

# Complex effects of winter warming on the physicochemical characteristics of a deep lake

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## *Abstract*

Recent winter warming over Central Europe associated with a positive phase of the North Atlantic Oscillation (NAO) strongly influenced the thermal and water column stability properties of deep Lake Constance ( $z_{\text{mean}} = 101$  m). Volumetrically weighted average water temperatures have increased since the 1960s by an average of  $0.017^{\circ}\text{C yr}^{-1}$ , and its interannual variability was strongly related to the variability in winter air temperature and the NAO winter index ( $\text{NAO}_w$ ). The influence of  $\text{NAO}_w$  on water temperature was more persistent than its influence on air temperature. The seasonal persistence of the  $\text{NAO}_w$  signal increased with water depth. Deep-water temperatures were related to the  $\text{NAO}_w$  from one spring mixing period to the next. This caused a time lag of 1 yr in the response of deep-water winter temperatures to the  $\text{NAO}_w$ . Reduced winter cooling during high- $\text{NAO}_w$  years resulted in the persistence of small temperature gradients that possibly resisted complete mixing. This, in turn, resulted in less upward mixing of nutrients (total phosphorus and total silica), which accumulated in the hypolimnion during the previous stratification period. A second effect of incomplete mixing was the lack of the replenishment of deep-water oxygen during high- $\text{NAO}_w$  years. Hence, besides its strong impact on the thermal regime, climate variability influenced both the causes (nutrient supply for phytoplankton growth) and symptoms (the degree of hypolimnetic oxygen deficiency) of trophic changes in Lake Constance.

During the past few decades, many large and deep Central European lakes have undergone strong eutrophication and subsequent oligotrophication (Sas 1989) as well as changes in temperature (Weyhenmeyer et al. 1999; Livingstone and Dokulil 2001; Livingstone 2003) associated with a positive phase of the North Atlantic Oscillation (NAO) (Hurrell 1995). The NAO is a large-scale fluctuation in the atmospheric pressure difference between the subpolar Icelandic low and the Azores high. Climatic conditions in Europe are influenced by the NAO predominantly during winter, when it is strongest and has the clearest teleconnections (Barnston and Livezey 1987). Hence, interannual variability in the NAO is usually expressed in terms of the winter NAO index ( $\text{NAO}_w$ ), which is the December through March average of standardized sea level pressure differences between Lisbon, Portugal, and Stykkisholmur/Reykjavik, Iceland (Hurrell 1995). The increased pressure difference during a positive phase of the NAO corresponds to more and stronger winter storms crossing the Atlantic Ocean, which results in high winter temperatures in western and northern Europe. A neg-

ative phase of the NAO is characterized by low pressure differences and results into colder-than-average winters (Hurrell 1995). The observed change in the NAO during past decades toward a more positive phase is suggested to be beyond natural variability and is likely due to increasing atmospheric gases (Gillett et al. 2003).

Several responses of freshwater ecosystems to NAO fluctuations have been documented (Straile et al. 2003). Surface temperatures in several lakes in Europe have been shown to be strongly related to the NAO (George et al. 2000; Straile and Adrian 2000; Livingstone and Dokulil 2001; Scheffer et al. 2001) and hence show a large degree of spatial coherence in winter and spring. In contrast to the impact of the NAO on the surface temperature of lakes, its effects on hypolimnetic temperatures are more variable (Gerten and Adrian 2001), and indirect effects of the NAO on the mixing intensity in lakes are not clear.

The spring mixing period in warm monomictic lakes is of central importance, because, during this period, nutrients that accumulate in the hypolimnion during the growing season are redistributed in the water column. Evidence from marine studies suggests that the NAO might affect mixing processes and, as a consequence, the supply of nutrients to surface waters (Oschlies 2001). Another important effect is on the downward transport of dissolved oxygen: Livingstone (1997) showed that reduced mixing in response to a series of warm winters severely reduced oxygen concentration in some Swiss lakes. Hence, changes in climate that affect mix-

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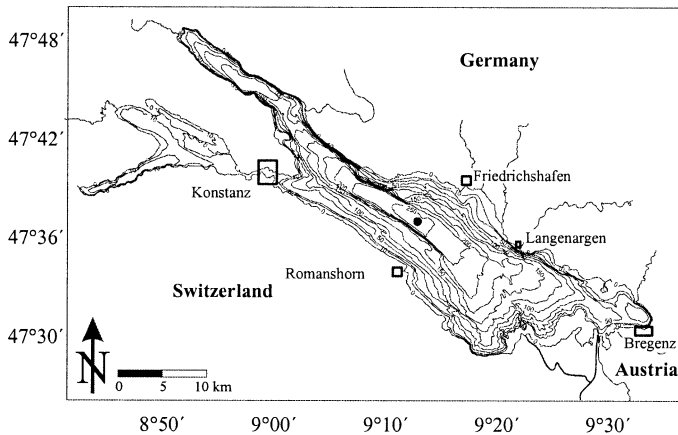


Fig. 1. Map of Lake Constance, showing the sampling station (black dot) at the deepest point of the lake.

ing intensity can influence the response of lakes to cultural eutrophication and oligotrophication.

