Long-term changes in hypoxia and soluble reactive phosphorus in the hypolimnion of a large temperate lake: consequences of a climate regime shift

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Abstract

The (Lower) Lake of Zurich provides an ideal system for studying the long-term impact of environmental change on deep-water hypoxia because of its sensitivity to climatic forcing, its history of eutrophication and subsequent oligotrophication, and the quality and length of its data set. Based on 39 years (1972–2010) of measured profiles of temperature, oxygen concentration and phosphorus (P) concentration, the potentially confounding effects of oligotrophication and climatic forcing on the occurrence and extent of deep-water hypoxia in the lake were investigated. The time-series of Nürnberg’s hypoxic factor (HF) for the lake can be divided into three distinct segments: (i) a segment of consistently low HF from 1972 to the late-1980s climate regime shift (CRS); (ii) a transitional segment between the late-1980s CRS and approximately 2000 within which the HF was highly variable; and (iii) a segment of consistently high HF thereafter. The increase in hypoxia during the study period was not a consequence of a change in trophic status, as the lake underwent oligotrophication as a result of reduced external P loading during this time. Instead, wavelet analysis suggests that changes in the lake’s mixing regime, initiated by the late-1980s CRS, ultimately led to a delayed but abrupt decrease in the deep-water oxygen concentration, resulting in a general expansion of the hypoxic zone in autumn. Even after detrending to remove long-term effects, the concentration of soluble reactive P in the bottom water of the lake was highly correlated with various measures of hypoxia, providing quantitative evidence supporting the probable effect of hypoxia on internal P loading. Such climate-induced, ecosystem-scale changes, which may result in undesirable effects such as a decline in water quality and a reduction in coldwater fish habitats, provide further evidence for the vulnerability of large temperate lakes to predicted increases in global air temperature.

Keywords: climate change, internal phosphorus loading, mixing dynamics, nutrients, oligotrophication, oxygen, wavelet analysis

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Introduction

Hypoxia occurs when dissolved oxygen (O_2) concentrations drop below the threshold at which life can no longer be sustained (Diaz & Rosenberg, 2008). This threshold is conventionally assumed to be 2 mg O_2 l^{-1}, although its value differs greatly among organisms (Vaquer-Sunyer & Duarte, 2008). Hypoxia is an important indicator of ecosystem health: as the extent, duration and frequency of occurrence of hypoxia increases, ecosystem health declines. The occurrence of a drastic increase in hypoxia in aquatic ecosystems over the past few decades has been attributed to the combined effects of eutrophication and climate change (Diaz, 2001; Diaz & Rosenberg, 2008; Vaquer-Sunyer & Duarte, 2008). Lakes are particularly susceptible to variations in climatic forcing (Adrian et al., 2009; Schindler, 2009; Shimoda et al., 2011). For numerous lakes across the globe, evidence is accumulating that their thermal regimes are undergoing fundamental changes as a result of climate warming, involving an increase in thermal stability and the partial suppression of mixing (e.g., Livingstone, 2003, 2008; Verburg & Hecky, 2009; Kaden et al., 2010; Schneider & Hook, 2010; Stainsby et al., 2011; North et al., 2013). As a result of these changes, lakes are likely to experience an increase in the frequency of occurrence, duration and extent of...
bottom-water hypoxia (e.g., Stefan & Fang, 1994; Rempfer et al., 2010; Foley et al., 2012).

The (Lower) Lake of Zurich, located on the Swiss Plateau, has been the focus of several previous studies of the impact of increasing air temperature on lake mixing patterns (Livingstone, 1993, 2003; Peeters et al., 2002) and O₂ depletion (Livingstone, 1997; Jankowski et al., 2006; Rempfer et al., 2009, 2010). This study continues this work, focusing on the long-term relationship between climatic forcing, mixing and bottom-water hypoxia, and assessing the potential implications of such a relationship for the nutrient dynamics of the lake. Particular emphasis is placed on the effect of the late-1980s climate regime shift (CRS) that resulted from a change in the behaviour of the Arctic Oscillation and the North Atlantic Oscillation (Yasunaka & Hanawa, 2002; Alheit et al., 2005; Rodionov & Overland, 2005), which in Switzerland has already been linked to sudden regime shifts in lakes, rivers and groundwater (Anneville et al., 2004, 2005; Hari et al., 2006; Figura et al., 2011; North et al., 2013).

