REPORT

Long-term development of hypolimnetic oxygen depletion rates in the large Lake Constance

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Abstract This study investigates over 30 years of dissolved oxygen dynamics in the deep interior of Lake Constance (max. depth: 250 m). This lake supplies approximately four million people with drinking water and has undergone strong re-oligotrophication over the past decades. We calculated depth-specific annual oxygen depletion rates (ODRs) during the period of stratification and found that 50% of the observed variability in ODR was already explained by a simple separation into a sediment- and volume-related oxygen consumption. Adding a linear factor for water depth further improved the model indicating that oxygen depletion increased substantially along the depth. Two other factors turned out to significantly influence ODR: total phosphorus as a proxy for the lake's trophic state and mean oxygen concentration in the respective depth layer. Our analysis points to the importance of nutrient reductions as effective management measures to improve and protect the oxygen status of such large and deep lakes.

Keywords Anoxia · Lake management · Statistical modeling · Water quality

INTRODUCTION

Dissolved oxygen (DO) is an important water quality indicator and has been used as a key variable in the classification of lakes and reservoirs for decades (Hutchinson 1938; Mortimer 1942). During stratification deep water layers are cut off from atmospheric exchange and hypolimnetic DO decreases due to respiration and microbial degradation. In these layers, small hypolimnetic volumes and/or large amounts of decomposing biomass may lead to high oxygen depletion rates (ODRs) potentially

giving rise to hypoxic or even anoxic conditions in hypolimnia. Besides the more immediate adverse implications for the state of lakes, including the production of toxic compounds such as ammonia or hydrogen sulfide, DO also plays an important role in the biogeochemical cycling of nutrients and metal ions (Wendt-Potthoff et al. 2014). Under anoxic conditions, for example, ferric iron is reduced to ferrous iron in lake sediments. As a result, ferrous phosphate complexes dissociate and mobilized phosphate molecules are released into the water column that lead to high internal phosphorus loadings and accelerating eutrophication (Einsele 1936; Frevert 1980; Hupfer and Lewandowski 2008; Carstensen et al. 2014). As the risk of anoxic conditions in hypolimnia increases with a lake's trophic state, such increases in internal phosphorus loads may act as a positive feedback in the eutrophication of surface waters. Furthermore, concentrations of Mn(II) may increase significantly in the bottom layers during incidences of anoxia (Davison et al. 1982). This reduced manganese accumulates in aquatic organisms with harmful effects including impairment of fish development (Hagenmaier 1974; Srivastava and Agrawal 1983) and poses a substantial health risk in drinking water supplies (Bryant et al. 2011).

Given the central importance of DO for aquatic ecosystems, it is not surprising that oxygen has been at the center of numerous investigations of lake ecosystems. As water managers require reliable predictions of short- and long-term DO levels (Hupfer and Hilt 2008; Uhlmann et al. 2011), a number of different concepts and approaches have been developed in the past to explain and predict observed oxygen concentrations (e.g., Hutchinson 1938; Nürnberg 1995; Livingstone and Imboden 1996).

Hutchinson, for instance, assumed that lake morphometry had a profound impact on volumetric hypolimnetic

oxygen depletion rates (VHOD, Hutchinson 1938). He concluded that as the VHOD of a lake is related to the average concentration of biodegradable material, the volume of hypolimnia must have some impact on ODR. He hypothesized for two given lakes, differing only in their hypolimnetic volume the lake with the larger volume would exhibit significantly lower depletion rates. To eliminate the effects of lake morphometry on ODR, Hutchinson developed a new concept of oxygen depletion rates which he referred to as the areal hypolimnetic oxygen deficit (AHOD):

$$\text{AHOD} = \frac{dm}{A_H \cdot dt}. \quad (1)$$

A_H refers to the upper horizontal boundary area of the hypolimnion and dm/dt to the change in the amount of hypolimnetic oxygen per unit of time. While the VHOD is susceptible to lake morphology (Molot et al. 1992), the AHOD is regarded as independent and was readily accepted by many scientists (e.g., Cornett and Rigler 1980) due to its assumed direct proportionality to trophic state.

However, Nürnberg (1995) pointed out that though AHOD and VHOD provide estimates of DO depletion rates, they fail to quantify both the spatial and temporal extent of anoxic conditions ($\text{DO} < 1 \text{ mg L}^{-1}$) within lake ecosystems. To provide comparative information on the spatial extent of anoxia in different lakes, Nürnberg introduced the concept of the anoxic factor (AF). The AF describes the ratio of the anoxic sediment area in relation to the total surface area of a given lake. Due to the scaling by lake surface area, the AF represents a relative quantity which can be compared between lakes of different sizes. Another major conceptual progress of Nürnberg's approach was her focus on sediment area, which was not included in the previous concepts of AHOD and VHOD.

