude in Swiss alpine lakes: a comparison with air temperature lapse rates. *Arctic, Antarctic, and Alpine Research*, 31: 341–352.
- Livingstone, D. M., Jankowski, T., and Lotter, A. F., 2005a: Patterns of deviation from linearity in the relationship between lake surface temperature and altitude above sea level in the Swiss Alps. *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie*, 29: 300–305.
- Livingstone, D. M., Lotter, A. F., and Kettle, E. H., 2005b: Altitude-dependent differences in the primary physical response of mountain lakes to climatic forcing. *Limnology and Oceanography*, 50: 1313–1325.
- Livingstone, D. M., Adrian, R., Arvola, L., Blenckner, T., Dokulil, M. T., Har, R. E., George, G., Jankowski, T., Järvinen, M., Jennings, E., Nöges, P., Nöges, T., Straile, D., and Weyhenmeyer, G. A., 2010: Regional and supra-regional coherence in limnological variables. In George, G. (ed.), *The Impact of Climate Change on European Lakes*. Aquatic Ecology Series, Volume 4. Berlin: Springer, 311–337.
- Magnuson, J. J., Benson, B. J., and Kratz, T. K., 1990: Temporal coherence in the limnology of a suite of lakes in Wisconsin, U.S.A. *Freshwater Biology*, 23: 145–159.
- Malík, P., Bačová, N., Hronček, S., Ivanič, B., Káčer, Š., Kočický, D., Maglay, J., Marsina, K., Ondrášik, M., Šefčík, P., Černák, R., Švasta, J., and Lexa, J., 2007: Zostavovanie geologických máp v mierke 1:50 000 pre potreby integrovaného manažmentu krajiny. Manuskript – archív Geofondu ŠGÜDŠ, arch. č. 88158. Bratislava: ŠGÜDŠ, 552 pp. (in Slovak).
- Miller, A., 2002: *Subset Selection in Regression*. 2nd edition. Boca Raton: Chapman and Hall/CRC, 234 pp.
- Pacl, J., and Wit-Joźwikowa, K., 1974: Teplota vôd. In Konček, M. (ed.), *Klíma Tatier*. Bratislava: Veda, 181–204 (in Slovak).
- Palecki, M. A., and Barry, R. G., 1986: Freeze-up and break-up of lakes as an index of temperature changes during the transition seasons: a case study for Finland. *Journal of Climate and Applied Meteorology*, 25: 893–902.
- Quinn, G. P., and Keough, M. J., 2002: *Experimental Design and Data Analysis for Biologists*. Cambridge: Cambridge University Press, 537 pp.
- R Development Core Team, 2011: *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Regier, H. A., Holmes, J. A., and Panly, D., 1990: Influence of temperature changes on aquatic ecosystems: an interpretation of empirical data. *Transactions of the American Fisheries Society*, 119: 374–389.
- Rich, P. M., and Fu, P., 2000: Topoclimatic habitat models. *Proceedings of the Fourth International Conference on Integrating GIS and Environmental Modeling*. (GIS/EM4): Problems, Prospects and Research Needs, Banff, Alberta, Canada, September 2–8.
- Rich, P. M., Dubayah, R., Hetrick, W. A., and Saving, S. C., 1994: Using Viewshed models to calculate intercepted solar radiation: applications in ecology. *American Society for Photogrammetry and Remote Sensing Technical Papers*, 524–529.

- Shao, J., 1993: Linear model selection by cross-validation. *Journal of the American Statistical Association*, 88: 486–494.
- Shao, J., 1997: An asymptotic theory for linear model selection. *Statistica Sinica*, 7: 221–264.
- Sommaruga-Wögrath, S., Koinig, K. A., Schmidt, R., Sommaruga, R., Tessadri, R., and Psenner, R., 1997: Temperature effects on the acidity of remote alpine lakes. *Nature*, 387: 64–67.
- Šporka, F., Livingstone, D. M., Stuchlík, E., Turek, H., and Galas, J., 2006: Water temperatures and ice cover in lakes of the Tatra Mountains. *Biologia Bratislava*, 61, Suppl. 18: 77–90.
- Stewart, K. M., and Haugen, R. K., 1990: Influence of lake morphometry on ice dates. *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie*, 24: 122–127.
- Thompson, R., Kamenik, C., and Schmidt, R., 2005: Ultrasensitive alpine lakes and climate change. *Journal of Limnology*, 64: 139–152.
- Thompson, R., Ventura, M., and Camarero, L., 2009: On the climate and weather of mountain and sub-arctic lakes in Europe and their susceptibility to future climate change. *Freshwater Biology*, 54: 2433–2451.
- Williams, S. G., and Stefan, H. G., 2006: Modelling of lake ice characteristics in North America using climate, geography, and lake bathymetry. *Journal of Cold Regions Engineering*, 20: 140–167.
- Williams, S. G., Layman, K. L., and Stefan, H. G., 2004: Dependence of lake ice covers on climatic, geographic and bathymetric variables. *Cold Regions Science and Technology*, 40: 145–164.
- Winder, M., and Hunter, D. A., 2008: Temporal organization of phytoplankton communities linked to physical forcing. *Oecologia*, 156: 179–192.

MS accepted August 2012