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Altitude-dependent differences in the primary physical response of mountain lakes to climatic forcing

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Abstract

Simultaneous hourly measurements of lake surface water temperature (LSWT) during summer and early autumn 2000 in 29 lakes in the Swiss Alps revealed the presence of two altitudinally distinct thermal regimes. The threshold separating the low-altitude from the high-altitude regime was located at ~2,000 m above sea level during early summer 2000 but rose as summer progressed. Within the low-altitude regime, LSWTs are strongly related to altitude and surface air temperature. On crossing the threshold to the high-altitude regime, the LSWT lapse rate increases sharply, but the relationship of LSWT to both altitude and air temperature weakens considerably. A difference in the response of low-altitude and high-altitude mountain lakes to climatic forcing in early summer may have implications for climate change studies in which mountain lakes are employed either for paleoclimate reconstructions or as sensitive indicators of current climate change. Any long-term temporal change in the threshold altitude would imply that lakes close to the threshold may not always have been located in the same thermal regime, with consequences for paleolimnological climate reconstructions. Predictions of the effects of future climate warming on high-altitude mountain lakes may have to take into account the possibility of a concomitant rise in the threshold altitude.

As the climate change debate continues, the importance of knowing how lakes respond to climatic forcing is becoming increasingly apparent. First, from a limnological perspective, an understanding of how lacustrine systems respond to climatic forcing is a necessary prerequisite to predicting their response to scenarios of future climate change. Second, from a climatological perspective, much of our knowledge of past climate changes is derived from the paleolimnological analysis of lake sediments. It is thus doubly important to establish the nature of the link between climatic forcing and lake response.

The most direct impact of climatic forcing is on physical lake variables. Of these, the one that is arguably the most directly affected by climatic forcing during the biologically productive months is lake surface water temperature (LSWT). Within the context of the climate change problem, the direct, immediate impact of climatic forcing on LSWT—the primary physical response—is of major relevance because the temperature conditions prevailing in the epilimnion often mediate the impacts of climate change not only on individual organisms, but on entire aquatic ecosystems (Regier et al. 1990).

In the context of the impacts of climate change on lakes, it is important to distinguish between climatic forcing on a regional scale, which can invoke a coherent response in lakes over a wide area, and local meteorological forcing, which, although always the ultimate driving force, is by definition specific to individual lakes. Although the effect of large-scale climatic forcing on lakes is often masked by locally specific conditions, it is becoming increasingly clear that lakes need not always be viewed merely as isolated points in the landscape. Based on seven lakes in Wisconsin, Magnuson et al. (1990) showed that several diverse limnological variables fluctuated coherently from year to year for lakes located a few kilometers apart and that this coherence was especially high for lake variables directly influenced by climatic forcing, while Benson et al. (2000) showed this coherence to extend over much larger spatial scales. In the European Alpine region, Livingstone (1993, 1997) showed that the response of deep-water temperatures and oxygen

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concentrations to climatic forcing is broadly coherent but that local, lake-specific conditions related to vertical mixing determine the mechanisms by which this coherence manifests itself. Close to the lake surface, the masking effect of lake-specific factors is much less, so regional coherence tends to be greater. Livingstone and Dokulil (2001), for instance, showed that LSWT was highly coherent between lakes up to several hundred kilometers apart in Austria and was related to coherent large-scale climatic forcing, including air temperature, cloud cover, and wind speed, which is ultimately governed by the climatic phenomenon known as the North Atlantic Oscillation (NAO). On short timescales (days to months), Livingstone and Lotter (1998) showed that the LSWTs of a large number of lakes on the Swiss Plateau respond coherently to regional air temperature, and subsequently Livingstone et al. (1999) showed not only that LSWT in the Swiss Alps responds coherently to regional climatic forcing over an altitude gradient exceeding 1,700 m, but that the decrease in LSWT with increasing altitude can be explained to a large extent by the linear decrease in surface air temperature with increasing altitude. Livingstone et al. (1999) also found exceptions to this general rule that suggested that the LSWT of high-altitude lakes might respond differently to climatic forcing than that of lower altitude lakes. In Switzerland, the surface mixed layer of some low-altitude lakes has warmed by over 1 K since the 1960s (Livingstone 2003). In view of such extreme warming at low altitudes, the present study was motivated by the need to investigate the nature of the primary physical response to climatic forcing exhibited by mountain lakes at high altitudes, for which long-term monitoring data are lacking, and for which, given the nature of the terrain, even short-term data are difficult to acquire.

With respect to climate change, mountain lakes take on a special significance. Not only are the effects of climate change expected to be greater at high altitudes than at low altitudes (Beniston et al. 1997), but also fluctuations in regional climate and local weather are the main sources of ecosystem variability in high-altitude lakes because their remoteness makes them less liable to anthropogenic disturbance (e.g., Catalan et al. 2002). In Switzerland, regardless of altitude, regional long-term rates of increase of air temperature substantially exceed corresponding global rates of increase (Beniston et al. 1994; Lister et al. 1998). Thus high-altitude lakes in the Swiss Alps are on the one hand potentially at risk from ecological changes induced by climate change, and on the other are likely to be sensitive indicators of such climate change. It is therefore necessary to gain an understanding of how such lakes respond to climatic forcing.

Data and study region—During summer 2000, miniature Minilog thermistors with integrated data loggers (Vemco Ltd., Shad Bay, Nova Scotia, Canada), attached to 15 cm × 15 cm styrofoam floats, were employed as described by Livingstone et al. (1999) to make simultaneous hourly measurements of water temperature 5 cm below the surface of each of 41 lakes in the central Swiss Alps. The study of Livingstone et al. (1999) had shown that the water temperature at a depth of 5 cm is easy to measure and, when averaged over 24 h, reflects the mean temperature of the epilimnion well. To enhance the representativeness of the data by minimizing local littoral effects, the thermistors were anchored close to the lakes' outflows, so that they would be exposed to a continual flow of epilimnetic water. The thermistors were anchored in ~1.5 m of water, close enough to the lakeshore to allow access without a boat, but far enough to reduce the likelihood of damage or unauthorized retrieval to an acceptable level. However, losses resulting from natural causes or vandalism meant that usable simultaneous data covering the time window 19 June to 1 October 2000 were available from only 29 of the 41 lakes. In 28 of these 29 lakes, the thermistor was recovered from the same location and depth at which it had been deployed (5 cm). In the remaining lake (Oberstockensee), the thermistor was found at a depth of 4 m, having apparently been moved from its initial place of deployment.

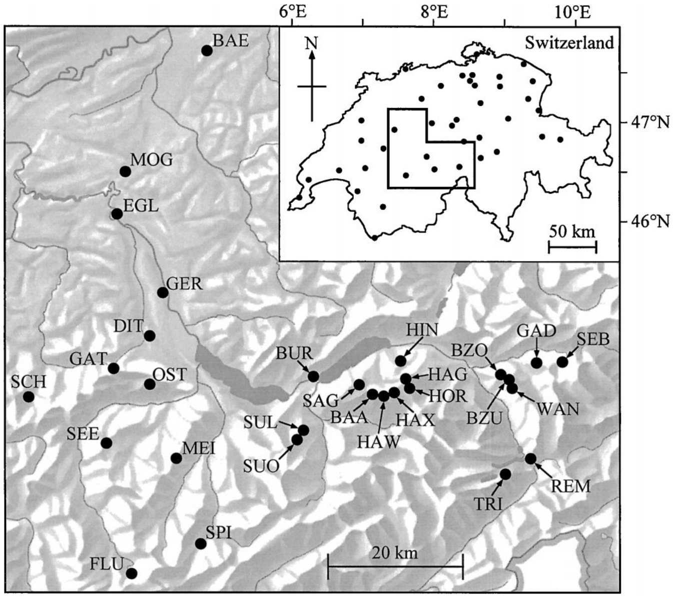

Fig. 1. Relief map of the study region in the Swiss Alps, showing the locations of the 29 lakes referred to in the text (*see Table 1* for further information on the lakes). The inset map of Switzerland shows the location of the study area and of the 40 meteorological stations (black dots) that provided air temperature data.

The lakes studied here are located in or close to the Bernese Alps in central Switzerland (Fig. 1). There are over 100 lakes in this region, ranging in altitude from 428 to 2,669 m above sea level (asl) (Guthruf et al. 1999). The 29 of these lakes for which data were available span an altitude range of over 2 km, viz. from 465 to 2,470 m asl. The lakes all lie within 50 km of the center of the region. They are generally fairly small, with only five having surface areas exceeding 0.1 km^2, but maximum depths vary widely, ranging from <3 to >40 m (Table 1). The shallowest of these lakes (or ponds) may be completely frozen during winter, but all are perennial. Most of the lakes (at least 23) have significant surface inflows. Of the 14 lakes located above 2,000 m asl, six have glaciers in their catchment area (Table 1), but in no case is the glacier located closer to the lake than ~1 km.