The conceptual developments by Nürnberg (1995) and Hutchinson (1938) suggest that mechanistic approaches to hypolimnetic oxygen dynamics should account for both sediment- and volume-related ODR. A simple framework for such a mechanistic approach—the point of departure for this study—was provided by Livingstone and Imboden's oxygen profile model (Livingstone and Imboden 1996). This mechanistic model (Eq. 2) is particularly interesting for both its novel approach to ODR as well as its simplicity.

$$J(z) = J_V + J_A \cdot \alpha(z). \quad (2)$$

Here, $J(z)$ represents the overall ODR at depth z , J_V the pelagic, volume-related ODR of water, J_A the benthic, sediment-related O_2 consumption, and $\alpha(z)$ the ratio of sediment area to water volume at depth z . Other studies have identified further variables which may significantly

affect hypolimnetic oxygen dynamics of lakes, including their nutrient loads and hypolimnetic water temperatures (Cornett 1989; Molot et al. 1992; Rippey and McSorley 2009). However, following the concept of maximum parsimony, Livingstone and Imboden (1996) intentionally neglected further parameters for the sake of the model's simplicity.

In view of the many adverse implications of hypoxic or even anoxic conditions, there is a clear need for effective tools helping to predict deep water oxygen concentrations in lakes. For an important system like Lake Constance, providing drinking water to four million people, continuous monitoring as well as reliable and applicable tools to predict hypolimnetic oxygen concentrations are crucial for societal welfare and a secured water supply. Though water quality and oxygen levels have been closely monitored in Lake Constance throughout the past decades, the prediction of oxygen levels has received comparatively little attention. The lake has undergone serious changes in trophic state—anthropogenic eutrophication shifted the lake into a eutrophic system around the late seventies and intense lake restoration measures turned it back into an oligotrophic system. This study focuses explicitly on the temporal and vertical variations of oxygen concentrations and ODR observed in Lake Constance in response to the divergent human influences in the past. We build upon the model suggested by Livingstone and Imboden (1996) and aim at identifying further relevant environmental variables. We primarily hypothesize that the lake's trophic state is significantly influencing ODR in such a way that the lake has now a stronger resistance against hypolimnetic anoxia than during times of intense eutrophication.

MATERIALS AND METHODS

Study site

Lake Constance is a large temperate, perialpine lake located on the northern slopes of the European Alps along the borders of Switzerland, Austria, and Germany. With major parts of its basin being deeper than 100 m, Lake Constance is considered a deep lake with a relatively large hypolimnetic volume (Fig. 1; Table 1). The natural state of Lake Constance was oligotrophic but since the sixties a continuous eutrophication was taking place which was peaking in the late seventies. During the past three decades Lake Constance has undergone re-oligotrophication with average total phosphorus concentrations (TP) decreasing from over $80 \mu\text{g L}^{-1}$ by the end of the seventies to less than $10 \mu\text{g L}^{-1}$ in 2010 (Fig. 2). For further information about Lake Constance we refer to Rinke et al. (2010).

Fig. 1 Contour map of the Lake Constance basin with the sampling station Fischbach-Uttwil (FU)

Table 1 Basic morphometric and hydrological characteristics of Lake Constance

Parameter	Value and unit
Altitude	395 m a.s.l.
Surface area	473 km ²
Max. depth	251 m
Average depth	100 m
Volume	48 km ³
Dimensions	63 × 14 km
Flow through	~ 10 km ³ a ⁻¹
Residence time	~ 5 a

Lake monitoring data

The water quality data on Lake Constance were provided by the BOWIS (Bodensee-Wasser-Informationssystem) database which is managed by the Internationale Gewässerschutzkommission für den Bodensee (IGKB; www.igkb.org) representing the international management board for Lake Constance. The monitoring program commissioned by the IGKB includes several physical, chemical, and biological water quality variables which are measured at bi-weekly or monthly intervals (station Fischbach-Uttwil, Fig. 1, see also Roßknecht 1998). We used data from the years 1977 until 2010 which include the period of maximum eutrophication and the following re-oligotrophication. Water samples were taken at 12 depths (0, 5, 10, 15, 20, 30, 50, 100, 150, 200, 230, and 250 m). The bathymetric map of Lake Constance and the corresponding hypsographic functions were provided by the IGKB.

