Oxygen depletion in lake hypolimnia

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Abstract

The Livingstone and Imboden (1996) model for the oxygen depletion rate in lake hypolimnia was evaluated with field results in 32 lakes. The volumetric oxygen consumption rate (J_V) was strongly related to lake trophic state, as represented by the growing season mean chlorophyll *a* (Chl *a*) and annual mean total phosphorus concentration, and might reach a maximum of 0.23–0.24 g O_2 m^{-3} d^{-1} in eutrophic lakes. The areal oxygen consumption rate (J_A) was not related to trophic state and was lower than the value estimated by the sediment core method, particularly in eutrophic lakes; the mean was 0.0816 ± 0.0150 g O_2 m^{-2} whole sediment d^{-1}. We modified the model and it was used to confirm that the field J_A, the average for the hypolimnion for the deoxygenation period, is influenced by J_V and the range of sediment area to water volume ratio, $\alpha(Z)$ (Z is water depth), in the hypolimnion, as well as the oxygen consumption rate in whole sediment (R). It was suggested that this is the reason for the difference between field and sediment core J_A values. The R in 10 lakes varied from 7 to 460 g O_2 m^{-3} whole sediment d^{-1}. Overall, the Livingstone and Imboden model with constant J_A and with a J_V value derived from an empirical relationship with either measure of trophic state was considered to be a suitable condensed model for oxygen depletion in lake hypolimnia.

Introduction

The depletion of oxygen in lake water, particularly in the hypolimnion, was one of the characteristics of lakes studied by the early limnologists. For example, Strom (1931) introduced the areal hypolimnetic oxygen deficit (AHOD) to summarize the behavior of oxygen in hypolimnia, and Hutchinson (1938) and Mortimer (1942) used it to classify lakes. Hutchinson (1957) has summarized this early research, after which the focus was to relate AHOD to measures of lake trophic state and to understand the influence of lake morphometry and other properties. The final result of this effort was the statistical model of Cornett and Rigler (1980), which allows AHOD to be predicted from lake water annual mean total phosphorus concentration, lake mean depth, and water temperature in the hypolimnion, although prediction by a nutrient loading model (Welch and Perkins 1979; Vollenweider and Janus 1982) should not be forgotten.

These AHOD models cannot simulate oxygen concentration–depth profiles, except in a general way; the mean oxygen concentration in a hypolimnion of mean depth Z after a period of days (t) would be the initial concentration − (AHOD/Z)/t. Cornett (1989), however, did develop a statistical model to predict the oxygen depletion rate in strata in the hypolimnion that used stratum water temperature, stratum water volume to sediment surface area, and phosphorus accumulation rate in the sediment, and it can be used to calculate the oxygen concentration–depth profiles at any time during stratification. Molot et al. (1992) also developed an empirical model to predict the oxygen concentration–depth profile at the end of the summer, and Clarke et al. (2002) have evaluated its wider application. The model uses stratum water volume to sediment surface area ratio, initial oxygen concentration and either the growing season mean epilimnetic total phosphorus concentration or

concentration in spring. During this period, Nurnberg (1995) introduced a new concept, the Anoxic Factor, to summarize the behavior of oxygen in lakes and developed a statistical model to predict its value.

Livingstone and Imboden (1996) developed a deductive model to describe the depletion rate of oxygen in lake hypolimnia. It separates the consumption of oxygen in water from consumption in the sediment to describe the influence of lake morphometry on the oxygen depletion rate. Morphometry was characterized by the sediment area to water volume ratio in the water strata, and the values for the consumption rate in water and sediment apply spatially over the hypolimnion and to the period of deoxygenation, which is seen as an additional advantage of the model (Pace and Prairie 2005). It is almost identical to that of Stefan and Fang (1994), in that they differ only in the degree of aggregation of model parameters. Pace and Prairie (2005) have recently synthesized what is known about respiration in lakes, integrated the results, and developed models to estimate the respiration of organic carbon in the global lake population.

Our motivation for returning to this topic was the European Union's Water Framework Directive (Directive 2000/60/EC), which requires that the quality of the structure and functioning of aquatic ecosystems associated with surface waters is used to establish the ecological quality of surface waters. Although biological properties are the main focus, oxygenation conditions are described as supporting them, and they can also be considered an important structural characteristic of lakes, with oxygen depletion an important process. Whether the hypolimnion is oxygenated, deoxygenated, or intermediate is part of the structure of a lake, in that this affects profundal macroinvertebrates (Dinsmore and Prepas 1997), fish habitat (Evans et al. 1996), and the internal loading and recycling of phosphorus (Nurnberg 1984) and iron and manganese (Davison 1993); the rate of oxygen depletion has already been used to classify lakes (Hutchinson 1957).

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We chose to investigate the Livingstone and Imboden (1996) model further. Those researchers encouraged it, and perhaps our models of the important physicochemical and biological properties of lakes need to be made more deductive or, at least, less empirical if climate change alters the interrelationships between lake properties. Also, perhaps the model has not been fully evaluated because it has only been used to model change in the oxygen profile during the eutrophication of one lake. Therefore, our aim in the work reported here was to evaluate the Livingstone and Imboden model for the oxygen depletion rate in hypolimnia; for this, we collected results from five Irish lakes and collated results for a further 28 from the literature.