The concentration of nutrients and dissolved oxygen at different depths in the water column can also be used as tracers of the impact of the NAO on mixing intensity. That is, reduced mixing during warm winters should result in negative correlations between the  $NAO_w$  and both hypolimnetic dissolved oxygen concentration and epilimnetic nutrient concentrations, as result of reduced downward mixing of dissolved oxygen and reduced upward mixing of nutrients. In the present study, we test this hypothesis and analyze the response of the Lake Constance temperature and mixing regime to warming and North Atlantic climate variability as expressed by the  $NAO_w$ .

### Study site and methods

Upper Lake Constance (Fig. 1) is a large (470 km<sup>2</sup>), deep ( $z_{\text{mean}} = 101$  m,  $z_{\text{max}} = 252$  m) lake at the northern fringe of the European Alps. The lake hardly ever freezes over completely (only once during the past century, in 1963). The lake is warm and monimictic, and mixing is strongest during late winter to early spring. Stratification starts between late March and April and lasts until late autumn/early winter. However, complete homeothermy is not reached by the end of the year and might not be reached at all during some winters. During summer stratification, the temperature gradient between the epilimnion and the hypolimnion is usually not steep, which results in a broad metalimnion that ranges from 5 m to below a depth of 30 m (Bäuerle et al. 1998). The first limnological studies of Lake Constance were in the late 19th century, and, since then, the lake has been studied thoroughly (Bäuerle and Gaedke 1998). The trophic status of Lake Constance changed dramatically during the past century. Total phosphorus (TP) during winter mixing increased almost 10-fold from the 1950s to the end of the 1980s and declined thereafter, as a consequence of sewage diversion and waste water treatment within the catchment area (Güde et al. 1998). The consequences of cultural eutrophication and reoligotrophication on plankton populations of Lake Constance were studied in great detail during the past few de-

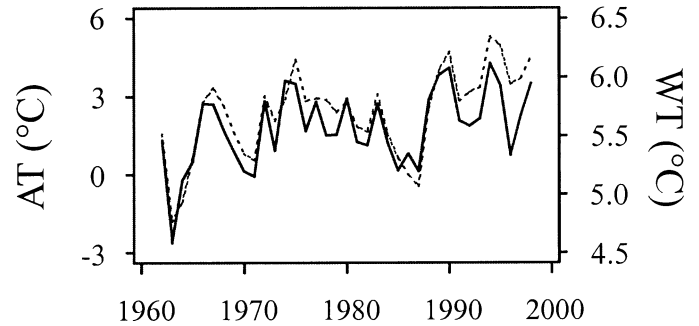


Fig. 2. Average winter air temperature (AT, solid line) and average annual water temperature (WT, dashed line) from 1962 to 1998 in Lake Constance.

acades (Walz et al. 1987; Gaedke 1998; Güde et al. 1998; Straile and Geller 1998a). More recently, it has been shown that the surface temperature and plankton development in Lake Constance is influenced by North Atlantic climate variability (i.e., the NAO; Straile and Geller 1998b; Straile 2000; Straile and Adrian 2000).

Water samples for the present study were taken by the Institut für Seenforschung at Langenargen at the deepest point of the lake (Fig. 1). Measurements of chemical variables were performed according to standard protocols (Rossknecht 1998). Typically, temperatures and chemical variables were measured at 0, 5, 10, 15, 20, 30, 50, 100, 200, and 250 m depth. Temperature profiles were recorded from 1962 to 1998. Profiles of silicate, TP, and oxygen concentrations are available from 1974 to 1998. Monthly measurements of deep-water oxygen (i.e., at 250 m depth) were available from 1962 to 1998. Monthly averages of air temperature at Lake Constance were obtained from the Deutscher Wetterdienst home page ([http://www.dwd.de/de/FundE/Klima/KLIS/daten/online/wwr/formatinfo\\_wwr.htm](http://www.dwd.de/de/FundE/Klima/KLIS/daten/online/wwr/formatinfo_wwr.htm)). Because we are interested in the effects and persistence of winter meteorological conditions, we used  $NAO_w$  for all analyses. We obtained this index from the NCAR Climate Analysis Section home page (<http://www.cgd.ucar.edu:80/cas/catalog/climind/>).