Data analysis and statistical modeling

The starting point of our statistical analysis is the model by Livingstone and Imboden (1996), it is based on four

assumptions. First of all, hypolimnetic oxygen depletion rate $J(z)$ is assumed to comprise both a pelagic (J_V) as well as a sediment consumption rate (J_A) described in Eq. 2. Secondly, J_V is assumed to be constant over depth while J_A scales linearly with $\alpha(z)$, the ratio between the sediment surface area and the water volume at a given depth z . Thirdly, it neglects turbulent diffusion. In other words, it assumes lakes to consist of individual, isolated water layers. Analysis of long-term data as well as modeling studies showed that turbulent diffusion is very low in the water body below 100 m (Boehrer 2000; Rinke et al. 2010; Straile et al. 2010). This water body refers to the deep hypolimnion as the seasonal thermocline is consistently shallower than 100 m between April and October (Rinke et al. 2010). To ensure that this assumption is justified for Lake Constance we only analyzed oxygen dynamics below 100 m depth. Finally, the fourth assumption of this approach is the horizontal homogeneity of the system so that one measurement of the vertical gradient is representative for the whole lake. This is an idealized assumption that is never perfectly fulfilled (e.g., compare Rinke et al. 2009) but largely met within the central deep basin of Lake Constance.

Observed oxygen depletion rates were calculated using oxygen concentration measurements between April and October at the depths of 100, 150, 200, 230, and 250 m. During these months, stratification in Lake Constance is stable and vertical exchange is minimal (see above). However, due to very high fluctuations in oxygen concentrations in 1989, for this year we decided to include all measurements from March until December in order to achieve a reliable ODR estimate. Vertical temperature distributions suggest that in 1989 the thermal stratification persisted during this extended period and that the thermocline was still shallower than 100 m in December. Oxygen depletion rates (ODRs, g m⁻³ day⁻¹) were determined as the slope of the linear regression of oxygen concentrations against time for each sampled depth layer and individual year (see Fig. 3 as an example). The calculated depth-specific ODRs correspond to $J(z)$ in Eq. 2. Note that ODRs are given as negative values since they describe the decrease in oxygen concentration.

The ratio between sediment area (A) and water volume (V) at a given depth, $\alpha(z)$, was derived from the hypsographic function of Lake Constance (Livingstone and Imboden 1996):

$$\alpha(z) = \frac{dA(z)}{dV(z)}. \quad (3)$$

To calculate J_V and J_A values, a linear regression was calculated using the ODRs [representing $J(z)$ in Eq. 2] measured at depths between 100 and 250 m as dependent variables and the corresponding estimates of $\alpha(z)$ at the respective depths as independent variables. The slope of this regression line provides an estimate of the sediment

Fig. 2 **a** Total phosphorus concentrations measured in Lake Constance (deepest point, Station Fischbach-Uttwil) between 1977 and 2010. **b** Dissolved oxygen concentrations measured in Lake Constance between 1977 and 2010. Incomplete mixing events in the years 1989, 1990, 2007, and 2008 are reflected in lower oxygen concentrations throughout the following years. White areas: no data

oxygen depletion rate J_A , whereas the intercept corresponds to the volumetric oxygen depletion rate J_V . As the available dataset covered more than 3 decades, it was possible to subdivide the data into 11–12-year-long time intervals representing periods of highly eutrophic (1977–1987, $TP > 40 \mu\text{g L}^{-1}$), mesotrophic (1988–1999, TP between 10 and $40 \mu\text{g L}^{-1}$), and oligotrophic (2000–2010, $TP < 10 \mu\text{g L}^{-1}$) states. The separate analysis of ODR of these three time intervals allowed testing the effect of the lake's trophic state on its hypolimnetic oxygen dynamics. Model selection of competing model formulations was conducted using the likelihood ratio test (Crawley 2013). All calculations were done with the statistics software R (R Development Core Team 2010).

Research questions

We believe that hypolimnetic oxygen depletion in the large Lake Constance is primarily driven by two factors: (i) characteristics of the basin determine the increase of

ODR along the vertical axis and (ii) long-term development of ODR is determined by the lake's productivity. We assume the approach of Livingstone and Imboden (1996) using $\alpha(z)$ to entirely represent the influence from the basin morphology and assume total phosphorus (TP) as proxy of lake productivity. Although we do not expect further significant influence factors we used the existing dataset to test for further variables determining the oxygen depletion in Lake Constance.