Materials and methods

Study lake

The Lake of Zurich is a perialpine lake with a surface area of 65 km², a volume of 3.3 km³ and a maximum depth of 136 m (Livingstone, 2003). The lake usually undergoes complete mixing once per year (i.e., it is holomictic and monomictic), but it can mix twice per year (i.e., it is facultatively dimictic: Peeters et al., 2002; Livingstone, 2003). During exceptionally cold winters when the lake freezes, it exhibits dimictic behaviour as it undergoes homothermy and complete mixing before ice-on and after ice-off. However, the Lake of Zurich has been completely ice-covered only once (1962–63) in the period 1944–2010 (Peeters et al., 2002; Rempfer et al., 2010). During milder winters with no ice cover the lake is generally monomictic, with homothermy and complete mixing occurring only in late winter or early spring. Finally, in exceptionally mild winters the lake can remain positively stratified throughout the entire winter, severely suppressing mixing (Livingstone, 1993, 1997; Rempfer et al., 2010). Vertical gradients of salinity remained fairly constant throughout the study period and therefore had a minimal effect on mixing patterns (Livingstone, 2003).

Several unique characteristics of the lake and its history make it an ideal study site for investigating the impact of climate warming on lake processes (Peeters et al., 2002). It has an extensive data set (~70 years) of lake profiles measured approximately 12 times per year (year-round) at consistent depths. Approximately 84% of the inflow into the lake is over a sill 3 m deep that connects it to the Upper Lake of Zurich (Omlin et al., 2001), thus limiting the impact of hydrology on lake processes (Livingstone, 2003). The lake is convectively mixed (Peeters et al., 2002), and even severe winter storms have only a limited effect on lake mixing during mild winters (Rempfer et al., 2010).

Field measurements

The Lake of Zurich data set dates back to 1936, but this study was restricted to the period 1972–2010 unless otherwise noted. During this period, water column profiles of temperature (T) and of the concentrations of dissolved O₂, total phosphorus (TP) and soluble reactive phosphorus (SRP) were measured at consistent depths (0.3, 1, 2.5, 5, 7.5, 10, 12.5, 15, 20, 30, 40, 60, 80, 90, 100, 110, 120, 130 and 135 m) at the deepest point of the lake (136 m) by the same agency, the City of Zurich Water Supply (WVZ) (Zimmermann et al., 1991), thus ensuring a high quality data set. Temperatures were measured by thermometer and regularly calibrated with a mercury thermometer (Livingstone, 2003). O₂ concentrations were measured using the Winkler method until 2001, an electrochemical O₂ sensor from 2002 to 2009, and an optode sensor thereafter. Sensor measurements at 2.5 m and 135 m depth were routinely compared with O₂ concentrations determined using the Winkler method (Jankowski et al., 2006). TP and SRP concentrations were consistently measured using VIS photometry (German standard methods D11: Gammeter et al., 1997). SRP samples were obtained by filtration through a 0.45 µm filter. The WVZ laboratory has been ISO accredited (ISO 17025 standard) since late 1999, after which measurement accuracy was 0.03–0.1 K for temperature, 0.1–0.3 mg l⁻¹ for O₂, and 0.79–1.8 µg l⁻¹ for TP and SRP. Before this time, measurement accuracies were estimated at ±10% for chemical variables and ±5% for physical variables. Further details on the Lake of Zurich data set are available from Zimmermann et al. (1991), Livingstone (2003) and Jankowski et al. (2006).

Data analysis

The water column profiles, which were measured irregularly at approximately monthly intervals, were subjected to a two-stage interpolation process to fill small data gaps and standardize both spatial and temporal sampling intervals. The measured water column profiles were first interpolated spatially at intervals of 1 m using linear interpolation (North & Livingstone, 2013). The resulting profiles were then interpolated temporally at daily (24-h) intervals using either cubic spline or linear interpolation. A comparison of cubic spline and linear interpolation for filling gaps in the time domain revealed that cubic spline interpolation was more accurate for temperature and O₂ concentration, but linear interpolation was more accurate for TP concentration and SRP concentration (R.P. North & D.M. Livingstone, unpublished data). In each case, the more accurate interpolation method was employed to yield profiles at consistent daily intervals. These daily profiles were then aggregated to yield monthly mean profiles. Based on the spatially and temporally uniform data sets resulting from the two-stage interpolation process, the following quantities were calculated: Nürnberg’s hypoxic factor (HF) for an oxycline at 2 mg O₂ l⁻¹ (Nürnberg, 2002, 2004); the concentrations of O₂, TP and SRP...
for various layers of the lake; and the Schmidt stability $S$ (Schmidt, 1928; Idso, 1973), which is a measure of the overall thermal stability of the lake.