The stability of the water column stratification was quantified as the Schmidt stability, which is the amount of mechanical work needed to homogenize the water column from the surface to maximum depth (Schmidt 1928; Idso 1973). In contrast to the Lake Number (Imberger and Patterson 1990), only morphological data, i.e., the area-depth dependence and the density profile itself, are required to calculate the Schmidt stability. Because profiles were taken on a monthly basis during most of the time interval considered, it is appropriate to use the Schmidt stability. Density was calculated from measured temperature and conductivity profiles. Statistical models were run with linearly detrended data—that is, prior to correlation analyses, the slope of a linear regression model with year as the independent variable was removed from of all data.

### Results

Average winter (December–March) air temperatures increased  $0.06^{\circ}\text{C yr}^{-1}$  ( $P < 0.01$ , Fig. 2) during the study pe-

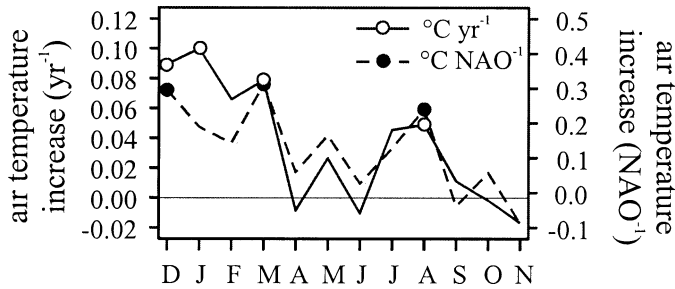


Fig. 3. Monthly average air temperature increase and average air temperature increase per unit increase in  $NAO_w$  during 1962–1998. For the latter regression models time series were linearly detrended. Slopes significantly different from zero are indicated by symbols ( $P < 0.05$ ).

riod. The average increase of volumetrically weighted annual mean water temperatures ( $0.017^{\circ}\text{C yr}^{-1}$ , Fig. 2,  $P < 0.01$ ) was approximately one-third of the increase in air temperatures and was highly related to winter air temperature ( $r = 0.88$ ,  $n = 37$ ,  $P < 0.0001$ ). Variability in both winter air temperature and annual mean water temperature were significantly correlated with the  $NAO_w$  ( $r = 0.53$ ,  $n = 37$ ,  $P < 0.001$  and  $r = 0.42$ ,  $n = 37$ ,  $P < 0.01$ , respectively).

Air temperatures increased significantly only during winter, with the exception of August (Fig. 3). The largest increase in air temperature was during February ( $0.1^{\circ}\text{C yr}^{-1}$ ). A rather similar pattern was observed in the increase of monthly air temperature per unit of  $NAO_w$  (Fig. 3). Water temperature increases were also depth specific (Fig. 4a–d). From January to April, temperature increased significantly during all months and at all depths, with the exception of the surface and 5 m depth in April (Fig. 4a,b). In these months the temperature increase was strongest in surface