Throughout the entire period during which the thermistors were anchored, air temperatures were being measured at 10-

Table 1. Information on the 29 lakes referred to in the text (*see Fig. 1* for locations; the lake abbreviations listed in parentheses correspond to those used in Fig. 1). E is the altitude of the lake surface, A_0 is the lake surface area, z_m the maximum lake depth, A_c the area of the catchment, E_{Cmax} the maximum altitude of the catchment area, and G the proportion of the lake catchment area covered by glaciers. All information is taken or derived from Guthruf et al. (1999) except that on Schwarzsee, which is from Lotter et al. (1997).

Lake	Location	E (m asl)	A_0 (10^3 m^2)	z_m (m)	A_C (km^2)	E_{Cmax} (m asl)	G (%)
Remersee (REM)	46°34′38″N, 8°21′22″E	2,470	5.6	2.1	0.83	2,979	3
Häxeseeli (HAX)	46°40′54″N, 8°03′35″E	2,464	24.3	—	0.50	2,919	9
Hagelseeli (HAG)	46°41′26″N, 8°05′24″E	2,410	6.4	—	0.15	2,532	0
Triebtenseewli (TRI)	46°33′13″N, 8°18′00″E	2,365	96.6	24.0	1.93	2,844	2
Hagelseewli (HAW)	46°40′27″N, 8°02′11″E	2,339	24.9	18.8	0.33	2,619	0
Bachsee (BAA)	46°40′15″N, 8°01′20″E	2,265	80.3	15.8	1.67	2,749	1
Oberes Bänzlauiseeli (BZO)	46°41′38″N, 8°17′16″E	2,216	11.4	—	0.28	2,528	0
Oberes Sulsseewli (SUO)	46°36′48″N, 7°51′01″E	2,191	7.2	2.4	0.31	2,383	0
Unteres Bänzlauiseeli (BZU)	46°41′27″N, 8°17′22″E	2,177	20.7	—	0.70	2,647	0
Gadenlauisee (GAD)	46°43′19″N, 8°21′31″E	2,155	8.2	7.5	0.71	2,775	15
Hornseeli 1 (HOR)	46°41′00″N, 8°06′21″E	2,147	4.3	—	0.14	2,324	0
Wannisbordsee (WAN)	46°41′00″N, 8°18′00″E	2,103	24.3	14.0	1.58	2,919	2
Flueseeli (FLU)	46°24′39″N, 7°30′00″E	2,045	34.7	8.5	0.64	2,506	0
Seebodensee (SEB)	46°43′29″N, 8°25′16″E	2,042	7.3	3.0	0.20	2,283	0
Sägistalsee (SAG)	46°40′52″N, 7°58′39″E	1,935	72.5	9.4	3.62	2,462	0
Sulsseewli (SUL)	46°37′07″N, 7°51′53″E	1,920	20.1	—	0.67	2,412	0
Meienfallseeli (MEI)	46°35′17″N, 7°53′07″E	1,900	15.2	—	0.97	2,445	0
Spittelmattesee (SPI)	46°26′54″N, 7°38′32″E	1,875	5.3	2.8	0.35	2,265	0
Seebergsee (SEE)	46°34′43″N, 7°26′39″E	1,831	57.6	15.3	0.28	2,060	0
Oberstockensee (OST)	46°41′17″N, 7°31′17″E	1,665	118.1	43.0	1.18	1,994	0
Gantrischseeli (GAT)	46°42′47″N, 7°26′28″E	1,578	14.1	2.2	1.11	2,174	0
Hinterburgseeli (HIN)	46°43′09″N, 8°04′06″E	1,514	45.0	11.4	1.36	2,319	0
Schwarzsee (SCH)	46°40′03″N, 7°17′00″E	1,046	455.4	10.0	19.70	2,102	0
Dittligsee (DIT)	46°45′25″N, 7°32′02″E	652	60.2	16.4	0.39	686	0
Burgseewli (BUR)	46°41′55′N, 7°53′11″E	613	52.5	19.1	0.72	1,602	0
Gerzensee (GER)	46°49′54″N, 7°32′54″E	603	251.6	10.7	2.73	839	0
Egelmösli (EGL)	46°56′45″N, 7°28′00″E	550	15.2	3.4	0.48	593	0
Moossee (MOG)	47°01′26″N, 7°28′45″E	521	303.5	21.1	20.81	685	0
Burgäschisee (BAE)	47°10′15″N, 7°40′10″E	465	206.5	30.0	3.83	541	0

min intervals at meteorological stations throughout Switzerland. Daily mean air temperatures from 40 of these stations, covering the altitude range 316–3,580 m asl, were employed in this study (*see Fig. 1* for station locations). Livingstone and Lotter (1998) showed that a composite mean air temperature series derived from measurements made at four meteorological stations (Basel-Binningen, Neuchâtel, Zürich-MZA, and Bern-Liebefeld) reflects the air temperature of the entire Swiss Plateau very well. Based on this composite series, the summer of 2000 (June–August) was the 25th warmest of the period 1901–2004, and lay within one standard deviation of the long-term mean. Thus, although the period of deployment of the thermistors in summer 2000 was warmer than average, it was not climatically extreme.

Results

Regional coherence of lake surface water temperature—An intrinsic property of any mountainous region is its morphological heterogeneity, so that mountain lakes within one geographical region can be exposed to very varied local meteorological forcing. It cannot therefore be assumed a priori that LSWT will respond coherently to regional-scale climatic forcing. In addition to heterogeneity in local weather, depending on the altitude and aspect of a lake's catchment area (which determine the duration of snow cover in summer), and the presence or absence of perennial glaciers in it, the lake can be fed by waters close to 0°C during much of the summer, further complicating the chain of cause and effect linking the LSWT to climatic forcing and tending to introduce further spatial heterogeneity into the pattern of response. Despite this, it is known that the surface temperatures of lakes throughout the European Alpine region, including several high-altitude alpine lakes, exhibit a high degree of regional coherence in both the short and long term and are highly correlated with regional air temperature (Livingstone and Lotter 1998; Livingstone et al. 1999; Livingstone and Dokulil 2001). During summer 2000, short-term temporal variability in daily mean LSWT was indeed very similar throughout the central Swiss Alps even between lakes with a vertical separation of as much as 2,000 m (Fig. 2a) and reflected the general temporal pattern present in the air temperatures that were measured simultaneously throughout the region (Fig. 2b).

Rather than calculating full correlation matrices—a rather unwieldy tool for 29 lakes—the approach of Livingstone and Dokulil (2001) was used to quantify the degree of short-term regional coherence exhibited by the LSWT of any one lake

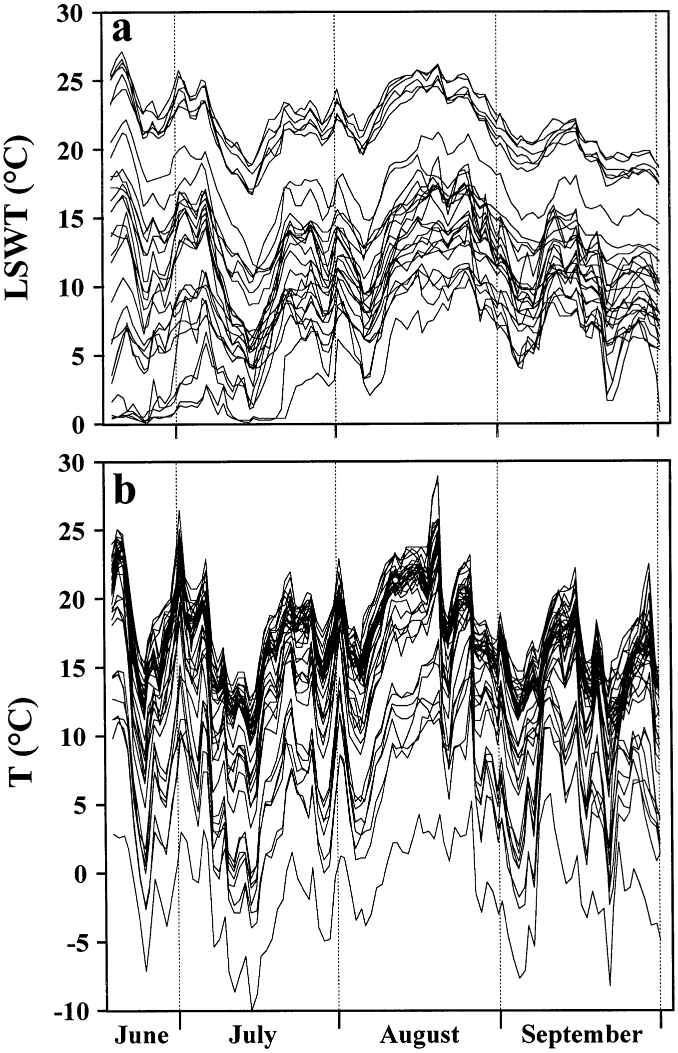

Fig. 2. (a) Daily mean lake surface water temperatures (LSWT, actually measured at 5 cm depth) of 29 Swiss lakes located between 465 and 2,470 m asl, from 19 June to 1 October 2000. (b) Simultaneously measured daily mean surface air temperatures (T) at 40 Swiss meteorological stations located between 316 and 3,580 m asl. *See Table 1* for information on the lakes, and *see Fig. 1* for the locations of the lakes and meteorological stations.