RESULTS

Lake Constance underwent a strong decrease in total phosphorus (TP) concentrations over the observation period starting in 1977 from over $80 \mu\text{g L}^{-1}$ TP to below $10 \mu\text{g L}^{-1}$ TP in 2010 (Fig. 2). Concentrations of dissolved oxygen (DO) varied considerably over time and depth in Lake Constance (Fig. 2). At water depths below 100 m oxygen depletion became evident and minimum DO

Fig. 3 Changes in oxygen concentrations over time at different depths in the year 1981. The lines indicate regression lines of a linear model between oxygen concentration and time for data from April to October (black points) as outlined in the methods, gray points were not included in the regression

concentrations approached 5 mg L^{-1} at the lake's deepest point in some years. Due to incomplete mixing in some winters, e.g., the winter of 1988/1989, DO concentrations did not completely recover and vertical gradients of DO persisted over the cold season.

In some years, particularly during the eutrophic phase, a strong supersaturation of DO has been recorded at the surface. A distinct metalimnetic oxygen minimum recorded in every year represents a regular pattern in this lake. Interestingly, this metalimnetic oxygen minimum was less intense during the eutrophic phases while the spatial extent and the oxygen deficit were larger during the mesotrophic and oligotrophic periods. Between 50 m and 100 m depth, DO concentrations showed only little fluctuation over time.

Calculated ODRs also showed a high variability over space and time and generally increased with depth (Fig. 4). The depth-specific ODRs, however, were subject to considerable interannual variation. As a consequence, the Livingstone model (i.e., $\alpha(z)$ as the sole explanatory variable) was able to explain only 50% of the observed variability in the ODR of Lake Constance (Table 2; Fig. 5).

According to the Livingstone model, i.e., splitting oxygen consumption into a benthic and pelagic compartment, the water body below 100 m is largely dominated by pelagic oxygen consumption. While 81% of the overall oxygen consumption occurs in the lake's pelagic zone, only the remaining 19% is sediment related. Even when considering only the water body below 200 m, 65% of the oxygen depletion still occurs in the pelagic zone while only 35% occurs in the sediments. Although $\alpha(z)$ scales systematically with water depth (Fig. 5), the residuals of the Livingstone model still showed a trend with water depth. Including depth as an additional factor into the Livingstone model led to a significant improvement of the predictive power (significance level for depth: $p < 0.001$, see also Table 2) of almost 60% of the observed variability in ODR. No interaction between $\alpha(z)$ and depth was significant.

Figure 4 indicated that oxygen depletion was more intense during eutrophic phases. Calculating the Livingstone model separately for the eutrophic (1977–1987), mesotrophic (1988–1999), and oligotrophic periods (2000–2010) revealed that the estimated volumetric and

Fig. 4 Calculated oxygen depletion rates (ODR) between 1977 and 2010 in Lake Constance

Table 2 Overview of the different statistical models evaluated. The models are described by the response variable on the left-hand side of the tilde and all explanatory variables on the right-hand side. The following explanatory variables are included: ratio of sediment surface over water volume (α), depth (z), total phosphorus concentration in the upper 50 m during overturn ($TP_{mix, 0-50}$), and the average oxygen concentration during stratification (April to October) in each depth ($O_{2, strat}$). R^2 coefficient of variation, BIC Bayesian information criterion, df degrees of freedom

Nr.	Model	R^2	BIC	df
1	$ODR \sim \alpha$	0.51	-1411.1	2
2	$ODR \sim \alpha + z$	0.60	-1437.0	3
3	$ODR \sim \alpha + z + TP_{mix, 0-50}$	0.62	-1444.5	4
4	$ODR \sim \alpha + z + TP_{mix, 0-50} + O_{2, strat}$	0.67	-1461.1	5