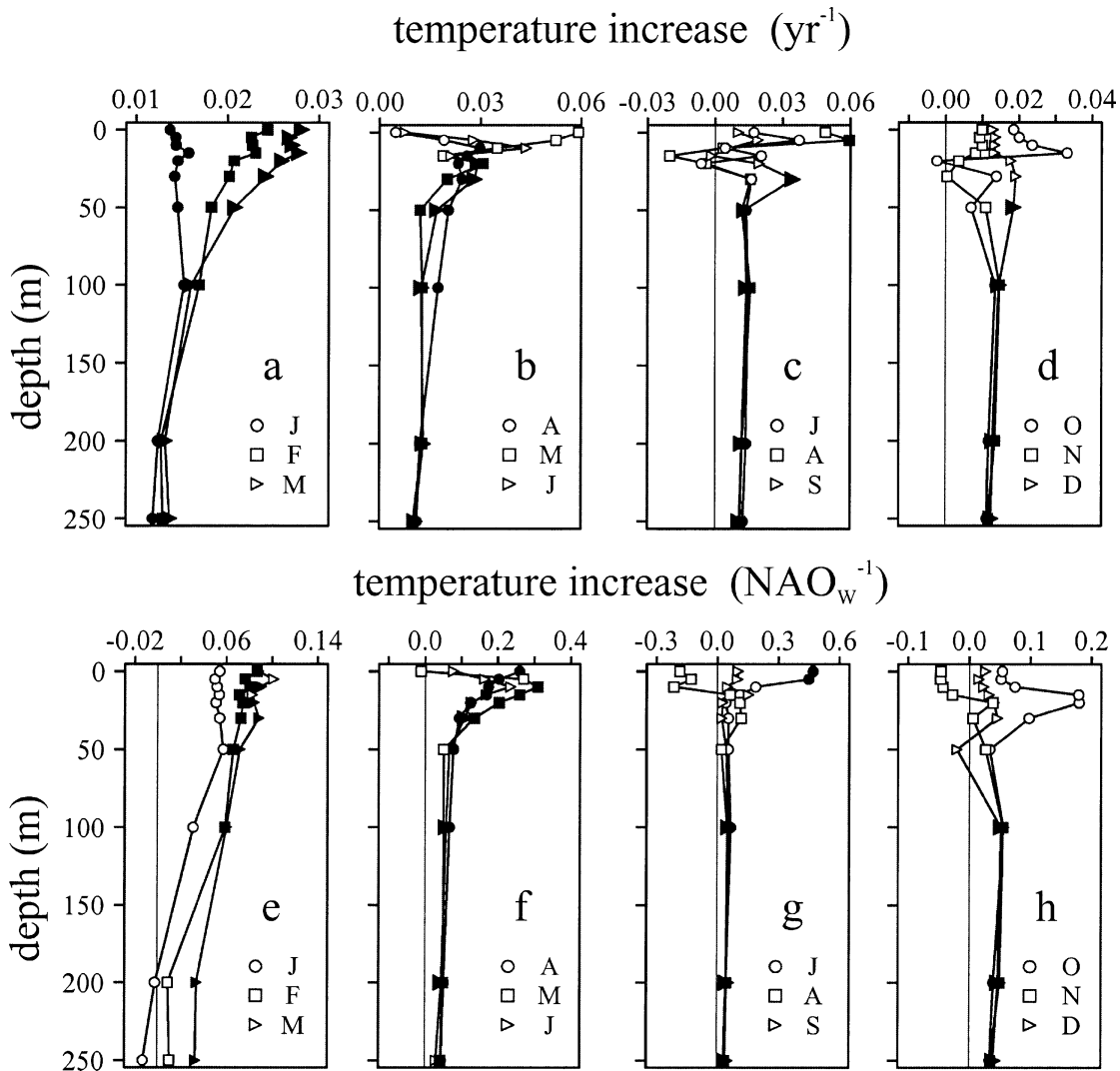


Fig. 4. Depth and month-specific water temperature increases (in  $^{\circ}\text{C yr}^{-1}$ ) and depth and month-specific water temperature responses to  $NAO_w$  (in  $^{\circ}\text{C } NAO_w^{-1}$ ) in (a and e) January–March, (b and f) April–June, (c and g) July–September, and (d and h) October–December. The response of water temperature to  $NAO_w$  was calculated with linearly detrended time series. Filled symbols indicate a significant relationship ( $P < 0.05$ ).

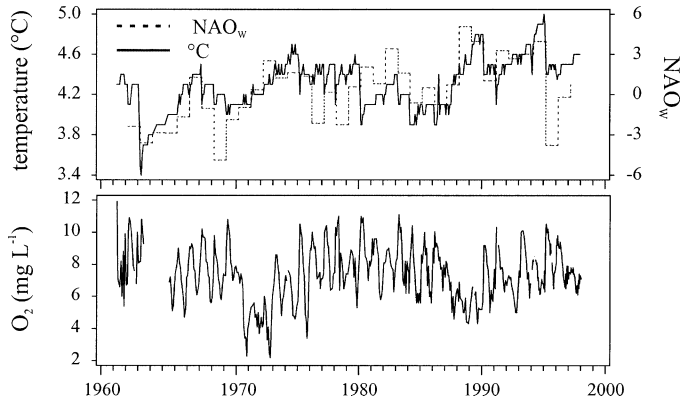


Fig. 5. (a)  $NAO_w$  and water temperature measured monthly at 250 m depth and (b) deep-water oxygen concentrations from 1962 to 1998 in Lake Constance.

layers and decreased with depth. At the surface, significant temperature increase rates were lowest in January ( $0.014^{\circ}\text{C yr}^{-1}$ ) and increased toward March ( $0.028^{\circ}\text{C yr}^{-1}$ ). From April onward, starting with the upper water layers and proceeding down through the water column, temperature increase rates lost significance. In April, the temperature increase at 10 m and below was significant, as it was in May at 20 m and below, and in June at and below 30 m (Fig. 4b), whereas from July to December almost no significant trends were observed above 50 m (Fig. 4c,d). In contrast, in the hypolimnion (i.e., below 50 m depth), temperatures continued to increase significantly from May to December.