Following the protocols of previous work on the Lake of Zurich (e.g., Örn, 1980; Livingstone, 2003), the upper boundary of the hypolimnion was defined at the fixed depth of 20 m. Mean deep-water $O_2$ and SRP concentrations were defined as volume-weighted means from 100 m to 135 m. Mean epi/metalimnetic SRP concentrations were defined as volume-weighted means from 0 m to 20 m. The lake was assumed to be stratified when $S > 200 \text{ J m}^{-2}$, and homothermic when $S \leq 200 \text{ J m}^{-2}$ (Livingstone, 2003). $S = 200 \text{ J m}^{-2}$ is equivalent to a uniform temperature profile of 6 °C within the epi/metalimnion and 4 °C within the hypolimnion. In the Lake of Zurich, the summer stratification period typically extends from April to September. The annual minimum hypolimnetic $O_2$ concentration occurs at the end of the stratification period, generally some time between September and November. This interannual variability in the timing of the annual minimum indicates that in some years mixing between the surface and the deep water occurred in October or November. Therefore, when estimating the annual maximum extent of the hypoxic zone, monthly mean $O_2$ concentrations in September (i.e., before the occurrence of any large-scale convective mixing events) were always used.

Monthly mean time-series of the measured and derived variables were either grouped by month to compare changes in seasonality or were aggregated to yield time-series of annual means. Available data on monthly mean loading rates ($t \text{ yr}^{-1}$) of TP entering the Lake of Zurich over the sill connecting it with the Upper Lake of Zurich cover the years 1976–2005. The loading was determined from measured TP concentrations at the sill and the measured flow of the Linth Canal, which is the major inflow to the Upper Lake of Zurich. This loading was multiplied by a factor of 1.6 to account for other, smaller inflows into the Upper Lake of Zurich (Gammeter & Forster, 2002; Dietzel et al., 2013).

The sequential $t$-test STARS (Rodionov & Overland, 2005) was used to detect abrupt regime shifts in the annual mean time-series of measured and derived variables. The magnitude of the shifts detected by STARS was determined by the threshold significance level ($P = 0.15$) and the cut-off length ($L = 10$ years) (Rodionov & Overland, 2005). The latter determines the detection scale of interest (decadal). When STARS detected a shift, the mean of each regime was calculated and tested with a second $t$-test. For this second test, any shift that satisfied a more stringent significance criterion of $P < 0.05$ was accepted (cf. North et al., 2013).

The time-series were tested for monotonic trends using the Mann–Kendall test as implemented in the ‘Kendall’ R-package (McLeod, 2011). If a time-series contained a significant shift (as detected by STARS), the Mann–Kendall test was applied to each regime separately. The Pearson product-moment correlation coefficient test built into $R$ was used to assess correlations computed between time-series (R Development Core Team, 2011). The lag-1 autocorrelation (the autocorrelation coefficient at a lag of one time unit: here, 1 month) and variance of a time-series (with seasonality and trend removed) were calculated based on the method outlined by Dakos et al. (2008).

Wavelet analysis was used to assess changes in seasonal and interannual variability in deep-water temperature and $O_2$ concentration. Wavelet analysis can be used to analyse non-stationary time-series and captures both the frequency distribution of the signal and how this distribution varies with time (Torrence & Compo, 1998; Benincà et al., 2009). Before conducting the wavelet analysis, the time-series were filtered using singular spectrum analysis, SSA (Ghil et al., 2002). Filtering removed trends, and also frequencies that were too low to be captured by the wavelet analysis. The filtered time-series were standardized by their standard deviation and then decomposed using the Morlet wavelet function. The wavelet and SSA analyses were accomplished using the R packages biwavelet (Gouhier, 2013) and Rssa (Korobeynikov, 2010), respectively.

**Results**

**Oxygen dynamics**

Based on annual HF values for the Lake of Zurich, the 39-year study period can be roughly divided into three segments (Fig. 1a). In Segment I (1972–1987), with the exception of the first 2 years, HF was never larger than 30 days yr$^{-1}$. Segment II (1988–2000) represents a transitional phase during which HF is extremely variable, ranging between approximately 8 days yr$^{-1}$ and 64 days yr$^{-1}$. Finally, in Segment III (2001–2010), with the exception of only 1 year (2003), HF consistently exceeded 30 days yr$^{-1}$. The transition from Segment II to Segment III corresponded to a statistically significant abrupt (upward) shift of 21 days yr$^{-1}$ ($P < 0.001$, $n = 39$) as detected by the STARS test (Table 1). No statistically significant monotonic trend was found before the shift (Segment I plus Segment II, $P > 0.05$, $n = 29$) or after (Segment III, $P > 0.05$, $n = 10$), suggesting that the shift was responsible for most of the overall increase in HF that has occurred since 1972 (Table 1).