Methods

The five Irish lakes used in this investigation are Lough Alina, Ballydugan Lough, Lough Macrory, Heron Lough, and White Lough. They are small lakes in the deglaciated landscape of Northern Ireland, with areas of 7, 12, 21, 5, and 6×10^4 m^2, respectively, and they were visited weekly between 06 April and 07 June 2005. The mean and maximum water depths are 5.5 and 14.0 m, respectively, in Alina, 4.9 and 12.0 m in Ballydugan, 2.8 and 10.5 m in Macrory, 3.9 and 10.5 m in Heron, and 6.2 and 10.7 m in White Lough. The thermal stratification in Lough Macrory was too weak to estimate the oxygen depletion rate, but the areal consumption rate was still estimated from sediment cores. The lakes were chosen so that they covered a range of trophic states, as represented by the annual mean total phosphorus concentration, which was 11, 20, 38, 40, and 110 μg P L^{-1} in Macrory, Alina, White, Ballydugan, and Heron, respectively.

Water samples from the mixed layer were taken with a Ruttner sampler, and a composite was produced. The concentration of chlorophyll *a* (Chl *a*) was determined by hot methanol extraction (Marker et al. 1980). The temperature and oxygen concentration depth profiles were recorded at a central site with a YSI MP556 Multi-Probe System with barometer and a YSI 5562 oxygen–temperature probe with 20 m of cable. The probe was calibrated in the field at each lake with water-saturated air and the barometric pressure.

The temperature results were used to estimate the eddy diffusion coefficient of heat for the main period of deoxygenation according to the flux-gradient method (Jassby and Powell 1975).

The Livingstone and Imboden (1996) model was used with the oxygen results for four of the Irish lakes to estimate values for the volumetric oxygen consumption rate and areal oxygen consumption rate. This model of the depletion of oxygen in the hypolimnion of a lake is

$$J(Z) = J_V + J_A \alpha(Z) \qquad (1)$$

where $J(Z)$ is the oxygen depletion rate (g O$_2$ m^{-3} water d^{-1}) at water depth Z (m of water), J_V is the volumetric oxygen consumption rate (g O$_2$ m^{-3} water d^{-1}), J_A is the areal oxygen consumption rate (g O$_2$ m^{-2} whole sediment d^{-1}), and $\alpha(Z)$ is the sediment surface area to water volume ratio (m^2 sediment m^{-3} water) at water depth Z. J_V and J_A

are assumed to be constant with water depth and time and the vertical diffusion of oxygen is assumed to be negligible. The slope of the linear regression of $J(Z)$ against $\alpha(Z)$ is, therefore, an estimate of J_A and the intercept an estimate of J_V. The consumption of oxygen in the sediment as a proportion of the total consumption in the water stratum at water depth Z is $(\alpha(Z)J_A)/J(Z)$.

Estimates of J_V and J_A in other lakes were also made with the use of field results collated from the literature. The Web Appendix (http://www.aslo.org/lo/toc/vol_54/issue_3/0905a.pdf) gives the sources of the results and how $J(Z)$ and $\alpha(Z)$ were derived. Results from 28 additional lakes, mostly from Canada, were available.

Between 3 and 14 data points were included in the regressions of $J(Z)$ against $\alpha(Z)$ (mean = 7.7, median = 8), and so the statistical power of some regressions to establish small J_A values was low. For example, for $\alpha = 0.05$, between 30 and 300 data points are needed for a test to establish a product moment correlation coefficient between 0.30 and 0.10, respectively, with a power of 0.50; for $\alpha = 0.10$, 19–180 data points are needed (Cohen 1988). As a result, we used an α significance criterion of >0.05 in some regressions; α was <0.05 in 17 lakes, >0.05 but <0.29 in seven, and >0.29 in the remainder. When the regression between $J(Z)$ and $\alpha(Z)$ was not considered significant, and so the value of J_A was indistinguishable from zero, the mean of the $J(Z)$ values was used as an estimate of J_V.

J_A in the Irish lakes was also estimated from sediment cores in the laboratory according to the method of Sweerts et al. (1989). The sediment cores were collected with a modified Kajak–Brinkhurst gravity corer, and three replicate cores were taken from sediment in the upper part of the hypolimnion—three from the middle and three from the deepest part—between 21 July and 23 August 2005. They were incubated at the average temperature of the hypolimnetic water (9.1°C in Alina, 8.7°C in Ballydugan and Heron, 10.2°C in Macrory, and 6.5°C in White) and aerated overnight. A stirring rate of 10 rpm was used to produce a diffusive boundary layer thickness of around 1 mm, which is considered typical of the conditions in the hypolimnion of lakes, and the oxygen concentration was measured with a HACH HQ10 oxygen–temperature probe. J_A was not correlated with water depth in any lake; *p* varied between 0.203 and 0.924 (average = 0.513, median = 0.566). The coefficient of variation of J_A (*n* = 9) for each lake was between 10.1% and 14.4%, and the standard error was between 0.019 and 0.036 g O$_2$ m^{-2} d^{-1} (mean = 0.028, median = 0.027). Graneli (1977) also found low spatial variability of J_A measured with sediment cores in three lakes; the standard error was between 3.1% and 10.5% of the mean value.