The persistence of the  $NAO_w$  signal in water temperature is also month and depth specific (Fig. 4e–h). Correlations between  $NAO_w$  and water temperatures were not significant in January (Fig. 4e). In February, water temperatures were significantly related to the  $NAO_w$  down to a depth of 100 m, whereas at 200 and 250 m correlations were not significant. From March to May, temperatures at all depths were, with occasional exceptions, significantly related to the  $NAO_w$  index (Fig. 4e,f). During the first half of the year, the slope of this relationship—that is, the increase in water temperature per unit of  $NAO_w$ —decreased with increasing depth from January to May (Fig. 4e,f). Within the upper water column, the slope increased from January toward May, despite air temperatures not being significantly related to  $NAO_w$  during April and May (Fig. 3). This suggests a positive feedback in the response of water temperatures to the NAO until April/May due to increased stability of the water column during high- $NAO_w$  years (see below). Increased stability reduces downward mixing of heat, which results in higher water temperatures and even stronger stratification. From July through December, significant correlations were mostly confined to depths below 50 m (Fig. 4g,h).

The strong association of deep-water temperatures with the  $NAO_w$  is evident from a time-series plot (Fig. 5a). Deep-water temperatures in Lake Constance exhibited seasonal and interannual variability, including “sawtooth” structures (Livingstone 1997)—that is, periods of gradual temperature increase of several years followed by an abrupt decrease from 1971 to 1975, 1981 to 1984, 1987 to 1991, and 1992 to 1995. These periods of gradual temperature increase were

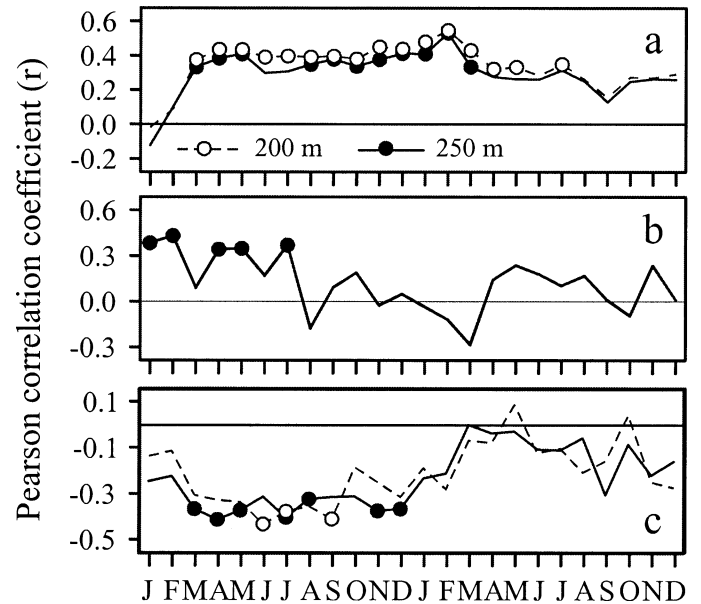


Fig. 6. Time series of correlation coefficients relating  $NAO_w$  to monthly values of (a) deep-water temperatures, (b) Schmidt stability, and (c) deep-water oxygen concentrations from the year the  $NAO_w$  index was taken and the following year. All correlations are for the time period 1962–1998, except for oxygen concentration at 200 m depth, for which only data from 1974–1998 were available. Symbols indicate correlations significant at  $P < 0.05$ . All time series were linearly detrended.

associated with high- $NAO_w$  winters (Fig. 5a). Deep-water oxygen concentrations varied seasonally and interannually (Fig. 5b). During most years, deep-water oxygen was replenished during the mixing period and decreased thereafter toward a late summer/autumn minimum. However, this was not the case in all years. A lack of deep-water oxygen replenishment during the early 1970s and the late 1980s was always associated with warm winters, when there was almost no cooling of deep waters (Rossknecht 1998). Maximum oxygen concentrations during the mixing period were highly correlated with the extent of deep-water winter cooling—that is, the temperature difference between December and March ( $r = 0.57$ ,  $n = 36$ ,  $P < 0.0002$ ), which in turn was related to the  $NAO_w$  index ( $r = -0.49$ ,  $n = 36$ ,  $P < 0.004$ ).