Fig. 5 **a** Scaling of the sediment surface to water volume ratio, $\alpha(z)$, in the deep hypolimnion of Lake Constance (below 100 m depth) against water depth. **b** Scatter plot of the model of Livingstone and Imboden (1996), i.e., depth-specific oxygen depletion rates in Lake Constance in response to the ratio of sediment surface to water volume, $\alpha(z)$; $n = 170$ (34 years times 5 depth levels). **c** Plot of observed versus simulated ODR for the best statistical model (see Table 4)

sediment-related ODRs in fact diminished with decreases in the lake's trophic state (Table 3). An ANCOVA with trophic state as explanatory variable and $\alpha(z)$ as covariate revealed that trophic state has a significant effect on ODR (ANCOVA, $F_{2,166} = 4.58$, $p = 0.01$). An extended version

of Livingstone's model included besides depth also the TP concentration of the upper 50 m during winter mixing ($TP_{mix,0-50}$) as a proxy for the nutrient availability and thus algal productivity (see Table 2). This extended model accounted for 62% of the observed variability in ODR. The

variable $TP_{\text{mix},0-50}$ turned out to be significant (linear model treatment contrast for $TP_{\text{mix},0-50}$: $p < 0.001$) while the interaction terms remained insignificant.

We tested whether water temperature (calculated as the average water temperature between April and October in each respective depth and year) would affect the lake's ODR. This turned out not to be the case and water temperature had no significant effect on the ODR. However, only very little variation was present below 100 m (ranging between 3.9 and 5.2 °C) making temperature unlikely to play a dominant role.

We used the long-term monitoring dataset to identify further significant variables determining the oxygen depletion rates. Among the available variables, the average oxygen concentration during stratification (April to October) in each depth appeared to be the most influential and leads to a substantial improvement of the statistical model (Table 2). The higher the oxygen concentration the more pronounced was the oxygen depletion in the respective depth. All interactions between these variables remained insignificant and the resulting model including all main factors explained 67% of the observed variability in ODR. This resulting multiple linear regression model, consisting of four main factors and no interaction terms, was found to be the most informative statistical model (Table 4). A comparison of simulated versus observed ODR illustrated the remaining, i.e., unexplained, variability (Fig. 5c).

We used this final model (see Table 4) to project hypolimnetic oxygen dynamics in a forward dynamic simulation under different trophic conditions in Lake Constance (oligotrophic: $TP = 8 \text{ mg m}^{-3}$ and eutrophic: $TP = 80 \text{ mg m}^{-3}$, Fig. 6). We assumed a worst case scenario of two consecutive years without any deep water renewal resulting in ongoing oxygen depletion over 1000 days. The projections show that Lake Constance is able to withstand two years without deep water renewal with respect to hypolimnetic oxygen concentrations, even in a eutrophic state. A reduced trophic state, however, clearly reduces ODR within the lake and the oligotrophic state is more resilient against hypolimnetic anoxia. Minimal oxygen concentrations at the deepest point approached

1 g m^{-3} under eutrophic conditions while at the oligotrophic state concentrations around 3 g m^{-3} prevailed. Due to the lake's oligotrophic state and the unlikelihood of a complete absence of mixing over several years, Lake Constance appears to be at present highly protected against anoxic conditions.

DISCUSSION

The statistical analysis of a dataset of over 30 years of oxygen measurements in the deep hypolimnion of Lake Constance revealed that oxygen depletion rates scale with several environmental factors. First of all, the simplified approach of Livingstone and Imboden (1996) which divided a lake's oxygen depletion into a pelagic and a benthic zone appeared to be important and valid but not overall statistically powerful. The Livingstone model, which accounts only for the morphological effects of the lake's basin, explained only 50% of the observed variability in ODR. Three further factors appeared to be important for predicting ODR in Lake Constance: water depth, phosphorus concentration, and oxygen concentration. These four variables together explained roughly two-thirds of the overall variability in ODRs. Given the extremely low variability in water temperature below 100 m depth in Lake Constance, water temperature was not significantly affecting ODR. Other authors comparing lakes with larger variation in hypolimnetic temperatures, however, provided strong evidence for the importance of temperature (e.g., Cornett and Rigler 1979).

Our analysis showed that oxygen depletion in Lake Constance is dominated by volume-related, i.e., pelagic, oxygen consumption and not by sediment-related oxygen consumption. Given the large volume and depth of Lake Constance this outcome was expected. This finding complies with comparable studies in estuaries (Kemp et al. 1992; Heip et al. 1995) where it was found that pelagic respiration dominates integrated water column respiration (pelagic + benthic) at depths larger than 10–20 m.