The Livingstone and Imboden (1996) model was modified as follows. J_A has been modeled by Bouldin (1968), and his steady-state model based on a zero-order reaction rate of oxygen consumption (Eqs. 2–5) has been widely used.

$$J_A = [2R\varphi C(0)D_S]^{0.5} \qquad (2)$$
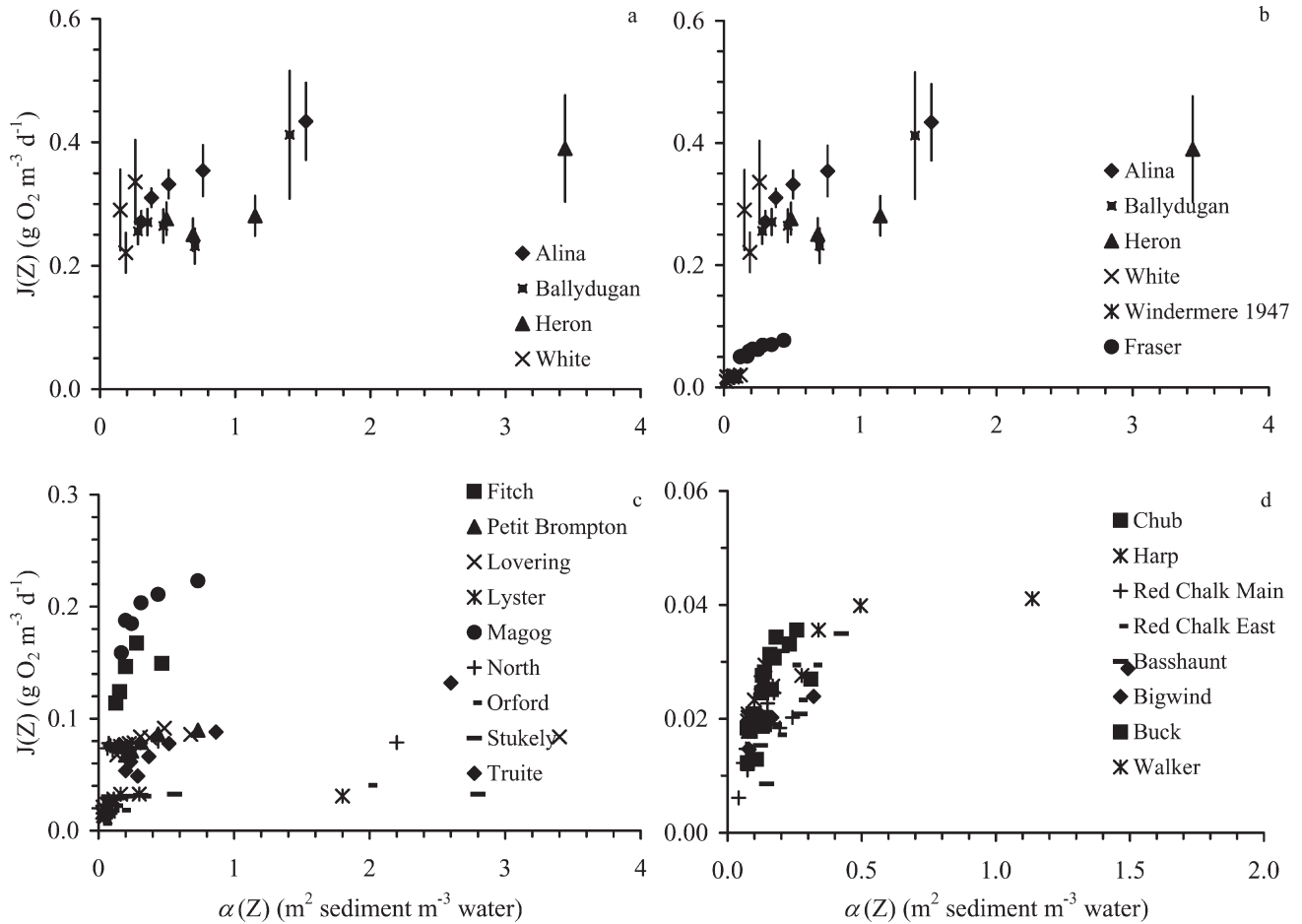
$$L = [2\varphi C(0)D_S/R]^{0.5} \qquad (3)$$

Fig. 1. The variation of oxygen depletion rate, $J(Z)$, at water depth Z with the sediment area to water volume ratio, $\alpha(Z)$, in strata in the hypolimnion of lakes. (a) Four Irish lakes, Alina, Ballydugan, Heron, and White. (b) Four Irish lakes and Lake Windermere North and Lac Fraser, Quebec. (c) Nine Quebec lakes. (d) Eight central Ontario lakes. Where shown, the error is standard error.

$$J_A = RL \qquad (4)$$

$$C(z) = (R/2\varphi D_S)z^2 - [2RC(0)/\varphi D_S]^{0.5}z + C(0) \quad (5)$$

$C(z)$ is the oxygen concentration in pore water (g O_2 m^{-3} water) at depth z in the sediment (m whole sediment), φ is the porosity of the sediment (m^3 water m^{-3} whole sediment), R is the zero-order rate of oxygen consumption in the whole sediment (g O_2 m^{-3} whole sediment d^{-1}), $C(0)$ is the oxygen concentration at the sediment–water interface (g O_2 m^{-3} water), D_S is the diffusion coefficient of oxygen in the whole sediment (m^2 whole sediment d^{-1}), and L is the depth of oxygen penetration in the sediment (m whole sediment). Steady-state conditions with φ, R, and D_S constant with depth are assumed. Hall et al. (1989) then improved the Bouldin model by including a diffusive boundary layer above the sediment–water interface (Eq. 6).