To analyze the persistence of the  $NAO_w$  signal in the hypolimnion, Fig. 6a shows the time series of correlation coefficients relating the  $NAO_w$  index of a specific year to monthly water temperatures of that and the following year. At 200 and 250 m depth,  $NAO_w$  was significantly related to water temperature from March until the next mixing period (i.e., the following March; Fig. 6a). Water-column stability, expressed as the Schmidt stability, was significantly associated with  $NAO_w$  during January–July, except during March and June (Fig. 6b), which shows the positive feedback between stability and  $NAO_w$ -related warming. Although the relationship between Schmidt stability and  $NAO_w$  was not significant in March, a comparison of depth profiles in high- $NAO_w$  years versus low- $NAO_w$  years revealed that, during high- $NAO_w$  years, there was a small temperature gradient during March, with surface temperatures approaching  $5^{\circ}\text{C}$

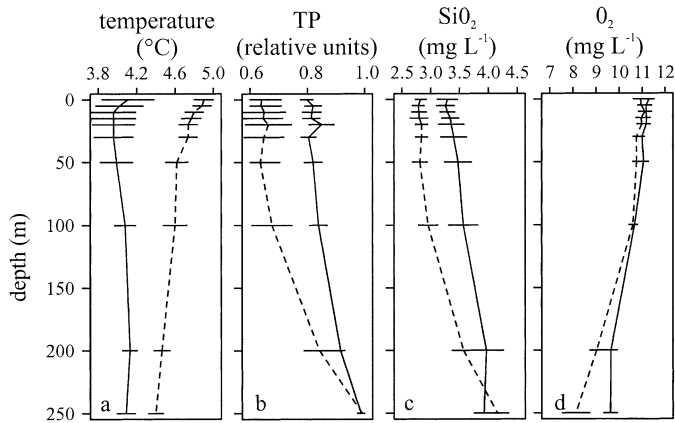


Fig. 7. Profiles of (a) temperature, (b) TP, (c) total silicate, and (d) oxygen in March in high- (dashed lines) vs. low- (solid lines) NAO<sub>w</sub> years (means  $\pm$  1 SE). High (low) NAO<sub>w</sub> years include those 25% of years with the highest (lowest) NAO<sub>w</sub> index during the study period (1962–1998 for water temperature profiles and 1974–1998 for TP, silica, and oxygen profiles). Multiple regression models indicate that, for all variables, there was a significant depth effect, NAO<sub>w</sub> effect, and interaction term during March (all  $P < 0.01$ ). Only for oxygen concentrations were there significant effects of depth ( $P < 0.001$ ) and a significant interaction term ( $P < 0.05$ ) but no overall effect of the NAO ( $P > 0.1$ ). For multiple regression models all data were used, not only the upper and lower quartiles.

and temperatures  $< 4.6^{\circ}\text{C}$  below 100 m depth (Fig. 7a). In contrast, during low-NAO<sub>w</sub> years, temperatures were close to  $4^{\circ}\text{C}$  at all depths, sometimes showing stable inverse stratification. Profiles of TP, SiO<sub>2</sub>, and O<sub>2</sub> in March of high- versus low-NAO<sub>w</sub> years also strongly suggest differences in overall mixing intensity (Fig. 7b–d). TP at a specific depth is expressed in units relative to the maximum value measured within the respective profile. This accounts for the long-term changes in TP due to eutrophication and oligotrophication. Maximum values in almost all years were measured near the sediment (i.e., at 250 m depth), which is indicated by a relative TP value approaching 1 during both high- and low-NAO<sub>w</sub> years (Fig. 7b). However, during high-NAO<sub>w</sub> years, at depths  $< 100$  m, TP reached only 70% of these maximum values, whereas, during low-NAO<sub>w</sub> years, TP reached 80%–90% of maximum values, which indicates a more homogenous distribution through the water column. Silica profiles in high- versus low-NAO<sub>w</sub> years showed similar patterns—strong differences between high- and low-NAO<sub>w</sub> years at depths  $< 100$  m and no differences at 200 and 250 m (Fig. 7c). In contrast, oxygen concentrations did not differ between high- and low-NAO<sub>w</sub> years during March at depths  $< 100$  m but were lower during high-NAO<sub>w</sub> years than during low-NAO<sub>w</sub> years at 200 and 250 m, respectively (Fig. 7d). Average upper water column (0–20 m) silica and relative TP during March were significantly related to each other ( $r = 0.42$ ,  $n = 25$ ,  $P < 0.05$ ), and both were related to deep-water oxygen concentrations ( $r = 0.4$ ,  $n = 25$ ,  $P < 0.06$  and  $r = 0.9$ ,  $n = 25$ ,  $P < 0.0001$ , respectively). Because stratification isolates the deep water from the atmosphere, decreasing oxygen concentrations cannot be replenished after the onset of stratification. As a consequence,

oxygen concentrations in deeper water layers were significantly related to NAO<sub>w</sub> until the end of the year (Fig. 6c).