Known precursors of abrupt shifts in complex systems, including ecosystems, include an increase in lag-1 autocorrelation and an increase in variance (e.g., Scheffer et al., 2009). Assuming HF to have undergone an abrupt shift from Segment II to Segment III, an increase in either or both of these variables might therefore be expected to have occurred prior to the shift. Analysis of the monthly mean HF time-series (with trend and seasonality removed) revealed a significant positive trend ($P < 0.01$, $n = 168$) in both lag-1 autocorrelation and variance from Segment I to Segment II leading up to the transition from Segment II to Segment III (Fig. S1). The lag-1 autocorrelation and variance of the time-series were calculated using a 14-year sliding window (168 months). This window size corresponds
to half the length of the time-series prior to the abrupt shift (i.e., 1972–1999).

The annual maximum areal extent of hypoxia (AEH) and the annual duration of hypoxia at a depth of 130 m (DOH) both showed approximately the same 3-segment pattern (Fig. S2a and b) and shift as the HF, with a significant abrupt shift ($P < 0.001$, $n = 39$) in all three variables occurring between 1997 and 2001 (Table 1).

The similarities among the three variables confirm that HF can be used as a reliable indicator to represent changes in the duration and spatial extent of hypoxia.

The time-series of the mean deep-water O$_2$ concentration in September (Fig. 1b) can also be divided into three distinct segments: mean O$_2$ concentrations below 100 m are generally above 4.4 mg l$^{-1}$ in Segment I, variable in the transitional Segment II, and at or below...
LONG-TERM CHANGES IN HYPOXIA IN A LARGE LAKE

Table 1 Statistical significance of abrupt shifts and monotonic trends in: annual hypoxic factor (HF) for a threshold of \([\text{O}_2 < 2 \text{ mg l}^{-1}]\); areal extent of hypoxia in September (AEH); annual duration of hypoxia (DOH) at a depth of 130 m; mean winter/spring (December to April) thermal stability (S); annual duration of the stratification period (DSP); annual volume-weighted mean total phosphorus concentration (TP); annual mean external TP loading (ETP); and annual volume-weighted mean deep-water soluble reactive phosphorus concentration (SRP). Shifts were detected using the STARS test (Rodionov & Overland, 2005) and trends were detected using the Mann-Kendall test (MK). Indicated in the table are the temporal locations of the abrupt shifts detected by STARS. When an abrupt shift was detected, the MK test was applied to the years before and after the shift, but not across the shift (indicated by NA = not applicable). The MK test was therefore applied to either Segment I (1972–1987), Segments I and II (1972–2000), Segments II and III (1988–2010) or Segment III (2001–2010). For the MK test, the sign of the only significant trend detected (which was negative) is also given. The ETP time-series was limited to 1976–2005.

<table>
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Statistical significance: \(P > 0.05 \text{ (ns); } P < 0.05 \text{ (*); } P < 0.01 \text{ (**); } P < 0.001 \text{ (***).}

4.5 mg l\(^{-1}\) in Segment III (Fig. 1b). The mean deep-water \(\text{O}_2\) concentration in September mirrors that in the preceding April (Fig. 1b; \(R^2 = 0.62, \ P < 0.001, \ n = 39\)), when the deep-water \(\text{O}_2\) concentration is generally at its annual maximum (Jankowski et al., 2006). This suggests that the deep-water \(\text{O}_2\) concentration in September is dependent to a large extent on the mixing conditions prevailing during the previous winter and spring, which in most of the deep Swiss perialpine lakes largely determine the annual maximum hypolimnetic \(\text{O}_2\) concentration (Livingstone & Imboden, 1996).

Eutrophication

An increase in the duration and spatial extent of hypoxia can often be attributed to eutrophication; that is, to an increase in the production of excess organic matter (Diaz, 2001). However, the study period (1972–2010) corresponds to a period of decreasing TP concentration (\(P < 0.001, \ n = 39\); Fig. 1c) and stable phytoplankton biomass (Posch et al., 2012) in the Lake of Zurich. This combination suggests that the observed increase in hypoxia from Segment II to Segment III was not the result of an increase in biomass decomposition in the hypolimnion linked to an increase in TP loading. The decrease in the mean lake TP concentration resulted from improved wastewater treatment and the banning of phosphates in detergents, and is reflected in decreasing external TP loading from the Upper Lake of Zurich (\(P < 0.001, \ n = 30\); Fig. 1e). After the late 1980s, external TP loadings were generally stable (Fig. 1e), and in the mid-1990s the rate of decline in the mean lake TP concentration slowed (Fig. 1c). The long-term downward trend in mean lake TP concentration continued, albeit less markedly, until the end of the time-series (Table 1). The mean lake TP concentration showed a noticeable jump in 2000, corresponding to the transition from Segment II to III (Fig. 1c). This increase can be entirely attributed to an increase in the deep-water SRP concentration (Fig. 1f), as no increase in TP concentration was found after removing the contribution of SRP, and there was no corresponding increase in external TP loading (Fig. 1e). The increase in deep-water SRP concentration in Segment III is discussed in more detail below.