$$J_A = [(R\delta_D D_S)/D]$$
$$\left(1 - \left\{[2D^2\varphi C_w]/[(RD_S\delta_D^2) + 1]\right\}^{0.5}\right) \qquad (6)$$

C_w is the oxygen concentration in the water stratum (g O_2

m^{-3} water) above the diffusive boundary layer, δ_D is the thickness of the diffusive boundary layer (m water), and D is the diffusion coefficient of oxygen in water (m^2 water d^{-1}). Rearranging Eq. 2, the oxygen concentration at the sediment surface at the bottom of the diffusive boundary layer is as shown in Eq. 7.

$$C(0) = J_A^2/(2R\varphi D_S) \qquad (7)$$

Values for D were taken from Broecker and Peng (1974), D_S was from Maerki et al. (2004), and a temperature of 10°C and sediment porosity of 0.98 were used; D was 0.000151 m^2 water d^{-1}, and D_S was 0.000136 m^2 whole sediment d^{-1}. A time step of 1 d and an initial value for C_w of 10 g O_2 m^{-3} were used. $\alpha(Z)$ was taken to be in the range 0.2–1.0 m^2 whole sediment m^{-3} water, with $\delta_D = 1$–5 mm and $J_V \leq 0.3$ g O_2 m^{-3} d^{-1}.

Results

The oxygen depletion rate in the hypolimnion, $J(Z)$, did not vary greatly with sediment area to water volume ratio, $\alpha(Z)$, in the four Irish lakes (Fig. 1a). Only in Lough Alina is the $J(Z)$–$\alpha(Z)$ regression significant at $p < 0.05$. The

Table 1. The volumetric oxygen consumption rate (J_V) and areal oxygen consumption rate (J_A) estimated by the Livingstone and Imboden (1996) model (Eq. 1) with field results in 32 lakes. The standard error (SE) of the value, number of points (n), maximum value of sediment surface area to water volume ratio [Max. $\alpha(Z)$], and coefficient of determination (R^2) of the regressions are also given. Where the J_A value was not significantly different from zero at $p > 0.05$, but a value is recorded, the p value is given in parentheses. Where no J_A value is recorded, the p value was >0.28, and where the regression was significant, but $J_V = 0$, the p value for J_V is given in parentheses. The maximum $\alpha(Z)$ value shown in parentheses was ignored.

Lake	J_V (g O_2 m^{-3} yr^{-1})	SE	J_A (g O_2 m^{-2} yr^{-1})	SE	n	Max. $\alpha(Z)$	R^2
Alina	0.257	0.0139	0.119	0.0169	5	1.52	0.94
Ballydugan	0.200	0.0352	0.135 (0.062)	0.0463	5	1.40	0.74
Heron	0.236	0.0140	0.0442 (0.18)	0.00752	4	3.44	0.95
White	0.282	0.0334			3	0.26	
Windermere North	0.0135	0.00132	0.0592	0.0214	9	0.12	0.52
Fraser	0.0407	0.00246	0.0866	0.00957	9	0.44	0.92
Magog	0.162	0.0110	0.0923	0.0275	6	0.73	0.74
Fitch	0.116	0.0194	0.0977 (0.26)	0.0706	5	0.47	0.39
Truite	0.0523	0.00431	0.0319	0.00401	7	2.60	0.93
Petit Brompton	0.0674	0.00343	0.0324	0.00916	7	0.73	0.71
Lovering	0.0700	0.00309	0.0318	0.00869	9	0.68 (3.40)	0.66
Stukely	0.0279	0.00064	0.00930	0.00262	9	0.56 (2.80)	0.65
Lyster	0.0145	0.00177	0.0746	0.0161	13	0.30 (1.80)	0.66
Orford	0.00905	0.00123	0.0672	0.00962	12	0.33 (2.00)	0.83
Brompton	0.0349	0.00104			13	3.80	
Central Memphremagog	0.0171	0.00215			14	1.70	
Massawippi	0.0191	0.00216			12	1.70	
North Memphremagog	0.0731	0.00142	0.0125 (0.12)	0.00701	8	0.44 (2.00)	0.35
Blue Chalk	0.0317	0.00745			3	0.35	
Chub	0.0160	0.00421	0.0499 (0.10)	0.0272	10	0.31	0.30
Crosson	0 (0.63)		0.227	0.0660	8	0.19	0.66
Dickie	0.0417	0.00860			3	0.54	
Harp	0.00977	0.00271	0.119	0.0257	12	0.17	0.68
Plastic	0.0335	0.0113			3	1.11	
Red Chalk Main	0.00877	0.00244	0.0636	0.0185	10	0.24	0.60
Red Chalk East	0.00390	0.0129	0.0811 (0.24)	0.0492	4	0.33	0.58
Basshaunt	0.0105	0.00470	0.0566	0.0220	9	0.42	0.48
Bigwind	0.0181	0.00062	0.00763	0.00138	12	1.49	0.75
Buck	0.00798	0.00370	0.114	0.0219	8	0.26	0.82
Gullfeather	0.0403	0.00337			3	0.50	
Solitaire	0 (0.10)		0.334	0.0498	6	0.12 (0.27)	0.92
Walker	0.0298	0.00502	0.0111 (0.28)	0.00765	4	1.14	0.51

slope is a field estimate of areal oxygen depletion rate (J_A), and the intercept is a field estimate of volumetric oxygen depletion rate (J_V). However, if a less severe criterion is used, then the results for Ballydugan Lough ($p = 0.062$) and Heron Lough ($p = 0.18$) also give field estimates of J_A and J_V for these lakes (Table 1). The reason for using $p > 0.05$ with a relatively small number of data points in the regression was described in *Methods*. The regression is not significant ($p = 0.75$) in White Lough, and the small range of $\alpha(Z)$ (maximum = 0.26 m^2 m^{-3}; Table 1) and very small number of data points ($n = 3$) make estimating what must be a low J_A value difficult; J_V was calculated as the average of the $J(Z)$ values (Table 1).