## Discussion

Water temperature in Lake Constance increased in concert with warming in the northern hemisphere in recent decades (Jones et al. 1999) and was strongly related to the variation in the phase of the NAO. Warmer winters are especially critical to deep temperate monomictic lakes, because temperature effects the duration and extent of winter mixing and, consequently, the annual heat budget of the lake and the vertical distribution of nutrients and oxygen. The increase in Lake Constance water temperatures as well as its response to the NAO were evident throughout the whole water column. This supports recent predictions of hydrodynamic models, which allow deep-water heat to carry over between successive years (Peeters et al. 2002). In contrast, models of dimictic lakes predict that only epilimnetic temperatures will warm and the stratification period will lengthen—that is, hypolimnetic temperatures are predicted to respond less strongly and inconsistently to warming (Hondzo and Stefan 1991).

Surface and epilimnetic water temperatures increased mainly during the first third of the year. A seasonally similar time span of the NAO influence on surface water temperatures: significant correlations in winter until April/May were reported from several perialpine lakes for the time period 1911–1990 (Livingstone and Dokulil 2001). Temperatures of deep waters in warm monomictic lakes are set during late winter/early spring, and this winter/early spring signal persists in the hypolimnion for a much longer time than in the epilimnion. However, even at a depth of 50 m, the NAO<sub>w</sub> signal vanished after early summer (Fig. 4g,h). Hence, spring and summer meteorological conditions unrelated to NAO<sub>w</sub> affect water temperature even down to a depth of 50 m, possibly because temperature gradients in the metalimnion of Lake Constance are low. The influence of NAO on hypolimnetic water temperatures was analyzed by Gerten and Adrian (2001) in three lakes of different depth; their data show that the persistence of the NAO<sub>w</sub> signal increases with increasing lake depth. In deep and dimictic Lake Stechlin, the NAO signal persisted throughout the whole summer and autumn until the mixing period in December (Gerten and Adrian 2001). In Lake Constance, which is deeper and monomictic, the NAO signal persisted even further—until the mixing period in March. However, it took longer for the NAO to affect the thermal regime in the actual winter in Lake Constance. In January, correlations between water temperatures and NAO<sub>w</sub> were not significant, and in February the NAO<sub>w</sub> signal was present down to a depth of 100 m but still not at 200 and 250 m (Figs. 4e, 6a). Hence, the specific mixing regime of Lake Constance resulted in a time lag of 1 yr in the relationship between winter meteorological conditions and winter deep-water temperatures.

The high correlation between winter air temperatures and water temperatures and NAO<sub>w</sub> suggests that the influence of the NAO on Lake Constance resulted from its influence on local air temperatures. Air temperature strongly influences lake temperature because it affects three of five heat-exchange processes between water and the atmosphere (Edin-

ger et al. 1968)—convective heat exchange, evaporative heat exchange, and the atmospheric emission of long-wave radiation. Reduced mixing intensity was most probably a consequence of reduced lake cooling during winter. The annual minimum water temperature in Lake Constance is usually attained in March. Significant positive trends or associations with the NAO of water temperatures obtained from December toward February hence indicate reduced winter cooling during recent and/or high-NAO years. The slopes of these trends and associations were greatest at shallow depths. Hence, winter cooling was more reduced in upper water layers, which resulted into the persistence of small temperature gradients possibly resisting complete mixes in more recent (high-NAO) years. In contrast, during low-NAO winters, hypolimnetic temperatures dropped more quickly, increasing the possibility of homeothermy and complete mixing. Winter cooling thus determined, to a large extent, the annual average water temperature (Fig. 2).

We cannot exclude the possibility that changes in wind speed also contributed to the observed trends and links. However, demonstrating the influence of wind in a large lake is complex, because there are strong spatial heterogeneities in wind speed and direction (Bäuerle et al. 1998). Gaedke et al. (1998) were not able to relate interannual differences in vernal warming and the start of stratification in Lake Constance to wind speed measurements. We did also not detect any significant relationship between wind-speed measurements at two Lake Constance stations (Konstanz and Kreuzlingen data not shown) and  $NAO_w$ . In contrast to heterogeneous winds at ground level, wind speed measured at a mountain top might reflect the more spatially homogenous geostrophic wind (Livingstone and Dokulil 2001). Indeed, Livingstone and Dokulil (2001) found a significant association of the wind speed on top of Mt. Säntis, located 20 km from Lake Constance at 2,500 m above sea level, and the mean spring surface temperatures of eight perialpine lakes, including Lake Constance. However, the coefficient of determination was rather low ( $r^2 = 0.11$ ), which suggests that the overall contribution of changes in wind speed to lake temperatures is probably low. Furthermore, hydrodynamic models have shown that an increase in air temperature alone is sufficient to explain temperature increase differences between epilimnetic and hypolimnetic water layers (Peeters et al. 2002).