for each month from July to September 2000. For each of the 29 lakes, two time series were constructed for each month by linearly detrending both the time series of the LSWT of the lake concerned and the mean time series of the LSWTs of the other 28 lakes. Pairwise coefficients of determination (r^2, expressed as a percentage) were then calculated between these two time series, giving a measure of the proportion of variance shared pairwise between each detrended LSWT series and a general detrended regional LSWT series that did not include any information from the lake being assessed. Detrending the monthly series effectively removes longer term (e.g., seasonal) effects that introduce autocorrelation into the time series, so that the resulting r^2 values reflect only short-term coherence. The results show regional coherence to have been high throughout the summer, with $p < 0.001$ and $r^2 > 40\%$ at all altitudes in all months (Fig. 3). As the summer progressed, the coherence underwent only a slight general decrease, with mean r^2 values declining from 88.7% in July to 87.4% in August and 82.7% in September.

However, although coherence was high at all altitudes, some altitudinal dependence was evident at the beginning of the study period. In July, regional coherence was high ($r^2 >$ 80%) for all lakes below 2,300 m asl, but substantially lower for four of the five lakes located above 2,300 m asl. By August, coherence had increased considerably at the highest altitudes but decreased somewhat at lower altitudes, so that very little altitudinal dependence remained. By September, coherence at all altitudes had declined, but the magnitude of the decline exhibited no apparent altitudinal dependence. Thus, except in the very highest lakes in early summer, short-term regional coherence of LSWT is essentially independent of altitude.

Relationship between regional mean lake surface water temperature and smoothed regional mean air temperature—Many empirical studies have shown LSWT to be strongly related to ambient air temperature (e.g., McCombie 1959; Webb 1974; Shuter et al. 1983), and the existence of such a relationship has been confirmed for the lakes of the Swiss Alps (Lister et al. 1998; Livingstone and Lotter 1998; Livingstone et al. 1999). Air temperature exhibits a high degree of coherence throughout the European Alpine region (e.g., Livingstone and Lotter 1998; Livingstone and Dokulil 2001). Therefore, the regional coherence found in LSWT is likely to be associated with the regional coherence in air temperature. For the lakes dealt with in this study, the similarity of the LSWT and air temperature time series is obvious from Fig. 2, where short-term changes in regional air temperature are seen to be reflected almost immediately (usually within 1 d) in the LSWTs of all the lakes for which data are available. Because air temperatures in Switzerland are very highly coherent in the short term, variations in the regional air temperature are captured well by constructing a mean air temperature time series based on data from very few meteorological stations (Livingstone and Lotter 1998). Therefore, a mean air temperature time series based on the data from the 40 meteorological stations employed in this study can be assumed to reflect the regional air temperature extremely well. Similarly, because of the high degree of regional coherence exhibited by LSWT, a mean LSWT time series constructed by averaging over the 29 lakes of this study can be assumed to give a good measure of the common short-term response of LSWT to regional climatic forcing (as opposed to specifically local forcing). These two mean time series are highly correlated, with 70.6% shared variance (Fig. 4a). However, a certain degree of inertia is apparent in the response of LSWT to air temperature, which manifests itself in the lower variance shown by the LSWT series as compared with the air temperature series (Fig. 2). This suggests that the relationship may be improved by low-pass filtering the air temperature series, as demonstrated by Kettle et al. (2004) for lakes in Greenland. Kettle et al. (2004) suggest applying an exponential smoothing filter to the daily mean air temperature as follows:

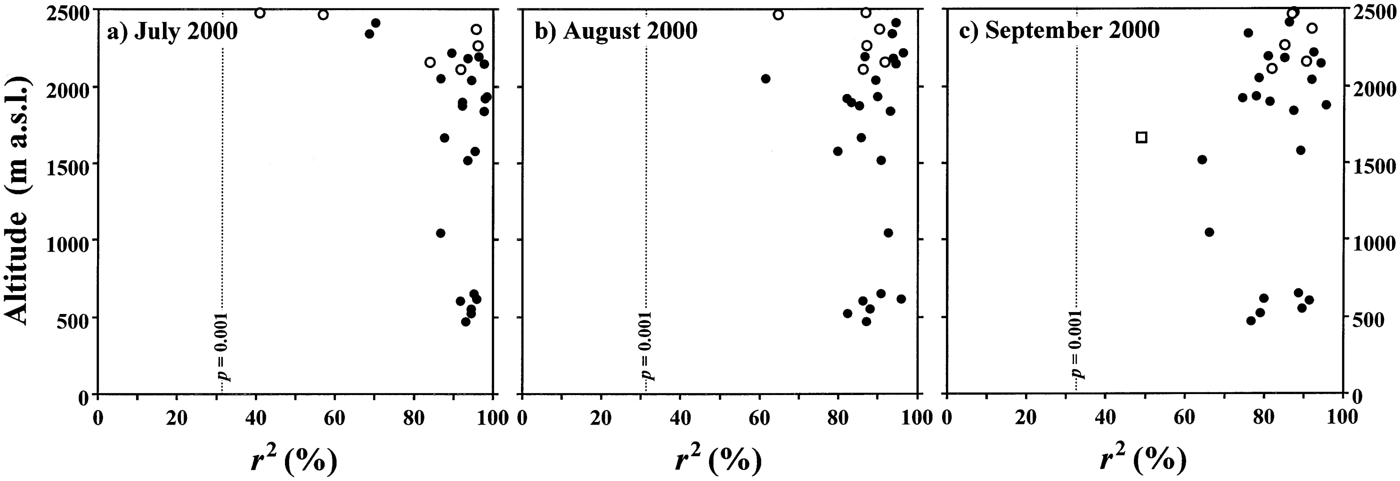

Fig. 3. Altitudinal dependence of regional coherence in lake surface water temperature (LSWT) exhibited by 29 lakes in the Swiss Alps in July, August, and September 2000. As a measure of short-term regional coherence exhibited by the LSWT of a particular lake in each month, pairwise coefficients of determination (r^2) were calculated between the linearly detrended time series of the LSWT of that lake and of the linearly detrended mean time series of the LSWTs of the other 28 lakes. The $p = 0.001$ significance level of the correlations is as shown. Lakes with glaciers in their catchment areas (Table 1) are denoted by open circles. The outlier in September (open square) is Oberstockensee, from which the thermistor was retrieved at 4 m depth (*see text*). *See Table 1* for information on the lakes, and *see Fig. 1* for their locations.

$$S_i = (1 - \alpha)S_{i-1} + \alpha T_i \qquad (1)$$

where S_{i-1} and S_i are the smoothed daily mean air temperatures on days $i - 1$ and i, respectively; T_i is the measured daily mean air temperature on day i; and α is the exponential smoothing coefficient, confined to the interval [0, 1]. Smoothing is absent at $\alpha = 1$ and increases to a maximum as $\alpha \rightarrow 0$. For the practical application of Eq. 1, S_1 was set to T_1 and the first 5 d of smoothed values were neglected (because of the transient effects of filtering at the beginning of a data series). The value of α that optimized the proportion of shared variance r^2 between the smoothed mean air temperature time series S and the mean LSWT time series was 0.33. Using this value for α resulted in an increase in r^2 from 70.6% (Fig. 4a) to 88.3% (Fig. 4b). The value chosen for α was not critical, however, and any value between 0.23 and 0.50 resulted in an r^2 value exceeding 85%. The cross correlation function of S and the mean LSWT time series had its maximum at zero lag, so at the level of resolution employed here (1 d) it was not necessary to include an explicit time delay in the model. The mean age of the measured air temperature data T incorporated into the smoothed air temperature data S, given by $1/\alpha$, is 3 d.

The regression of LSWT on S illustrated in Fig. 4b was employed to estimate the mean LSWT time series, and the results compared with the measured data (Fig. 5). This figure confirms that the temporal structure of the regional mean LSWT time series is almost identical to that of the smoothed regional mean air temperature time series S, underlining the strength of the empirical link between air temperature and LSWT. The overall root mean square difference (RMSD) between the measured and estimated LSWT time series was 0.76 K (24 June–1 October). However, the RMSD increased from 0.51 K in July to 0.71 K in August and 0.82 K in September, implying that the strength of the link between LSWT and air temperature decreases somewhat as summer wears on.