External forcing and mixing dynamics

The transition from a low to a variable HF (Segment I to Segment II) coincided with an abrupt shift in the mean air temperature on the Swiss Plateau (Hari et al., 2006; Figura et al., 2011; North et al., 2013). This abrupt shift was linked to the now well-documented large-scale late-1980s CRS. In the Lake of Zurich, the increase in air temperature was reflected in an abrupt increase in the mean water temperature of the epi/metalimnion and, to a smaller degree, of the hypolimnion (North et al., 2013). As a result of the difference in warming between the epi/metalimnion and the hypolimnion, the Schmidt stability of the lake (S) in winter/spring (December to April) increased abruptly from Segment I to Segment II (Fig. 1d; \(\Delta S = 86 \text{ J m}^{-2}, \ P < 0.01, \ n = 39\)).

Wavelet analysis was used to assess temporal changes in dominant mixing cycles. In Segment I, the power spectrum of deep-water temperature shows a peak centred on a period (\(T_w\)) of approximately 2–3 years (Fig. 2a). In Segments II and III, additional peaks appear, with periods ranging up to approximately 7 years (Fig. 2a). Throughout the time-series, there is little power at a period of 1 year, indicating that there is no marked annual cycle in deep-water temperature.
In contrast, the power spectrum of deep-water O$_2$ concentration shows a significant peak at a period of 1 year throughout most of the time-series (Fig. 2b). However, in Segments II and III, the annual component is less consistently present, and the power in the multiannual cycles (approximately 2 years < $T_W$ < 5 years) is greater than in Segment I (Fig. 2b). The decrease in power at lower periods in the time-series of deep-water O$_2$ concentration, and the increase in power at higher periods in both the deep-water temperature and O$_2$ time-series, suggests that annual renewal of the deep water occurred less consistently in Segments II and III than in Segment I. Instead, multiannual cycles began to dominate lake mixing patterns after the late-1980s CRS.

To confirm the results of the wavelet analysis, we assumed that if the deep-water temperature (O$_2$ concentration) increased (decreased) over two or more consecutive years, then the lake did not completely mix.

The transition from a variable to a consistently high HF (Segment II to Segment III) does not correspond to an abrupt change in any of the climatic or physical lake variables considered in this study. However, Livingstone (2003) found that in the Lake of Zurich the duration of the stratified period (DSP) has been steadily increasing over the past few decades, with the date of the onset of stratification (in spring) occurring earlier and the date of the onset of homothermy (in early winter) later. In the DSP time-series (1972–2010), the STARS test detected an abrupt increase from 1999 to 2000 (Table 1; ΔDSP = 14 days yr⁻¹, P < 0.01, n = 39) that corresponds approximately to the timing of the abrupt increases in HF, AEH and DOH at the end of Segment II, suggesting that the abrupt shift in the hypoxia indicators might be related to the abrupt increase in the DSP (Fig. S2c).

**Phosphorus dynamics**

The annual mean deep-water SRP concentration increased sharply at the end of Segment II and, after a short decrease, continued to increase with a small but significant trend (P < 0.01, n = 6) from 2005 onwards (Fig. 1f). The increase occurred after almost 20 years of declining mean lake TP concentrations (Fig. 1c). Three possible causes of the abrupt increase in deep-water SRP were investigated: (i) increased external TP loading; (ii) reduced deep-water renewal leading to an accumulation of SRP in the deep water; and (iii) increased internal P loading from the sediments.

**External loading.** While TP concentrations in the Lake of Zurich have declined since the 1970s, it is possible that a change in weather patterns (e.g., increased rainfall) in Segment III might have led to an increase in external TP loading. However, as discussed earlier, external TP loading from the Upper Lake of Zurich remained relatively stable throughout Segments II and III (Fig. 1e), and there was no significant correlation between annual mean external TP loading and annual mean deep-water SRP concentration (P > 0.1, n = 18; note that data on external TP loading were available only up to 2005). Additionally, there was no observed increase from Segment II to Segment III in P input from wastewater discharge (AWEL, 2010).