The effect of the NAO on water-column stability is also manifest in the vertical distribution of oxygen and nutrients during March. The March profiles of TP, silica, and oxygen provide evidence for the depth of NAO-related mixing strength. They suggest that winter mixing was sufficient to homogenize the upper 100 m of the water column in Lake Constance, independent of the state of the NAO, but that there was less mixing below 100 m during high- $NAO_w$  years. Deep-water oxygen levels were also lower during the high-NAO winters from 1988 to 1990 in several nearby perialpine lakes (Livingstone 1997). Simulation models also predict reduced turnover frequencies in the Great Lakes that results in secondary changes of nutrient upmixing and oxygenation of deep water (Croley et al. 1998). Another mechanism that can transfer oxygen into deep waters is gravity currents generated by plunging cold water masses due to faster cooling of littoral water during winter (Fer et al. 2001; Hollan unpubl. data). Because winter air temperatures at

Lake Constance were closely linked to the NAO, cooling of littoral water masses and the development of cold gravity currents are more likely to occur during low-NAO years. Hence, this mechanism can contribute to the observed negative correlations of the NAO with deep-water oxygen. However, it cannot account for the lower concentrations of epilimnetic silicate and TP in high-NAO years, whereas reduced mixing does. Hence, cold density currents may contribute to some of the observed patterns, but mixing is an adequate explanation for all observed depth specific patterns and is thus the more parsimonious explanation.

The influence of the NAO on deep-water oxygen concentrations carries over almost until the next mixing period. In addition to the influence of the NAO on oxygen supply during the mixing period, the NAO can influence hypolimnetic oxygen concentrations via other mechanisms. In the eutrophic Pluss-See, oxygen concentrations in the hypolimnion in autumn, but not during spring and summer, were negatively related to the meteorological conditions of the previous winter (Güss et al. 2000), probably because of the increased degradation of organic matter originating from more intense summer blooms of phytoplankton after mild winters. Oxygen consumption in the hypolimnion of Lake Constance should increase because of higher deep-water temperatures during high- $NAO_w$  years. In contrast, reduced nutrient supply for phytoplankton and increased grazing of daphnids during spring during high- $NAO_w$  years (Straile 2000) might result into lowered phytoplankton biomass and, thus, decreasing sedimentation rates. As a consequence, less organic material might reduce bacterial oxygen demand for decomposition during high- $NAO_w$  years. The net result of these opposite effects on deep-water oxygen concentrations in Lake Constance is unclear, and the supply of oxygen during mixing thus probably most strongly influences deep-water oxygen concentrations year-round (Rossknecht 1998).

Our results show that the temperature and the mixing regime during late winter in Lake Constance changed during the recent decades in response to winter warming and the NAO. This has affected oxygen and nutrient dynamics in this deep lake. Reduced upward mixing of nutrients during high-NAO years supports management efforts to reduce nutrient availability to phytoplankton. On the other hand, reduced downward transport of oxygen during high-NAO years results in lower hypolimnetic oxygen concentrations, thereby increasing one symptom of eutrophication. Hence, deep-water oxygen is only partially amenable to management procedures. Because several models predict that the current positive phase of the NAO will persist at least for the first few decades of the 21st century (Paeth et al. 1999), a reduction of oxygen concentrations in the hypolimnion as a result of incomplete mixing cannot be excluded in Lake Constance in the near future, despite continuing efforts to reduce nutrient loading.

Our study adds information on the multiple effects of climate change on lake ecosystems. Within one lake, we have now evidence that water temperatures, the mixing regime, oxygen concentrations, the vertical distribution of nutrients, population growth of *Daphnia*, the timing of the suppression of algae by *Daphnia* (i.e., the clear-water timing; Straile 2000, 2002; Straile and Adrian 2000), and the year-class strength of fish species (Straile et al. unpubl. data) were affected by the NAO. Considering the multitude of effects and

mechanisms and their possible interactions and resulting indirect effects, the prediction of further changes of lake ecosystems in response to climatic change will be a demanding task.

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