Air temperature lapse rates—In summer, air temperatures measured near the land surface in mountain regions decrease approximately linearly with altitude (Tabony 1985; Barry 1992). The magnitude of this decrease, the surface air temperature lapse rate (or apparent lapse rate), is similar to the adiabatic lapse rate of moist air in the free atmosphere, which is ~6 K km^{-1} (Tabony 1985). Based on the data from the same 40 meteorological stations that supplied data to the present study, Livingstone et al. (1999) calculated monthly mean surface air temperatures as a function of altitude above sea level for summer and early autumn 1997. They found the surface air temperature to have decreased linearly with altitude at lapse rates of 6.0 K km^{-1} (July 1997), 5.7 K km^{-1} (August 1997), and 4.1 K km^{-1} (September 1997). Data from summer 2000 confirmed that the surface air temperature had exhibited a uniform linear decrease with increasing altitude during the period of deployment of the thermistors (Table 2; Fig. 6). In this case, the mean lapse rates obtained for July 2000 (6.1 K km^{-1}) and August 2000 (5.6 K km^{-1}) were almost identical to those obtained for the corresponding months in 1997. However, the mean lapse rate obtained for September 2000 (5.1 K km^{-1}) differed substantially from that obtained for September 1997, owing mainly to a difference in the frequency of temperature inversions, which began to affect lapse rates in September (Livingstone et al. 1999). No evidence was found of any alteration in the magnitude of the lapse rate from low to high altitudes.

For each individual day from 19 June to 1 October 2000, a linear regression of air temperature on altitude was conducted. All 105 daily regressions were significant at the $p < 0.001$ level, and the mean proportion of variance ex-

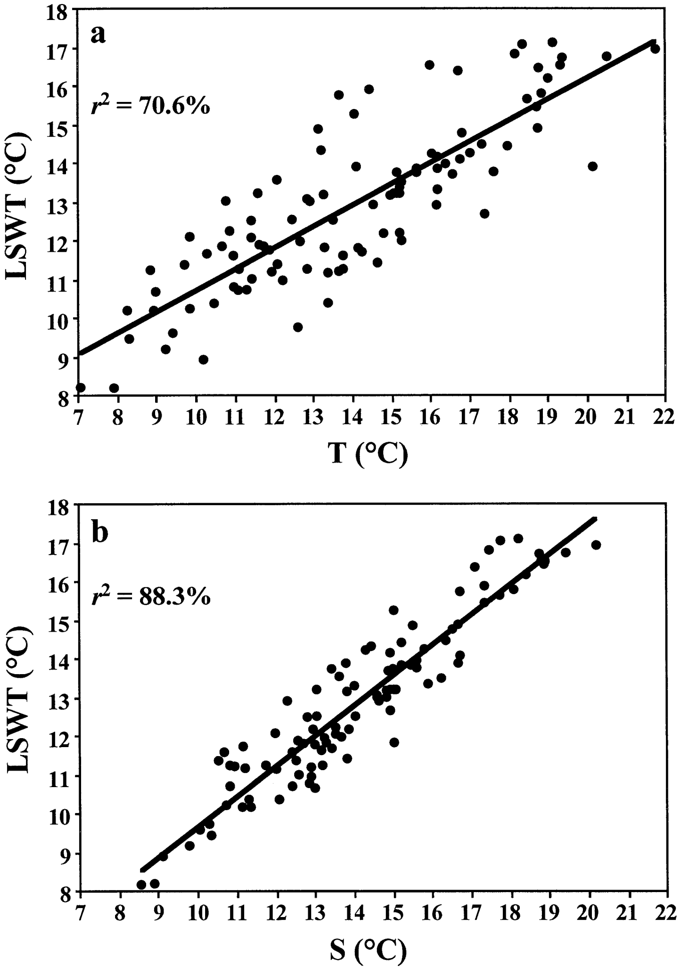

Fig. 4. Linear regressions of regional mean lake surface water temperature (LSWT) (a) on unsmoothed regional mean air temperature (T) and (b) on exponentially smoothed regional mean air temperature (S), smoothed using Eq. 1 with $\alpha = 0.33$. Both regressions are significant at the $p < 0.001$ level. The regional mean LSWT and air temperature series were computed from daily mean temperature data from 29 lakes (Table 1; Fig. 1) and 40 meteorological stations (Fig. 1) from 19 June to 1 October 2000.

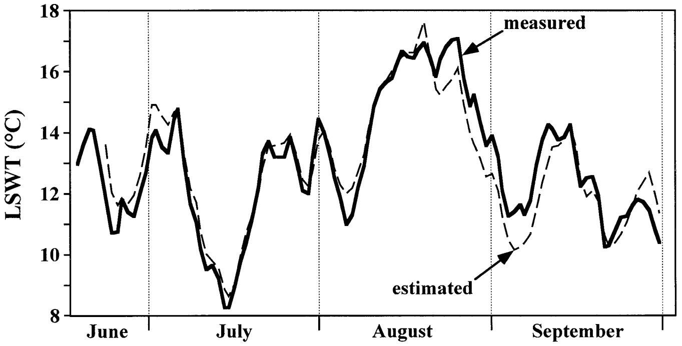

Fig. 5. Comparison of estimated and measured values of regional mean lake surface water temperature (LSWT). The measured regional mean LSWT was computed as the arithmetic mean LSWT of 29 lakes (Table 1; Fig. 1). The estimated LSWT was obtained from the smoothed regional mean air temperature S (Eq. 1, $\alpha = 0.33$) by linear regression (Fig. 4b).

plained was 94% (Fig. 7a). The gradient (the surface air temperature lapse rate) and the 2,000-m intercept (the estimated air temperature at 2,000 m asl) calculated for each day (Fig. 7b,c) could then be employed to provide an accurate estimate of the air temperature time series over the entire study period at any given altitude. The accuracy of the estimates was confirmed by computing estimated air temperature time series for the altitudes of the 40 meteorological stations that had provided the original air temperature measurements and comparing the estimated time series with the measured time series. In all cases, the proportion of shared variance lay between 92% and 99%, and the RMSD between the measured and estimated time series lay between 0.4 K and 2.0 K, with a mean RMSD of 0.9 K. No significant linear trend in RMSD with altitude was found ($n = 40$, $r^2 = 2.5\%$, $p > 0.1$), so the estimates at high altitudes are as accurate as those at lower altitudes. During the entire study period, estimated daily mean air temperatures below 2,000 m asl always exceeded 0°C (Fig. 7d).

Lake surface water temperature lapse rates at low and high altitudes—Although air temperature decreases at one

Table 2. Comparison of linear regressions of monthly mean air temperature and lake surface water temperature (LSWT) on altitude above sea level. The air temperature regressions covered the entire altitude range from 316 to 3,580 m asl (Fig. 6), whereas the LSWT regressions were carried out for low-altitude lakes (<2,000 m asl) and high-altitude lakes (>2,000 m asl) separately (Fig. 10). The coefficient of determination (r^2) gives the proportion of variance explained by the relevant linear regression, the lapse rate is the rate of decrease of temperature with increasing altitude (CI = confidence interval), and the 2,000-m intercept is the estimated temperature at 2,000 m asl.

	Air temperature			LSWT (lakes <2,000 m asl)			LSWT (lakes >2,000 m asl)		
	July	August	September	July	August	September	July	August	September
Number of data points	40	40	40	15	15	15	14	14	14
Coefficient of determination (r^2) (%)	98	98	97	91	91	89	38	30	26
Significance level	$p<0.001$	$p<0.001$	$p<0.001$	$p<0.001$	$p<0.001$	$p<0.001$	$p<0.05$	$p<0.05$	$p<0.1$
Altitudinal dependence	strong	strong	strong	strong	strong	strong	weak	weak	very weak
Lapse rate (K km^{-1})	6.1	5.6	5.1	7.1	7.1	6.5	12.6	8.7	5.4
Lapse rate, 95% CI (K km^{-1})	0.3	0.3	0.3	1.3	1.3	1.3	10.1	8.4	5.8
2,000-m intercept (°C)	7.2	10.9	7.5	11.1	13.0	10.4	10.2	13.3	10.2
2,000-m intercept, 95% CI (°C)	0.4	0.3	0.4	1.3	1.3	1.3	2.8	2.4	1.6