**Reduced deep-water renewal.** A reduction in either the frequency of occurrence or the intensity of deeply penetrative mixing events (deep-water renewal) could hinder the transport of SRP from the hypolimnion to the epilimnion. SRP derived from decaying particulate matter would then be trapped in the hypolimnion and would begin to accumulate over consecutive years. However, throughout Segment III, minimum annual deep-water SRP concentrations (determined from monthly means) remained relatively consistent over consecutive years (Fig. 3). For all three segments, a month-by-month comparison showed an increase in mean deep-water SRP concentration from March/April to October/November and a decrease from October/November to March/April (Fig. 4). During the period of weak stratification from October/November to

![Fig. 3 Time-series of the volume-weighted monthly mean deep-water SRP concentration (≥100 m depth) in the Lake of Zurich during Segment III (2001–2010).](image-url)
March/April, SRP concentrations increased in the epi/metalimnion and simultaneously decreased in the deep water (Fig. 4). This indicates that SRP was consistently mixed from the deep water into the epi/metalimnion once per year between October/November and March/April in all three segments. Therefore, despite the change in mixing patterns after the late-1980s CRS (Fig. 2), during Segment III mixing was still strong enough to hinder the carry-over of SRP in the deep water from one year to the next.

Internal P loading. To investigate whether deep-water SRP concentrations were quantitatively related to the extent of hypoxia, September deep-water SRP concentrations were compared to annual HF values. Before analysing lake nutrient time-series for the effects of interannual variability in climatic forcing, long-term trends resulting, for instance, from eutrophication or oligotrophication need to be removed (George et al., 2004; Jankowski et al., 2005). Because the behaviour of the O₂ and SRP time-series differed among the three segments, linear detrending over the entire time-series, as often practised (e.g., George et al., 2004), would be neither sufficient nor justifiable. Instead, linear detrending was carried out on each of the three segments separately. The detrended values from the three segments were then recombinated prior to comparing the two variables. Even after detrending by segment, the annual HF values and the September deep-water SRP concentrations still share the 3-segment pattern described earlier – consistently low values (Segment I), high variability (Segment II) and consistently high values (Segment III) – and are highly correlated (Fig. 5a; \( R^2 = 0.54, P < 0.001, n = 39 \)). Significant correlations were also found between the (detrended) September deep-water SRP concentration and the other two indicators of hypoxia; that is, the (detrended) AEH in September (Fig. 5b; \( R^2 = 0.64, P < 0.001, n = 39 \)) and the (detrended) annual DOH at a depth of 130 m (Fig. 5c; \( R^2 = 0.51, P < 0.001, n = 39 \)). The strong correlations suggest that the increase in the deep-water SRP apparent in Segment III has at least in part resulted from changes in redox conditions at the sediment-water interface, resulting in an increase in internal P loading from the sediment, related to the increasing extent and duration of hypoxia.

Discussion

An abrupt rise in air temperature over the Swiss Plateau in the late 1980s, associated with a large-scale climate regime change, was accompanied by abrupt increases in the temperature of lakes, rivers and groundwater (Anneville et al., 2004, 2005; Hari et al., 2006; Figura et al., 2011; North et al., 2013). Specifically in the case of the Lake of Zurich, water temperatures and thermal stability underwent an abrupt increase in winter and spring that altered the mixing regime (North et al., 2013), limited replenishment of O₂ to the hypolimnion, and eventually resulted in an increase in the extent and duration of seasonal hypoxia. The period of consistent seasonal hypoxia (Segment III) coincided with an increase in deep-water SRP concentrations; this increase is most likely predominantly the result of internal P loading.

The observed changes in winter thermal stability, mixing patterns and deep-water O₂ concentrations had been predicted in previous studies of the Lake of Zurich through the use of models (Peeters et al., 2002) or by inference from the analysis of isolated extreme events, such as particularly mild winters or hot summers (Livingstone, 1997; Jankowski et al., 2006; Rempfer...
et al., 2010; Gallina et al., 2011). The consistency between the predictions of these studies and the observations presented here provides a good indicator of the validity of models and case studies when predicting the impacts of climate change on lakes. This is particularly important for infrequently monitored lakes, for which the type of time-series analysis used in this study is not possible.

What is driving the increase in hypoxia?