Table 3 Table of volumetric (J_V) and sediment-related (J_A) oxygen depletion rates in Lake Constance according to the Livingstone model and calculated for the overall study period as well as for the periods of eutrophic, mesotrophic, and oligotrophic state of Lake Constance. Values are given $\pm$ standard errors, coefficients of variation (R^2) are given for the corresponding linear models between ODR and α as given in Eq. 2

Period	J_V ($\text{g O}_2 \text{ m}^{-3} \text{ day}^{-1}$)	J_A ($\text{g O}_2 \text{ m}^{-2} \text{ day}^{-1}$)	R^2
Eutrophic (1977–1987)	$-5.43 \times 10^{-3} \pm 0.77 \times 10^{-3}$	$-75 \times 10^{-3} \pm 10.5 \times 10^{-3}$	0.489
Mesotrophic (1988–1999)	$-4.58 \times 10^{-3} \pm 0.57 \times 10^{-3}$	$-64 \times 10^{-3} \pm 7.8 \times 10^{-3}$	0.531
Oligotrophic (2000–2010)	$-3.93 \times 10^{-3} \pm 0.52 \times 10^{-3}$	$-64 \times 10^{-3} \pm 7.1 \times 10^{-3}$	0.603
All years (1977–2010)	$-4.64 \times 10^{-3} \pm 0.37 \times 10^{-3}$	$-67 \times 10^{-3} \pm 5.1 \times 10^{-3}$	0.514

Table 4 Summary of the model statistics for the best multiple linear regression model (model four in Table 2). The full expression of the statistical model is: $ODR(z) = f_0 + f_1 \cdot \alpha(z) + f_2 \cdot z + f_3 \cdot TP_{\text{mix}, 0-50} + f_4 \cdot O_{2, \text{strat}}$. See Table 2 for parameter description

Target variable	Factor name	Estimate	SE	p
Intercept	f_0	1.9×10^{-2}	3.7×10^{-3}	<0.001
α	f_1	-4.8×10^{-2}	6.0×10^{-3}	<0.001
z	f_2	-5.4×10^{-5}	6.9×10^{-6}	<0.001
$TP_{\text{mix}, 0-50}$	f_3	-3.2×10^{-5}	8.4×10^{-6}	<0.001
$O_{2, \text{strat}}$	f_4	-1.4×10^{-3}	3.0×10^{-4}	<0.001

Fig. 6 Simulated projections of oxygen concentrations in Lake Constance under the assumption of two consecutive years without any deep water renewal as predicted by the statistical model in Table 4. An initial oxygen concentration of 12 mg L^{-1} was chosen as this is a typical concentration in a year with complete winter overturn. Projections were computed for a eutrophic state (left, $TP_{0-50} = 80 \text{ } \mu\text{g L}^{-1}$, around year 1980) and for an oligotrophic state (right, $TP_{0-50} = 8 \text{ } \mu\text{g L}^{-1}$, current situation)

The significant effect of water depth on ODR was unexpected as the original Livingstone model already accounted for the basin morphology by including $\alpha(z)$, i.e., the ratio between sediment surface area and water volume. We interpret the observed significance of depth as a particularity of very deep lakes where processes are at work that increase ODR in greater depth. Based on our data we can only speculate on the reasons. Process studies in Swiss lakes documented that the flux of reduced substances from the sediment (e.g., ammonia, Fe(II), etc.) are an important cause of oxygen consumption (Matzinger et al. 2010; Müller et al. 2012). It was also shown that ground water inflow into Lake Constance contributes significantly to the import of dissolved substances (Müller and Gächter 2012), which implies a flux of reduced substances into the basin. However, these processes are unlikely to influence the water body below 100 m depth significantly. We rather hypothesize that sinking seston particles from the upper pelagic productive zone are already degrading during sedimentation and therefore intensify oxygen consumption in deeper layers before reaching the sediment. Algal cells, for example, stay physiologically active for some time

when sedimenting out of the euphotic zone (Benndorf 1968) and die only after a sufficiently long time in the dark interior of lakes. Since Lake Constance is a very deep lake, the duration of sedimentation is long and probably lasts several weeks (assuming sinking velocities between 1 and 10 m day^{-1} , Benndorf 1968; Wetzel 2001). This implies that in deep lakes many algal cells die while sinking down and their decay takes place in greater depths during sinking. The additional oxygen demand of decaying algae during sedimentation might be the cause for the increasing oxygen depletion with depth and the corresponding significant effect of depth in our statistical analysis.