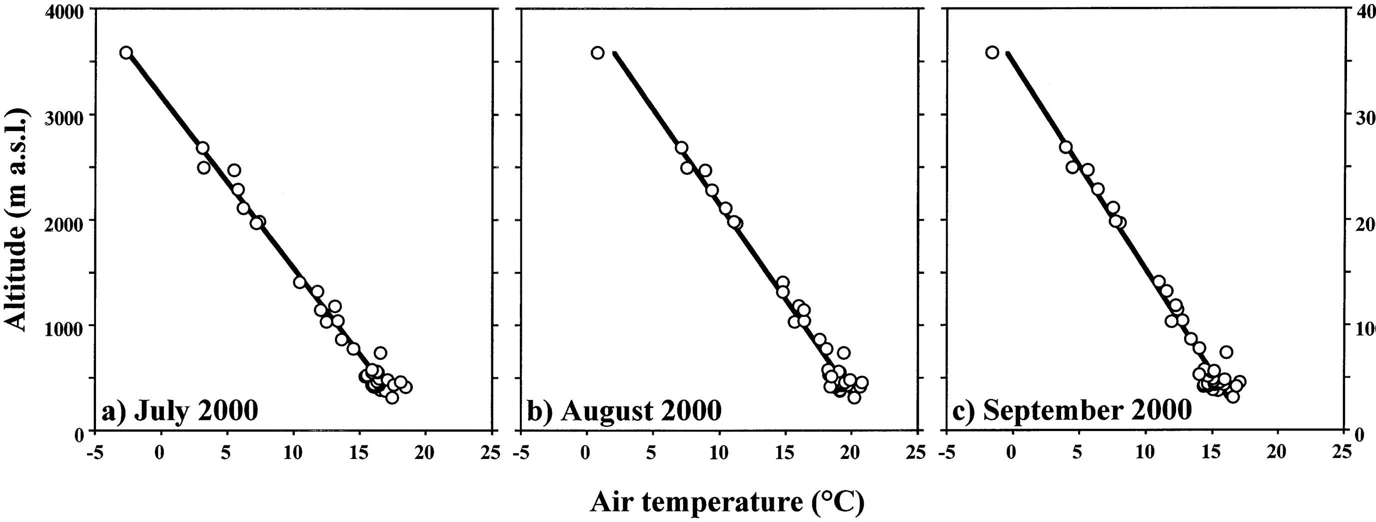

Fig. 6. Linear decrease in monthly mean air temperature in Switzerland with altitude above sea level in July, August, and September 2000. The monthly mean air temperatures (open circles) were measured at the 40 meteorological stations of Fig. 1. The regression lines shown are significant at the $p < 0.001$ level. *See Table 2* for further details of the regressions.

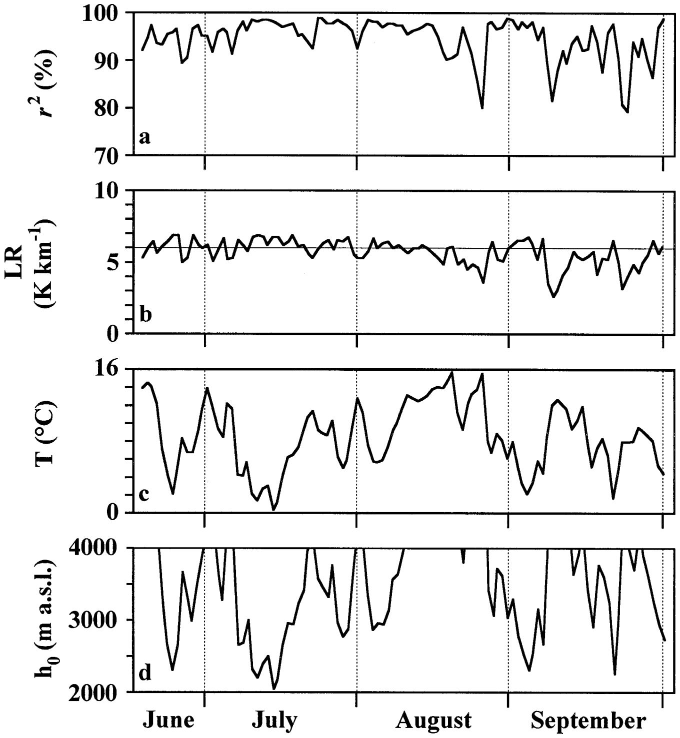

Fig. 7. Results of 105 linear regressions of daily mean air temperature on altitude, 19 June–1 October 2000. (a) Proportion of variance explained (r^2). (b) Computed surface air temperature daily lapse rates (LR). The adiabatic lapse rate for moist air in the free atmosphere (~6 K km^{-1}, Tabony 1985) is given by the thin horizontal line. (c) The 2,000-m intercept (i.e., computed air temperature T at 2,000 m asl). (d) The computed altitude of the 0°C isotherm (h_0). All regressions are significant at the $p < 0.001$ level. Air temperature measurements were supplied by the 40 meteorological stations of Fig. 1.

constant rate with altitude, it is clear by inspection that this is not necessarily true of LSWT (Fig. 8). In contrast to air temperature, a simple linear regression therefore does not suffice to describe the altitudinal dependence of LSWT in all summer months. Instead, the behavior of lakes at higher and lower altitudes can differ in some months, with the former often exhibiting a substantially higher LSWT lapse rate than the latter. To take account of this difference and to determine objectively the altitude of the hinge point or threshold at which the change in behavior of LSWT most likely occurs, a two-component linear model with a common but unknown hinge point was formulated and applied to the data in 10-d time windows. Beginning at the lowest altitude lakes, the group of 29 lakes was split successively into a low-altitude and a high-altitude subgroup, each of which was then described by a linear model. The equations of the two models were given by joining the centroid of each subgroup to the common, unknown hinge point (equivalent to forcing a linear regression through a given, but unknown, point). The optimal subgroup division and the coordinates of the optimal hinge point (its altitude and its corresponding LSWT) were determined objectively by minimizing the RMSD between the measured and modeled LSWTs. The results, an example of which is illustrated in Fig. 8, showed that the altitude of the hinge point increased from 1,875 m asl at the end of June to 2,177 m asl at the end of July. At the beginning of August, the linear models above and below the theoretical hinge point became practically indistinguishable from one another, so that a simple linear regression model covering all altitudes within the data set suffices for August and September.

To investigate further the existence of a difference in the altitudinal dependence of LSWT below and above an assumed threshold located between 1,875 and 2,177 m asl, i.e., at ~2,000 m asl, traditional linear regressions of daily mean LSWT on altitude were computed for each day of the study period, treating the 15 low-altitude lakes located below 2,000

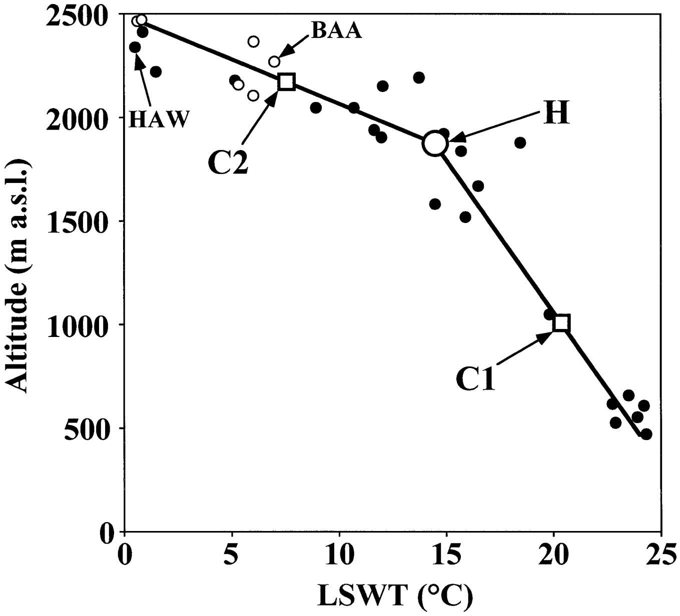

Fig. 8. Example of the pronounced difference between the rate of decline of lake surface water temperature (LSWT) with altitude prevailing at high and low altitudes (for the 10-d period 19–28 June 2000). Also shown is the two-component linear model with common hinge point constructed to characterize this difference, as described in the text. The small circles represent 10-d mean measured LSWTs of the 29 study lakes (open and filled circles denote, respectively, lakes with and without glaciers in their catchment areas). C1 and C2 are the centroids of the low-altitude and high-altitude subgroups that are defined by the altitude of the optimum hinge point H. The two-component linear model is defined by the straight lines joining H to C1 and C2, whereby the coordinates of H are determined objectively by minimizing the root mean square difference between measured and modeled LSWTs. Hagelseewli (HAW) is subject to local topographic shading, whereas Bachsee (BAA), a lake adjacent to Hagelseewli, is not. *See Table 1* for information on the lakes, and *see Fig. 1* for their locations.