The linear relationship between $J(Z)$ and $\alpha(Z)$ in the hypolimnion of Windermere North Basin in 1947 and in Lac Fraser (Quebec, Canada) is shown in Fig. 1b, and the J_V and J_A values derived from the regressions are given in Table 1. With the lakes in Quebec there was no sensible relationship between $J(Z)$ and $\alpha(Z)$ in Central Memphremagog and Massawippi, so the mean $J(Z)$ was used as an estimate of J_V (Table 1). Linear relationships between $J(Z)$

and $\alpha(Z)$ in the other lakes (Fig. 1c) were used to estimate field J_A and J_V values, in two cases (Fitch and North Memphremagog) with $0.27 > p > 0.05$ (Table 1). With five of these lakes, the data point with the highest $\alpha(Z)$ value was ignored (3.40 m^2 m^{-3} in Lovering, 2.80 in Stukely, 1.80 in Lyster, 2.00 in Orford, and 2.20 in North Memphremagog) because the relationship was strongly linear with the remainder of the results (Fig. 1c). A reason for this behavior is proposed in *Discussion*. The linear relationships in the central Ontario (Canada) lakes were used to derive field J_V and J_A values, in three cases (Chub, Red Chalk East, and Walker) with $0.05 < p < 0.29$ (Table 1). The data point with the highest $\alpha(Z)$ value in Solitaire was ignored.

Overall, $J(Z)-\alpha(Z)$ results for 32 lakes were collected or collated from the literature, and 32 J_V and 24 J_A values were derived (Table 1). The range of $J(Z)$ is large, ≤ 0.4 g O_2 m^{-3} d^{-1}, and the range of the $\alpha(Z)$ variable varied from 0.08 to 3.80 m^2 m^{-3}, with a typical value of 0.50 m^2 m^{-3} (Fig. 1).

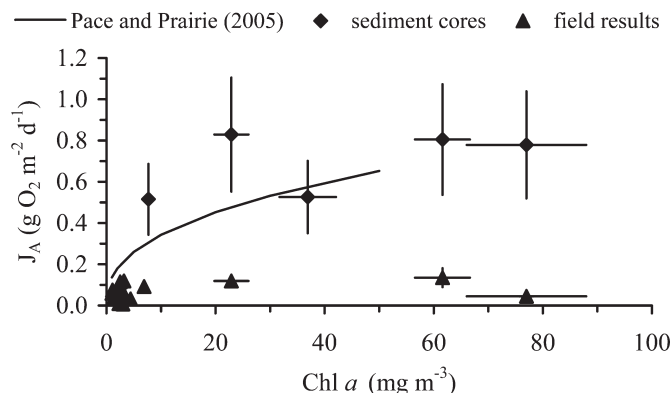J_A was also measured in the five Irish lakes by the sediment core method. Because no relationship between J_A

Fig. 2. The variation of areal oxygen consumption rate (J_A) with mean growing season lake water chlorophyll *a* (Chl *a*) concentration. The empirical relationship developed by Pace and Prairie (2005) for sediment cores, the value measured from sediment cores in the five Irish lakes, and the value estimated by the Livingstone and Imboden (1996) model (Eq. 1) with field results in four Irish lakes are given. Where shown, the error is standard error.

and water depth appeared in any of these lakes, the mean value for each lake was calculated. It increases with mean growing season Chl *a* concentration, and this behavior agrees with the empirical relationship derived with sediment cores by Pace and Prairie (2005) (Fig. 2). The field J_A values derived from the Livingstone and Imboden (1996) model (Table 1) are also included in Fig. 2. If the empirical relationship is used to indicate the J_A value that would be estimated from sediment cores, as was found to be reasonable with the five Irish lakes, then Fig. 2 shows that all but two of the 22 field-derived J_A values are less than the sediment core values; the sediment core value is greater by between -0.16 and 0.73 g O_2 m^{-2} d^{-1} (mean = 0.19, median = 0.12). The largest difference is found in the three Irish lakes because the field J_A value does not increase with Chl *a* concentration once the value is >5–10 mg m^{-3}. Although the sediment core method attempts to reproduce the hydrodynamic conditions at the sediment–water interface in lakes, as was the case with the method used in the Irish lakes (Sweerts et al. 1989), the difference between the field and sediment core values appears to be too great, particularly in eutrophic lakes, to be caused by the somewhat artificial nature of sediment cores.