We found oxygen depletion in a given depth to be dependent on the average oxygen concentration in this layer. A direct dependence of respiration rates on oxygen concentrations, however, was clearly ruled out by previous experiments (Cornett and Rigler 1984). The effect of the oxygen concentration on ODR, however, was also found in other statistical analyses (Molot et al. 1992; Wagner and Kruse 1995) and is therefore most likely a proxy for another causal factor. High oxygen concentrations could be interpreted as indicators of a strong vertical mixing in the

last winter. The corresponding supply of easily degradable organic carbon from the euphotic zone might result into intensified oxygen depletion. Alternatively, a fertilization effect could be a mechanism that links vertical mixing with intensifying oxygen depletion. Intensified upward flux of nutrients due to mixing may fertilize algal growth in the euphotic zone during the following spring period and thus increase sedimentation rates and ODRs. Empirical evidence supporting such mechanisms, however, has not been found in our data.

We rather hypothesize that the significant effect of mean oxygen concentration results from the diffusive oxygen fluxes through the sediment water interface. Oxygen consumption of lake sediments is fed by oxygen fluxes from the water into the sediments through the benthic boundary layer where transport is only possible by diffusion (e.g., Jørgensen and Revsbech 1985; Bryant et al. 2010). In fact, this diffusive transport can be limiting so that the thickness of the benthic boundary layer determines the flux of oxygen from the water into the sediment (Lorke et al. 2003; Bryant et al. 2010). Since the flux through the benthic boundary layer is proportional to the prevailing oxygen gradient, the resulting rate of sediment oxygen uptake necessarily scales with the average oxygen concentration in the open water (the bulk concentration according to Bryant et al. 2010). In the studies mentioned above, the open water oxygen concentration at distances more than 50 cm above the sediment surface was in the order of $3\text{--}6\text{ g O}_2\text{ m}^{-3}$ (Jørgensen and Revsbech 1985; Bryant et al. 2010).

Robustness of results

We evaluated the robustness of our results by calculating ODRs on the basis of different time spans. That is, instead of using the oxygen concentrations between April and October for calculating the average oxygen depletion rate we also tried time spans from April to November or March to November. Although the computed ODRs differed slightly from those calculated from April to October, the significance levels and estimates of the different statistical models (compare Table 4) remained similar and the conclusion on the best model was always the same. The same held true if oxygen depletion was calculated based on percent saturation instead of using absolute concentrations.

Implications from global warming

Global warming poses a substantial threat to the hypolimnion of lakes due to the increased risk of anoxia. In Lake Zurich, a large perialpine lake in the vicinity of Lake Constance, warming rates of water layers above 20 m have been approximately twice as high per decade over the last 50 years than for layers below 20 m (Livingstone 2003).

This difference in warming rates has enhanced the lake's thermal stability, thus extending the annual stratification period by 2–3 weeks. Such prolonged periods of limited vertical oxygen exchange and continuous oxygen depletion may, in turn, lead to deteriorating oxygen conditions in the hypolimnia of lakes.

Worse still, oxygen replenishment through overturn may become inefficient in deep temperate lakes due to increasingly milder winters. Following global warming, winter circulation may become a rare event in deep temperate lakes, turning monomictic into oligomictic lakes (Livingstone 2003). In fact, model simulations for large perialpine lakes have predicted a change towards an oligomictic mixing type pointing to an increased risk of hypolimnetic anoxia (Danis et al. 2004). In warmer winters, surface water does not cool down to hypolimnetic temperatures and winter mixing remains incomplete. In such situations winter mixing does not penetrate deep enough to affect water at all depths. This effect was also observed in Lake Constance (Straile et al. 2010) and may be responsible for low oxygen concentrations in some of the recent years when the lake has already turned into an oligotrophic state but winter mixing was incomplete (see Fig. 2). In Lake Zurich, an increase in frequency of such incomplete mixing events has intensified anoxic conditions in the deep hypolimnion. This, in turn, has promoted an increased phosphorus release from the sediments (North et al. 2014) leading to a new phase of eutrophication. A particularly harmful situation may arise from such developments if deep waters are subject to increasing levels of salinity. Even if such increases take place at slow rates, e.g., due to the release of carbonates from the sediments or geogenic salt water intrusions (Boehrer and Schultze 2008), a sufficiently long period of incomplete mixing may still lead to critically high salinity gradients. The resulting high-density water cannot be mixed by convective forces after a critical salinity threshold has been surpassed. This phenomenon turns oligomictic lakes into meromictic lakes—a development that seems to be already at work in some of the large perialpine lakes on the southern slope of the European Alps (Ambrosetti and Barbanti. 2005).