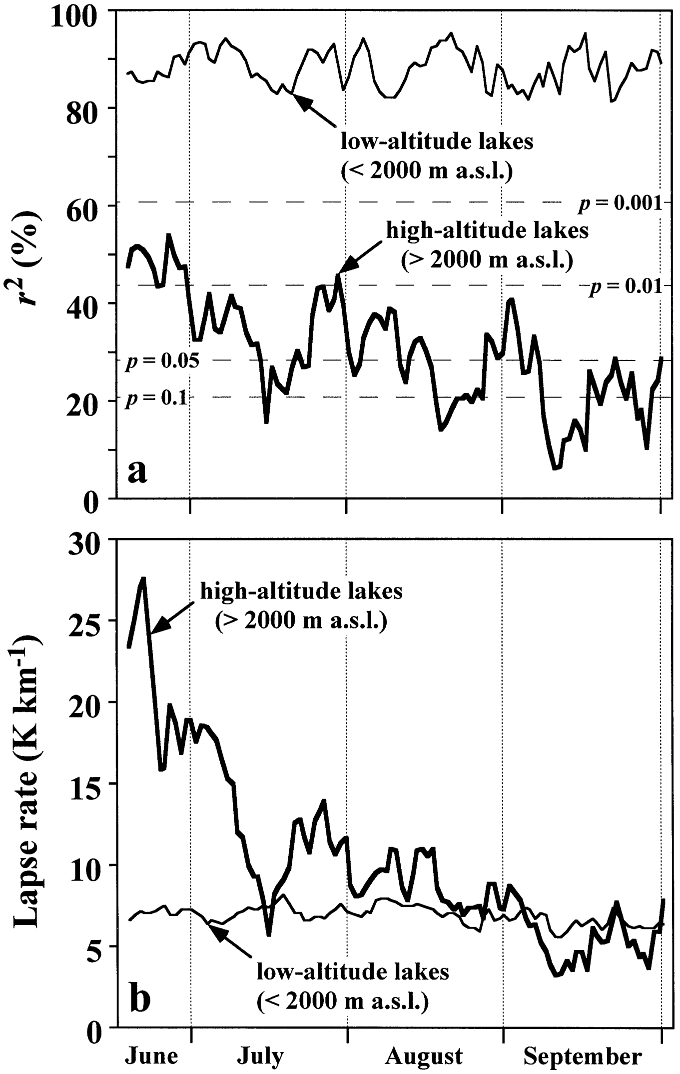

Fig. 9. Results of linear regressions of 105 sets of daily mean lake surface water temperature (LSWT) on altitude for 29 lakes in the Swiss Alps, 19 June–1 October 2000. The regressions were computed separately for 15 low-altitude (<2,000 m asl) and 14 high-altitude (>2,000 m asl) lakes. (a) Proportion of variance explained (r^2), with significance levels. (b) Computed daily LSWT lapse rates, i.e., the rate of decrease of LSWT with increasing altitude above sea level. *See Table 1* for information on the lakes, and *see Fig. 1* for their locations.

m asl and the 14 high-altitude lakes located above 2,000 m asl separately (hereafter, low-altitude refers to <2,000 m asl and high-altitude to >2,000 m asl). Within the group of low-altitude lakes, the altitudinal dependence of LSWT is consistently strong throughout the entire study period, with a highly significant linear relationship ($p < 0.001$) and over 80% variance explained by each of the 105 daily regressions (Fig. 9a). The lapse rates for the low-altitude lakes vary little about a mean value of 6.9 K km^{-1} during the study period (Fig. 9b), exceeding the corresponding mean surface air temperature lapse rate (5.7 K km^{-1}, Fig. 7b) by 1.2 K km^{-1}. Among the high-altitude lakes, however, the linear dependence of LSWT on altitude is much weaker, with only 30% shared variance on average during the study period. In addition, the proportion of shared variance does not remain constant, as it does for the lower altitude lakes, but exhibits a continual decline from over 50% at the end of June to below 30% in September (Fig. 9a). Despite this, however, the regression is still statistically significant at the $p < 0.05$ level on 98 of the 105 d. The lapse rates of the high-altitude lakes differ considerably in their behavior from those of the low-altitude lakes (Fig. 9b). They decline rapidly in June and July from very high values (over three times the corresponding values for the low-altitude lakes) to attain values in August that are comparable with, but still slightly greater than, those of the low-altitude lakes. During August and September, the decline is more gradual, but sufficient to result in a situation in September in which the lapse rates of the high-altitude lakes begin to fall below those of the low-altitude lakes.

To illustrate the change in LSWT lapse rate from low-altitude to high-altitude lakes more clearly, Fig. 10 shows the altitudinal dependence of LSWT for each month separately, including separate linear regressions for the low-al-

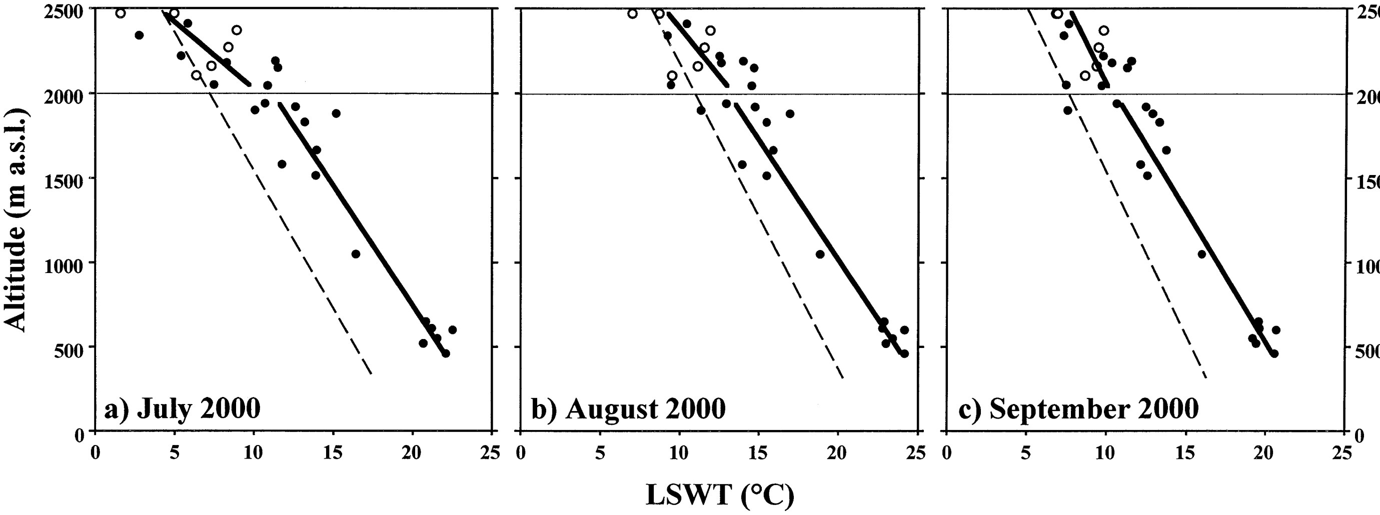

Fig. 10. Altitudinal dependence of monthly mean lake surface water temperature (LSWT) exhibited by 29 lakes in Switzerland (Table 1; Fig. 1) in July, August, and September 2000. Solid lines: linear regressions of LSWT on altitude for lakes below and above 2,000 m asl (thin horizontal line). Dashed lines: linear regression of air temperature on altitude (Fig. 6) for comparison purposes. Details of the regressions are given in Table 2. *See Table 1* for information on the lakes, and *see Fig. 1* for their locations. Lakes with glaciers in their catchment areas (Table 1) are denoted by open circles.

titude and high-altitude lakes, and also including, for comparison purposes, the air temperature regression lines of Fig. 6. In Table 2, selected statistics summarizing the monthly regressions are compared. For the low-altitude lakes, the altitudinal dependence of the monthly mean LSWT is strong in all three months, with a highly significant linear relationship and a high proportion of variance explained (Table 2). In all three months, the monthly mean LSWT of any low-altitude lake is almost always substantially higher than the monthly mean air temperature at the same altitude (Fig. 10). For the high-altitude lakes, the linear dependence of LSWT on altitude is much weaker, with a lower degree of statistical significance and a much lower proportion of shared variance (Table 2). The high-altitude LSWTs still tend to lie above the equivalent air temperatures, but, especially in July and to a lesser extent in August and September, the discrepancy is much less than in the case of the low-altitude lakes (Table 3). In all three months, LSWT lapse rates for both low-altitude and high-altitude lakes exceed air temperature lapse rates. High-altitude LSWT lapse rates exceed low-altitude LSWT lapse rates in July and August, but not in September (Table 2; Fig. 10).