The observed increase in the duration and extent of hypoxia can be linked to three major drivers: a reduction in the frequency and/or intensity of deep-water renewal, an increase in the lake’s recovery time (with regard to deep-water $O_2$ concentrations), and an increase in the duration of the stratification period. In a monomictic lake, deep-water renewal typically occurs once a year, some time in the winter or early spring. Deep-water $O_2$ is depleted during summer stratification and is replenished by deep mixing events. If the annual renewal of the deep water does not occur, or is incomplete (weak), deep-water $O_2$ concentrations will decrease over consecutive years (Livingstone, 1997). Wavelet analysis showed that after the late-1980s CRS, the power spectrum of deep-water $O_2$ concentration and temperature shifted to include more power at low frequencies, which represent multiannual cycles of deep-water renewal. This change in the power spectrum provides strong evidence that the increase in

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Fig. 5 Plot of the detrended September deep-water ($\geq 100$ m) SRP concentration in the Lake of Zurich against detrended values of (a) the hypoxic factor (HF); (b) the areal extent of hypoxia (AEH) in September; and (c) the annual duration of hypoxia (DOH) at 130 m depth. The dashed line is the fit of the linear regression. For each time-series, linear detrending was carried out on each of Segments I (1972–1987), II (1988–2000) and III (2001–2010) separately prior to plotting.
winter thermal stability has resulted in a reduction in the frequency and/or intensity of the occurrence of deeply penetrative winter mixing events.

In Segment II, just after the late-1980s CRS, both the lag-1 autocorrelation and the variance of the monthly mean HF time-series began to increase. An increase in either of these variables indicates a decrease in the resilience of the system and an increase in its recovery time, suggesting an upcoming change point (e.g., Dakos et al., 2008; Scheffer et al., 2009). This slowdown in the response of the system to stochastic perturbations can be seen in the results of the wavelet analysis. In Segment I, the deep-water O\(_2\) concentration shows a strong annual cycle (Fig. 2b), indicating that nearly every year the deep-water O\(_2\) that was consumed during the stratification period was replenished; the lake therefore recovered nearly every spring to a ‘normal’ O\(_2\) concentration. In Segments II and III, the annual cycle of advective mixing and aeration was weaker, with power being shifted to multi-annual cycles (Fig. 2b). During this period, deep-water renewal in winter and early spring was less intense and the O\(_2\) that had been depleted was not fully replenished every year. As a result, it took longer for the lake’s deep-water O\(_2\) concentration to return to ‘normal’ levels, suggesting the system could not recover as quickly as it used to.

Finally, the largest increase in the duration and extent of hypoxia – the transition from a variable HF (Segment II) to consistently high HF (Segment III) – corresponded to an abrupt increase in the duration of the stratification period at the end of the 1990s. Therefore, the likely cause of the increase in hypoxia in the Lake of Zurich can be summarized as follows: an abrupt decrease in the frequency or intensity of winter/spring mixing at the end of Segment I led to an increase in the variability of the duration and extent of hypoxia, and to an increase in the lake’s recovery time with respect to deep-water O\(_2\) replenishment. At the end of Segment II, an abrupt increase in the duration of the stratification period increased the stress on the system and initiated, or accelerated, the critical transition that occurred at the end of Segment II. In general, less O\(_2\) in the deep water available at the start of the stratification period, combined with a longer stratification period, meant that hypoxic conditions were reached earlier in the summer, and therefore tended to occur more consistently, last longer and extend across a larger area during Segment III than during Segments I and II.

What are the impacts of increasing thermal stability and hypoxia on nutrient dynamics?

Three potential causes of an observed increase in deep-water SRP concentration from Segment II to Segment III were investigated; viz., an increase in external TP loading, a reduction in the frequency and/or intensity of deep-water renewal and an increase in internal P loading. The data presented here suggest that the third of these is the most likely cause: as the deep-water SRP concentration was strongly correlated with the extent and duration of hypoxia, the increase in deep-water SRP concentration was most probably the result of an increase in internal P loading from the sediment, associated with the observed increase in extent and duration of hypoxia. Several of the indicators of internal P loading in stratified lakes, as outlined by Nürnberg (2009), were present in the Lake of Zurich. The profiles of the concentrations of TP and SRP increased with depth, indicating a sediment source. The deep-water SRP concentration increased from March/April to October/November, corresponding to the stratification period, when hypoxic conditions develop and internal P loading is expected to occur. Although the Lake of Zurich does not experience severe anoxia, both the duration and spatial extent of seasonal hypoxia have increased. The combination of indicators suggests that internal P loading is likely the dominant process contributing to the observed increase in deep-water SRP concentration in Segment III.