Alternative ways of oxygen import into deep hypolimnia

A central assumption of the Livingstone model is that the vertical transport of O_2 via turbulent mixing is negligible during the stratified period. This is, of course, an idealized assumption as some degree of mixing will always take place. Field studies in the western Lake Constance suggest that vertical diffusion may still be sufficient to transport DO across the thermocline during summer stratification (Heinz et al. 1990) thus mediating a small oxygen flux into

the hypolimnion. However, given the large dimensions of the lake's basin with a maximum depth of over 250 m and a thermocline depth of approximately 10–40 m (Rinke et al. 2010), these low oxygen fluxes through the thermocline will hardly affect oxygen concentration in the deep interior of the lake. Empirical estimates of vertical mixing in the hypolimnion of Lake Constance indicated mixing coefficients in the order of $10^{-5} \text{ m}^2 \text{ s}^{-1}$ (Boehrer 2000). Vertical mixing at this intensity results in effective vertical length scales of 10–20 m over one stratification period. In conclusion, in Lake Constance vertical mixing during the stratified period is very limited and cannot mediate oxygen transport from the thermocline into the lake's deep hypolimnion. However, at water layers deeper than 220 m where $\alpha(z)$ and ODR each change very quickly with depth (compare Fig. 5) the model predictions may well be influenced by these low vertical mixing intensities. As a result, predicted oxygen gradients may become steeper than observed gradients.

Winter mixis always results in a positive oxygen flux into the deep hypolimnion. Interestingly, we also found such positive oxygen fluxes in years with incomplete mixing pointing to alternative processes that mediate a transport of oxygen-rich water into the hypolimnion. During the winter of 1988/1989, for example, the lake remained thermally stratified and convective mixing did not occur deeper than 200 m. Yet, the oxygen concentration in 250 m depth increased substantially from 6 to 10 mg L^{-1} . Sometimes large inflow volumes from the river Rhine, the major inflow into the lake, penetrate into the deep hypolimnion due to high sediment load (Fink et al. 2016). During these events, the density of the inflowing water is substantially increased by mineral particles and a plume is formed that quickly penetrates into the deep interior of the lake sometimes reaching the deepest point. Such density-driven inflow plumes are also documented in other lakes and reservoirs (Byun et al. 2005). A recent analysis by Fink et al. (2016) indicated that these plumes constitute a regular characteristic of Lake Constance and contribute substantially to the oxygen dynamics within the deep hypolimnion. In brackish environments, e.g., the Baltic Sea, similar plumes can be generated by saline intrusions into the deep waters (Rosenberg et al. 2016). Differential cooling has also been shown to represent another origin of density-driven plumes of oxygen-rich water into the deep hypolimnion (Boehrer and Schultze 2008). This phenomenon occurs during autumnal cooling when the surface water in shallow bays cools down faster than in the center of the basin, reaches the temperature of maximum density, and subsequently sinks down along the slopes of the basin. Previous reports hypothesized that differential cooling may significantly contribute to the deep water renewal in Lake Constance (KLIWA 2007).

Trophic state and lake management

Lake Constance as a large and deep lake with a huge hypolimnetic water volume is able to store large quantities of dissolved oxygen. In the water volume below 100 m depth around 60 tons of dissolved oxygen constitute a relatively large oxygen storage compared to the areal oxygen consumption at the sediment surface (121 km^2). Lake Constance is therefore well protected against anoxia due to its basin morphometry, remaining fully oxygenated even during its highly eutrophic phase with TP concentrations of about $80 \text{ } \mu\text{g L}^{-1}$.

Our statistical model clearly indicated a significant effect of TP concentrations on the lake's hypolimnetic oxygen levels predicting higher oxygen depletion rates under eutrophic than under oligotrophic conditions (Fig. 6; Table 3). Given the variables in our model, the TP concentration in the lake remains the only factor which can be influenced by lake management. This points to the importance of a comprehensive phosphorus management (e.g., Kleinman et al. 2015; Schoumans et al. 2015) for safeguarding the water quality in aquatic ecosystems. Decreases in the phosphorus content of Lake Constance over the past 35 years have already reduced the oxygen depletion to a rather low—most probably close to natural—level. As a result, the lake's resilience to anoxia is close to its maximum and the current state of Lake Constance makes the occurrence of anoxia very unlikely even in spite of global warming. In view of climate change and the expected increased likelihood of incomplete winter mixing, the decision of the international lake management board (IGKB, Internationale Gewässerschutzkommission für den Bodensee, www.igkb.org) to reduce phosphorus inputs to the very low level prevailing today has proven to be right.

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