Altitudinal dependence of the strength of the relationship between lake surface water temperature and smoothed regional air temperature—Because air temperature decreases uniformly with increasing altitude during the entire study period but LSWT does not, a change in the relationship between LSWT and air temperature must occur close to the altitude of the threshold. That the intercept in the relationship between LSWT and air temperature (i.e., the discrepancy between LSWT and air temperature) decreases with increasing altitude above ~2,000 m asl is clear from Fig. 10 and Table 2. Of more interest in this context is whether the strength of the relationship also changes at high altitudes, i.e., whether the LSWT of high-altitude lakes is as strongly related to air temperature as the LSWT of low-altitude lakes. The significance of this lies in the use of high-altitude lakes as particularly sensitive indicators of climate change (e.g., Koinig et al. 1998; Battarbee et al. 2002; Catalan et al. 2002).

The daily regression coefficients describing the dependence of daily mean air temperature on altitude (Fig. 7b,c) were used to compute air temperature time series for the altitudes of each of the 29 lakes, thus allowing the relation-

Table 3. Monthly mean lake surface water temperatures (LSWT), air temperatures (T), and the discrepancy between the two (ΔT = LSWT − T), interpolated at various altitudes using the regression equations detailed in Table 2 and illustrated in Fig. 10.

	Based on equation for lakes <2,000 m asl												Based on equation for lakes >2,000 m asl					
	500 m asl			1,000 m asl			1,500 m asl			2,000 m asl			2,000 m asl			2,500 m asl		
	LWST (°C)	T (°C)	ΔT (°C)	LWST (°C)	T (°C)	ΔT (°C)	LWST (°C)	T (°C)	ΔT (°C)	LWST (°C)	T (°C)	ΔT (°C)	LWST (°C)	T (°C)	ΔT (°C)	LWST (°C)	T (°C)	ΔT (°C)
July 2000	21.6	16.4	5.3	18.1	13.3	4.8	14.6	10.2	4.4	11.1	7.2	3.9	10.2	7.2	3.1	3.9	4.1	−0.2
August 2000	23.6	19.2	4.4	20.1	16.4	3.7	16.6	13.6	2.9	13.0	10.9	2.2	13.3	10.9	2.4	8.9	8.1	0.9
September 2000	20.1	15.2	4.9	16.9	12.7	4.2	13.6	10.1	3.5	10.4	7.5	2.9	10.2	7.5	2.7	7.5	5.0	2.5

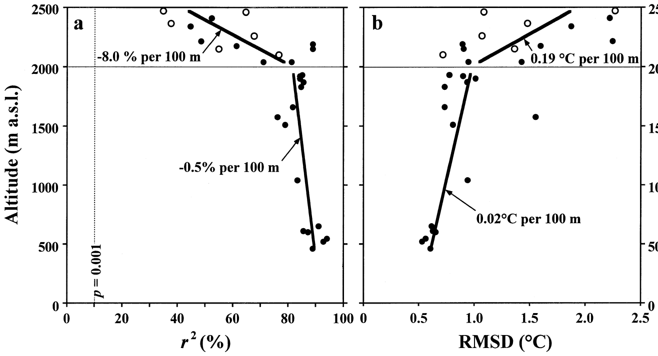

Fig. 11. Altitudinal dependence of the strength of the relationship between lake surface water temperature (LSWT) and smoothed air temperature (*S*) in the Swiss Alps. (a) Coefficient of determination (r^2) between LSWT and *S*, with $p = 0.001$ significance level. (b) Root mean square difference (RMSD) between the measured LSWT series and the LSWT series estimated from *S* by linear regression. All series were linearly detrended to remove seasonal effects prior to computing the regressions, which covered the period from 19 June to 1 October 2000. The straight lines shown are additional linear regression lines of r^2 and RMSD on altitude, for lakes below and above 2,000 m asl (thin horizontal line). These linear regressions are significant at the $p < 0.01$ level for r^2 and the $p < 0.1$ level for RMSD; the gradients of the four regression lines are as shown. *See Table 1* for information on the 29 lakes, and *see Fig. 1* for their locations. Lakes with glaciers in their catchment areas (Table 1) are denoted by open circles.

ship between LSWT and air temperature to be investigated for each lake individually. From the above description of the relationship between regional mean LSWT and regional air temperature, the importance of smoothing the air temperature series before attempting to model LSWTs has clearly emerged (Fig. 5). Each of the 29 air temperature time series was therefore smoothed using Eq. 1. Two approaches were employed: (1) smoothing was conducted using a constant value $\alpha = 0.33$ for the smoothing coefficient, and (2) an optimal value for α was determined for each lake separately by maximizing the proportion of LSWT variance for the lake (r^2) that was explained by the relevant smoothed air temperature time series. Smoothing using a constant value of 0.33 for α increased the mean proportion of LSWT variance explained (the mean r^2 over the 29 lakes) from 55.8% (no smoothing) to 72.6%. Smoothing using individually determined values of α resulted in only a slight further improvement to 74.8%, confirming that the exact value of α is not critical. Thus, for the sake of generality, all smoothing was conducted with $\alpha = 0.33$.

After linear detrending to reduce the effects of seasonal variation, pairwise linear regressions were computed between the LSWT series and the smoothed air temperature series (*S*). For all 29 lakes, the linear relationship found between the detrended LSWT and *S* series was highly significant ($p < 0.001$). For each lake, the proportion of shared variance (r^2) was plotted against altitude (Fig. 11a). A distinct decrease in r^2 with increasing altitude is apparent over the whole range of altitudes, but the magnitude of the rate of decrease is substantially higher above 2,000 m asl (-8.0% per 100 m) than below 2,000 m asl (-0.5% per 100 m). The linear regression equations were then used to obtain a time series of estimated LSWT values for each lake from the smoothed air temperature series, and the RMSD between the estimated and measured values computed and plotted against altitude (Fig. 11b). Again, a distinct altitudinal dependence is apparent over the whole range of altitudes, but with a substantial difference between the mean rate of increase in RMSD above 2,000 m asl (0.19 K per 100 m) and below 2,000 m asl (0.02 K per 100 m).

The empirical relationship between LSWT and air temperature is therefore strongest at the lowest altitudes (~500 m asl), becoming gradually weaker with increasing altitude up to ~2,000 m asl. At ~2,000 m asl the relationship suddenly begins to worsen rapidly, weakening much faster with increasing altitude above ~2,000 m asl, so that the proportion of shared variance for lakes at ~2,500 m asl is only about half that for lakes at ~500 m asl, and the RMSD between estimated and measured LSWTs is approximately three times more (Fig. 11). While 12 of the 15 low-altitude lakes have both $r^2 > 80\%$ and RMSD < 1 K, this is true of only 2 of the 14 high-altitude lakes.

Discussion

During summer and early autumn in the Swiss Alps, surface air temperature clearly decreases linearly with increasing altitude over the entire range of altitudes for which data are available (Fig. 6), allowing the decrease on any one day to be characterized by a lapse rate that is essentially invariant with altitude (Fig. 7b). This does not apply to LSWT, for which two distinct altitudinal regimes appear to exist, each with its own LSWT lapse rate (Fig. 9b). In early summer 2000 (June and July), the threshold between these regimes lay at ~2,000 m asl, but as summer progressed, the threshold rose continually, so that by August 2000 it had risen above the highest lakes in the data set employed here, i.e., to above ~2,500 m asl. Expressed in terms of time rather than altitude, the high-altitude lakes can be thought of as lagging the low-altitude lakes seasonally.