One of the assumptions of the Livingstone and Imboden (1996) model that was used to derive the field J_A and J_V values is that vertical diffusion of oxygen is negligible. The effect of this on the observed values of $J(Z)$, and so on J_V and J_A in the Irish lakes, was established by correcting the observed $J(Z)$ for diffusion. This was completed by using the eddy diffusion coefficients of heat, estimated for each stratum for the main period of deoxygenation from late April to early May to early June 2005. The mean coefficient was 0.118 ± 0.022 m^2 d^{-1} in Alina ($n = 5$), 0.0604 ± 0.0036 m^2 d^{-1} in Ballydugan ($n = 5$), 0.0158 ± 0.0053 m^2 d^{-1} in Heron ($n = 4$), and 0.056 ± 0.013 m^2 d^{-1} in White ($n = 4$). The eddy diffusion coefficient of heat was applied to mass and so, because the coefficient for mass can be less than for heat in strongly

thermally stratified layers of water (Quay et al. 1980), the diffusion of oxygen should not be larger than the values based on the diffusion coefficient of heat. Ignoring heat loss to the sediment should also not lead to much of an underestimate of the eddy diffusion coefficient.

The observed vertical oxygen concentration gradient in the strata of a lake, along with areas of the upper and lower boundaries of the strata and the eddy diffusion coefficient, were used to calculate the differences between the masses of oxygen entering and leaving the strata. The differences were then converted to changes in concentration by using the volumes of the strata. There was no relationship between the strata and water depth, so the average net vertical transport of oxygen was calculated for each lake: -0.091 ± 0.024 g O_2 m^{-3} d^{-1} in Alina, -0.047 ± 0.0085 in Ballydugan, -0.019 ± 0.015 in Heron, and -0.001 ± 0.011 in White; a negative net vertical transport indicates that transport is toward the sediment surface. These values are small compared with the mean $J(Z)$, -0.317 ± 0.018 g O_2 m^{-3} d^{-1} in Alina, -0.2557 ± 0.0085 in Ballydugan, -0.235 ± 0.035 in Heron, and -0.249 ± 0.041 in White (average = 13%; range, 0.22–29%). If $J(Z)$, corrected for the net effect of diffusion, is used instead of the observed value, then only small changes in the values of J_V and J_A are derived by Eq. 1. The estimates of J_V are not statistically different, except at Alina, and the mean difference between corrected and observed is -0.024 g O_2 m^{-3} d^{-1} (range, -0.001 to -0.043 g O_2 m^{-3} d^{-1}). The mean difference between corrected and observed J_A values for the three lakes is -0.061 g O_2 m^{-2} d$^-$ (range, -0.033 to -0.079), and the estimates of J_A made with the observed and corrected $J(Z)$ values are statistically different, except at Ballydugan.

This analysis of the effect of vertical transport on the estimates of J_V and J_A from Eq. 1 in these four eutrophic lakes shows that it alters the values only a little; it changes J_V by an average of -0.024 g O_2 m^{-2} d^{-1}, which is small compared with the range of observed values of -0.200 to -0.282 (Table 1). The effect on J_A is larger: the average change is -0.061 g O_2 m^{-2} d^{-1} and the observed values are -0.0442, -0.119, and -0.135 for Heron, Ballydugan, and Alina, respectively (Table 1); only in Heron is the effect important, but this is because of the low J_A value in this lake. However, because J_V and J_A were also estimated from the literature, this assumption needs to be assessed further. Although the effect of vertical transport on AHOD has been widely assessed, only Cornett and Rigler (1987) considered the net effect of transport in and out of strata on the depletion rate in the strata; the assessment was completed mainly from oligotrophic lakes, and these are included in Table 1. They found that transport into and out of strata were highly correlated and that net vertical transport was much smaller than the total flux of oxygen. Of the 160 strata in 12 mainly oligotrophic lakes, net transport into these strata was $>20\%$ of $J(Z)$ in only 26% of the strata. Their assessment does indicate that the J_V and J_A values estimated from field results should not be affected much by assuming that net transport of oxygen is negligible in oligotrophic lakes. Overall, the influence of diffusion is so small in oligotrophic and eutrophic lakes

that this assumption does not reduce the advantage of estimating J_V and J_A from field results. The true J_A values might be a little greater than those estimated by Eq. 1.

Discussion

Field values of J_V *and* J_A—The volumetric oxygen consumption rate, J_V, and areal oxygen consumption rate, J_A, were derived from the Livingstone and Imboden (1996) model in 32 lakes (Table 1), and these values, along with the sediment area to water volume ratios, $\alpha(Z)$, in the hypolimnia, do reproduce the generally linear variation of oxygen depletion rate, $J(Z)$, with $\alpha(Z)$ (Fig. 1). If J_A is taken to be constant during the deoxygenation period, then the applicability of this model to reproducing field observations is given by the value of the coefficient of determination of the regression (mean = 0.68; median = 0.67; range, 0.30–0.95). Some of the lower values could be caused by the smaller $\alpha(Z)$ range in those lakes, for the linear regression between coefficient of determination and maximum $\alpha(Z)$ is significant (p = 0.020, 23 df). An examination of Fig. 1 does indicate that any departure from linearity in a lake occurs at the upper end of the $\alpha(Z)$ range; a reason for this is suggested below.

No relationship exists between the field J_A and J_V values in the lakes (Fig. 3a); the linear regression is not significant (p = 0.85, 23 df). This finding is not influenced by the groups of lakes that were used; in particular, the seven lakes at the bottom left of Fig. 3a and the 10 at the upper left are not distinguished by the origin of the results, mainly the 12 lakes in Quebec and 14 in central Ontario.