The internal P loading hypothesis could not, however, be confirmed with 100% certainty because of the difficulties associated with separating out the effects of changing mixing patterns and internal P loading, especially in view of the fact that the observed increase in mean annual deep-water SRP concentration occurred over a relatively short period of time. Instead, it is likely that a variety of factors control the nutrient flux across the sediment-water interface, and a much more detailed assessment would be required to fully understand the effect of the observed change in deep-water O\(_2\) concentrations on redox processes.

What are the lake management implications?

The observed increase in temperature and thermal stability in the Lake of Zurich (Livingstone, 2003; North et al., 2013) has been previously linked to changes in phytoplankton community composition (Anneville et al., 2005) and phytoplankton richness (Pomati et al., 2012). In addition, there has been an increase in the predominance of the cyanobacterium *Planktothrix rubescens* (Gallina et al., 2011; Posch et al., 2012), a known toxin producer (Microcystis-RR; Blom et al., 2001) that has been linked to animal deaths and poses a human health risk (Fortin et al., 2010). If the limiting nutrient for primary producers in the lake is P, changes in P dynamics as a result of internal P loading can be expected to have
consequences for the water quality of the lake. Although an investigation of nutrient limitation does not lie within the scope of this work, the topic does deserve further consideration, particularly in view of the current debate over whether we should be managing our lakes and oceans for P only (Schindler et al., 2008), or a combination of P and nitrogen (Scott & McCarthy, 2010).

In addition to the negative impacts on the lower trophic levels in the lake, there are also ramifications for fish. The lake is home to a commercial coldwater fishery, with lake trout (Salvelinus namaycush) the most abundant fish species (Massol et al., 2007). The observed increase in water temperature and decrease in deep-water O2 concentration combine to reduce the size and range of the coldwater fish habitat, a phenomenon referred to as the ‘thermal-dissolved O2 squeeze’ (Coutant, 1985; Arend et al., 2010). Throughout Segments II and III in the Lake of Zurich, O2 concentrations throughout the entire hypolimnion were below the hypoxic threshold for juvenile lake trout (O2 < 7 mg l−1; Evans, 2007) at least once every year. In contrast, this only occurred in 50% of years in Segment I. Combined with observed increases in epi/metalimnetic water temperatures, it is likely that in autumn, the habitable region for lake trout has decreased since the late-1980s CRS. The combined effect of the thermal-dissolved O2 squeeze and the increasing abundance of P. rubescens (Posch et al., 2012), a poor source of nutrition for higher organisms (Martin-Creuzburg et al., 2008), could begin to have a negative effect on all levels of the Lake of Zurich food web.

Outlook

Like any environmental system, lakes are driven by a multitude of competing factors, making it difficult to associate an observed change with any one specific driver. In this study, external P loading was clearly excluded as the main driver of increasing deep-water hypoxia. However, it cannot be eliminated as an indirect driver. During a period of high external P loading (e.g., pre-1980 in the Lake of Zurich), large amounts of P can be buried in the lake sediment. Eventually, the buried P may be reintroduced into the lake through internal loading. Similarly, the response of a lake variable to change is rarely straightforward, as demonstrated by the deep-water O2 concentration in the Lake of Zurich. Instead of reacting in an abrupt manner to the late-1980s CRS (e.g., by an abrupt increase in the extent of hypoxia), the deep-water O2 concentration underwent a transitional phase of high variability during Segment II, before steadying in Segment III (an approximately 13-year delay).

Previous studies have shown that lakes respond coherently to changing climatic forcing, particularly in the case of physical lake variables (Magnuson et al., 1990; Kratz et al., 1998; Magnuson & Kratz, 2000; Anneville et al., 2005; Livingstone et al., 2010). While chemical and biological variables behave less coherently than physical variables (Magnuson et al., 1990; Kratz et al., 1998; Magnuson & Kratz, 2000), there is growing evidence that an increase in hypoxia, as observed in the Lake of Zurich, is becoming more common across the Northern Hemisphere (e.g., Foley et al., 2012; Rössner et al., 2012) in response to a large-scale increase in lake surface water temperature (Schneider & Hook, 2010). The effect of the 1980s CRS on the Lake of Zurich is therefore an important example of how a continued global rise in air temperature could have a negative impact on lakes around the world, by resulting in an increase in the frequency of occurrence and extent of hypoxia and in an increase in internal P loading from the sediment.

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References


Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Time-series of the monthly hypoxic factor (HF) and of its lag-1 autocorrelation and variance, after removing trend and seasonality.

Figure S2. Time-series of the areal extent of hypoxia in September, the annual duration of hypoxia at a depth of 130 m and the annual duration of the stratification period.