Within the low-altitude regime (i.e., below ~2,000 m asl in early summer 2000 and below ~2,500 m asl in late summer 2000), LSWT can be modeled empirically very well as a linear function of smoothed air temperature, with over 80% variance explained (Fig. 11a). Like air temperature, LSWT decreases linearly with increasing altitude (Fig. 10), but its lapse rate exceeds that of air temperature by 16–28% (Table 2). Despite the gradual convergence of LSWT and air temperature with increasing altitude apparent in Fig. 10, the LSWT of a given low-altitude lake almost always remains substantially above the air temperature computed for the altitude of that lake. The results for the low-altitude regime confirm those of the previous studies of Livingstone and Lotter (1998) and Livingstone et al. (1999), who have discussed and explained them in detail. Briefly, the altitudinal decrease in LSWT is governed predominantly by the altitudinal decrease in the theoretical lake surface equilibrium temperature (LSET), to which the LSWT tends exponentially. The LSET, introduced by Edinger et al. (1968) to explain how water temperatures respond to meteorological forcing, is defined as the LSWT at which the computed net heat flux across the air–water interface is zero (Edinger et al. 1968; Dingman 1972). In addition to air temperature, only three other meteorological variables (cloud cover, wind speed, and relative humidity), and one essentially astronomical variable (clear-sky solar radiation), govern the LSET of most lakes (Edinger et al. 1968; Sweers 1976; Livingstone and Imboden 1989). Of these five variables, air temperature shows the strongest altitudinal dependence, implying that the vertical decrease in LSET is governed primarily by the vertical decrease in air temperature (although, as shown by Beniston et al. 1994 and Blumthaler et al. 1996, the attenuation of solar radiation by cloud cover in the Alps also exhibits some altitudinal dependence). Computations by Kuhn (1977) for the Swiss Alps indicate that the LSET, like air temperature, decreases linearly with increasing altitude. Various studies have shown that temperature measurements in Swiss lakes can be explained well using the equilibrium temperature concept (Marti and Imboden 1986; Livingstone and Imboden 1989; Gabathuler 1999), and according to Arai (1981) summer LSWTs generally coincide quite well with corresponding LSETs. Thus, the decrease in LSWT with altitude in the Swiss Alps—and presumably in other mountain regions—is also expected to be approximately linear. Within the low-altitude regime, the LSWT measurements conform to these theoretical expectations, since there are very few complicating factors to disrupt a direct empirical dependence of LSWT on air temperature or LSET. At no time during early summer (19 June–31 July) did the hourly LSWT ever fall below 4.5°C in any of the 15 low-altitude lakes, implying that none of these lakes experienced either ice cover or inverse stratification. In addition, none of the low-altitude lakes have glaciers in their catchment areas (Table 1), so their LSWTs were not affected by glacial meltwater. The only complicating effect that cannot be entirely ruled out for the low-altitude lakes is that of meltwater from old snow. Although the 0°C surface air temperature isotherm always lay above 2,000 m asl during early summer, implying that no new snow fell close to any of the low-altitude lakes (Fig. 7d), pockets of old snow persist in the higher parts of mountainous catchment areas well into early summer (from Table 1, only 7 of the 15 low-altitude lakes have catchment areas that lie wholly below 2,000 m asl).

Within the high-altitude regime (i.e., above ~2,000 m asl in early summer 2000 and above ~2,500 m asl in late summer 2000), the situation is more complex. Although the LSWT also exhibits a linear decrease with increasing altitude in the high-altitude regime, its altitudinal dependence is weaker and its lapse rate substantially higher than in the low-altitude regime. The difference between the low-altitude and high-altitude regimes must therefore reflect an altitudinally dependent difference in the processes governing the response of LSWT to climatic forcing. Of the various possible hypotheses that can be advanced to explain this, several can be rejected immediately based on the available data:

(1) Partial ice cover. In some high mountain lakes, ice and open water coexist for several weeks during the thawing period or even during the whole summer (Livingstone et al. 1999; Goudsmit et al. 2000; Ohlendorf et al. 2000). This essentially decouples the LSWT from the ambient air temperature because any heat input to the lake is used to melt the remaining ice rather than to increase the LSWT. However, 9 of the 14 high-altitude lakes had LSWTs that exceeded 1°C at all times during the study period (Fig. 2) and were therefore ice free. Thus, of the lakes in the data set, partial ice cover can have affected the LSWT only of five of the very highest of the high-altitude lakes.

(2) Local topographic shading. The blocking of incident solar radiation by local topography is known to depress the LSWT of Hagelseewli, the fifth highest lake in the current data set, which lies in the shadow of a steep cliff immediately to the south of the lake (Livingstone et al. 1999; Goudsmit et al. 2000; Ohlendorf et al. 2000). The sixth highest lake in the current data set, Bachsee (2,265 m asl), is located only 1 km from Hagelseewli (Fig. 1) but is not shaded by a cliff. However, its LSWT behaves like that of the other high-altitude lakes and not like that of the low-altitude lakes (Fig. 8). Thus, although the LSWT of Hagelseewli is consistently considerably lower than that of Bachsee, indicating that the effect of local topographic shading (which is often coupled with partial ice cover) cannot always be ignored, it cannot explain the general difference between the low-altitude and high-altitude thermal regimes.

(3) Glaciers in the catchment area. Although 6 of the 14 high-altitude lakes have glaciers in their catchment areas, 8 do not (Table 1). From Figs. 3, 8, 10, and 11, no difference is apparent in the behavior of the LSWTs of high-altitude lakes with and without glaciers in the catchment area.

(4) Morphometric effects. There is no detectable decrease (t-test, $p < 0.1$) in the ratio of lake surface area to catchment area (Table 1) from low-altitude to high-altitude lakes that might make low-altitude lakes more vulnerable to catchment effects (e.g., meltwater) than high-altitude lakes. In addition, the effect of removing shallow ponds ($z_m \leq 2.5$ m) from the data set was found to be negligible: for July 2000, when the difference in LSWT lapse rate between the low-altitude and high-altitude regimes was greatest, removal of the shallow ponds increased the high-altitude lapse rate by only 0.1 K km^{-1} (from 12.6 K km^{-1} to 12.7 K km^{-1}).

Three plausible hypotheses remain that might explain the difference between the low-altitude and high-altitude thermal regimes, but none of these can be confirmed or rejected with certainty based on the currently available data.

(1) The first hypothesis is that the lakes of the warmer low-altitude regime are stably stratified, with a thin surface mixed layer that responds sensitively to climatic forcing. Under this hypothesis, thermal stratification in the lakes of the cooler high-altitude regime is weak or unstable, leading to a thick mixed layer, possibly encompassing the entire water column, that responds insensitively to climatic forcing.

(2) The second hypothesis is that the lakes of the warmer low-altitude regime are essentially unaffected by meltwater, whereas in the high-altitude regime inflowing meltwater from snow in the catchment area results in either a strengthening of inverse stratification or in cabbeling and an upward displacement of the thermocline.

(3) The third hypothesis is that the LSET, and hence the LSWT, is affected by differences in the amount and opacity of cloud cover at low and high altitudes, which are known

to occur in the Alps (e.g., Beniston et al. 1994; Blumenthaler et al. 1996). Measurements at meteorological stations in the Bernese Alps show that the mean relative sunshine duration during the period 19 June to 31 July 2000 decreased with increasing altitude from 45% at Interlaken (580 m asl) to 42% at Adelboden (1,325 m asl) and 40% at Jungfraujoch (3,580 m asl).

In the Swiss Alps, one of the primary responses of high-altitude lakes to climatic forcing—the response of LSWT to air temperature—has been shown here to differ substantially from that of lakes at lower altitudes during a large part of the biologically productive summer season. This has implications not only for the response of present-day mountain lake ecosystems to climatic forcing, but also for the study of the development of such aquatic ecosystems in relation to past and future climate change. Paleolimnological studies of lake sediments at remote high-altitude sites represent an important tool for the reconstruction of past climate history (e.g., Battarbee et al. 2002; Catalan et al. 2002). Empirical climate inference models based on biota–temperature relationships (e.g., Lotter et al. 1997; Heiri et al. 2003) are normally employed to carry out these reconstructions. In these models, the problem of the unrepresentative nature of infrequent spot LSWT measurements, especially at remote mountain lakes, is often circumvented by calibrating the models against summer air temperature instead of LSWT. However, because the form of the relationship between LSWT and summer air temperature changes close to the temporally variable threshold altitude, summer air temperature cannot be used as a direct surrogate for LSWT in this region. Even well within the high-altitude regime, the use of summer air temperature as a surrogate for LSWT is questionable because of the deterioration in the empirical relationship between the two temperatures apparent from Fig. 11. In fact, summer air temperature may not be the major factor controlling biota in high-altitude lake ecosystems at all. Instead, as shown by Lotter and Bigler (2000), factors such as the duration and extent of ice cover together with catchment-related features may exert the strongest influence on the occurrence and abundance of planktonic and benthic organisms in such lakes.

Paleolimnological studies of high-altitude lakes must also take account of long-term temporal changes in the threshold altitude and cannot assume that any given lake has always belonged to the altitude regime in which it is currently located. This implies additionally that the results of paleolimnological studies of high-altitude lakes cannot be directly extrapolated to future conditions without taking account of the possibility of an upward shift in the threshold altitude. A major future challenge for paleolimnologists may be to trace the location of the threshold in time as a climate proxy, analogous to the climate-dependent treeline ecotone. One possible effect of global warming might be to cause the difference between the LSWT lapse rates at low and high altitudes to be eradicated earlier in the summer than is now the case.

This study has demonstrated the existence of two distinct, altitudinally dependent, thermal regimes during part of the biologically productive summer season, in which lake surface water temperatures exhibit clearly differing responses to climatic forcing. Because lake biology is strongly dependent on the temperature prevailing in the upper layers of the water column, the results are potentially of great significance not only for explaining the response of high-altitude lake ecosystems to current climatic forcing, but, perhaps even more so, for interpreting the results of paleolimnological studies of high-altitude lake sediments aimed at reconstructing past climate history, and for predicting the impact of future climate change on high-altitude lakes.

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