Volumetric oxygen consumption rate—J_V is related to two measures of lake trophic state: the growing season mean Chl a concentration (Fig. 3b) and the annual mean total phosphorus concentration (Fig. 3c). The relationship is more precise with Chl a, with a suggestion that J_V reaches a maximum value in eutrophic lakes. Although only the four Irish lakes are considered, this value is 0.244 $\pm$ 0.0174 g O_2 m^{-3} d^{-1} (Table 1). If the relationship with total phosphorus is used, then five values can be employed, the four Irish lakes and Magog, and the maximum value is 0.227 $\pm$ 0.0212 g O_2 m^{-3} d^{-1} (Table 1).

The literature supports the relationship between J_V and trophic state described by Fig. 3b and c. To use the results in the literature, however, it must be assumed that J_V is approximately the mean value of $J(Z)$ for the hypolimnion, which is true in many, but not all, lakes in which $J(Z)$ does not vary much with $\alpha(Z)$ (Fig. 1), and that the consumption of oxygen in the sediment, $\alpha(Z)J_A$, is small compared with total consumption [mean $J(Z)$]. The mean $J(Z)$ would be greater than J_V if consumption in the sediment is not small compared with total consumption. J(60 m) in Lake Rotoiti increased from 0.024 to 0.071 g O_2 m^{-3} d^{-1} from 1957 to 1984 (*see* fig. 5 in Vincent et al. 1984), and because the mean Chl a concentration was 6.7 mg m^{-3} during the 1967–1970 period and 9.6 mg m^{-3} during 1981–1982, these results (Fig. 3d) are consistent with the J_V–Chl a relationship in Fig. 3b. The relationship between the volume-weighted average $J(Z)$ value in the hypolimnion of five
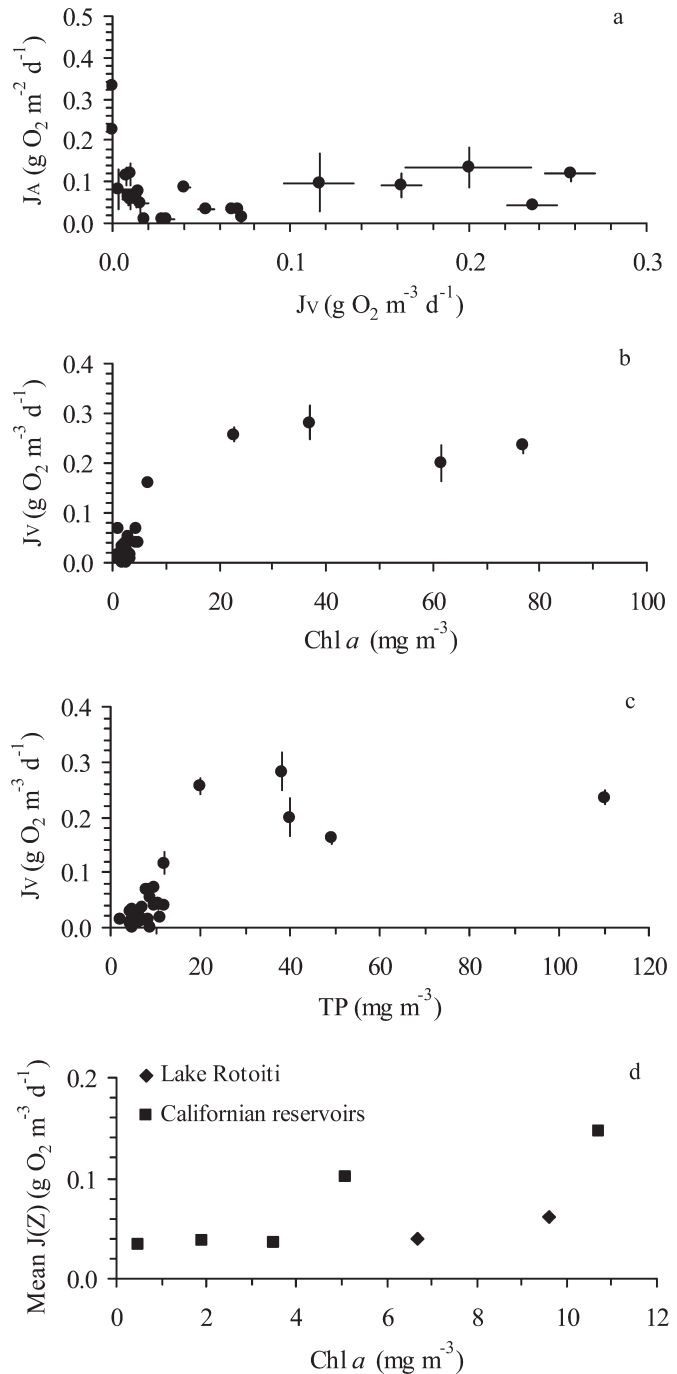
Fig. 3. The variation of (a) areal oxygen consumption rate, J_A, with volumetric oxygen consumption rate, J_V, in the hypolimnion of 22 lakes; (b) J_V with growing season mean lake water chlorophyll a (Chl a) concentration in 29 lakes; (c) J_V with annual mean lake water total phosphorus concentration (TP) in 32 lakes; (d) mean oxygen depletion rate in the hypolimnion, $J(Z)$, at water depth Z with Chl a in Lake Rotoiti and six reservoirs in California. Where shown, the error is standard error.

reservoirs in California and the Chl a concentration (*see* table 1 in Beutel 2003; Fig. 3d) is also consistent with the relationship in Fig. 3b. Mathias and Barcia (1980) found that, although the volume-weighted average $J(Z)$ value in the hypolimnion is related to $\alpha(Z)$, the average $J(Z)$ is

higher in eutrophic lakes; lakes with Chl $a > 5$ mg m^{-3} and $\alpha(Z)$ values of 0.6–0.8 m^2 m^{-3} have an average $J(Z)$ value of ≤ 0.22 g O$_2$ m^{-3} d^{-1}. Finally, the volume-weighted hypolimnetic oxygen concentration at the end of the summer can be used to estimate the mean $J(Z)$ in 80 lakes in south-central Ontario (Quinlan et al. 2005). Because spring overturn occurs between the last week of April to mid-May and autumn overturn is around 1 September (Molot et al. 1992), the time period available for deoxyenation is 120 d. If the oxygen concentration at spring overturn is 8 g O$_2$ m^{-3}, the average of 14 lakes in central Ontario (Molot et al. 1992), then the mean $J(Z)$ for the 80 lakes is ≤ 0.067 g O$_2$ m^{-3} d^{-1}. The maximum value could be higher than this because deoxygenation could have occurred before September in the eutrophic lakes, but these values are generally consistent with the relationship in Fig. 3c, in that the 90th percentile annual mean total phosphorus concentration for these lakes is approximately 24 mg m^{-3} (Quinlan et al. 2005).

The form of the relationship between J_V and Chl a or total phosphorus concentration is not clear (Fig. 3b,c). J_V could reach an upper limit value; if so, it could be in the range 0.227–0.244 g O$_2$ m^{-3} d^{-1}. The relationship could be logarithmic, although the number of data points that are >5 mg m^{-3} Chl a or >15 mg P m^{-3} total phosphorus is not sufficient to conclude this; the logarithmic relationship described by Fig. 3b is $J_V = 0.0657$ ln(Chl a) $- 0.0275$ ($R^2 = 0.79$).

An explanation of the form of the J_V–trophic state relationship could be based on the volume of water within which the oxygen concentration is reduced as a result of diffusion to the surface of the particles that are responsible for oxygen consumption in the hypolimnetic water; the sphere of water around a particle that is affected in this way is 20 times the radius of the particle (Koch 1971). As the concentration of particles in hypolimnetic water increases as trophic state increases (Baines and Pace 1994), the spheres begin to overlap and so the rate of increase of J_V decreases (logarithmic relationship) or becomes zero (upper limit value). The effect of particles moving through water during sedimentation on the size of the spheres also needs to be taken into account (Karp-Boss et al. 1996). An upper limit value of 0.23–0.24 g O$_2$ m^{-3} d^{-1} is also realistic; use of the oxygen uptake rate for detritus of 1–2 mg O$_2$ g^{-1} hr^{-1} from Fig. 1 in Hargrave (1972) and a solids concentration in hypolimnetic water of 5–10 g m^{-3} in eutrophic lakes suggests that J_V would be 0.12–0.48 g O$_2$ m^{-3} d^{-1}.

Areal oxygen consumption rate—J_A and the two measures of lake trophic state—growing season mean Chl a (p = 0.93, 21 df) and annual mean total phosphorus concentration (p = 0.88, 23 df)—are not related; the mean J_A value is 0.0816 $\pm$ 0.0150 g O$_2$ m^{-2} whole sediment d^{-1} (n = 24, median = 0.0654; range, 0–0.334; Table 1). These field results suggest that the consumption of oxygen in hypolimnetic sediment does not increase with trophic state, although it should be pointed out that only three lakes have Chl $a > 7$ mg m^{-3}, so further results are needed to clarify this indication.

J_A has been widely estimated from sediment cores, and it was found that these values are greater than the field values by ≤ 0.73 g O$_2$ m^{-2} d^{-1} (mean = 0.19, median = 0.12) and that this depends on the trophic state of the lake (Fig. 2). The possibility that this difference was due to the assumption in the Livingstone and Imboden (1996) model that vertical diffusion of oxygen can be ignored was evaluated; it was found to change the field J_A values very little and not enough to account for the lower field J_A values.

The basis of comparison of the sediment core J_A, which relates to a part of the sediment at one time during deoxygenation, with the field value, which characterizes the areal oxygen consumption over the hypolimnion for the period of deoxygenation, is not clear, even ignoring the somewhat artificial nature of sediment cores. It is, however, possible to assess how the field value relates to J_A through a modification of the Livingstone and Imboden (1996) model. It could be that J_A does not have a constant value in all water strata in the hypolimnion for the whole period of deoxygenation. Its value might be determined by the oxygen consumption rate in the whole sediment, R, and modified by the oxygen concentration in the water at the sediment surface, $C(0)$, which changes during deoxygenation of the stratum. The value of $C(0)$ is further influenced by oxygen consumption in the water stratum, J_V, and also by the sediment area to water volume ratio, $\alpha(Z)$, in that the higher this value, the greater is the effect of consumption in the sediment on the concentration in the stratum, $\alpha(Z)J_A$ (Eq. 1). Because R, J_V, and $\alpha(Z)$ should influence the value of J_A, and because J_A changes during deoxygenation, the Livingstone and Imboden model was modified by replacing the constant J_A parameter with the Hall et al. (1989) model for J_A. The modified model, described in *Methods*, was used to investigate the effect of R, J_V, and $\alpha(Z)$ and of the diffusive boundary layer thickness (δ_D), on the average value of J_A for the whole hypolimnion for the period of deoxygenation.

A low value of R (20 g O$_2$ m^{-3} whole sediment d^{-1}) is needed to produce an average J_A for the period of deoxygenation between 0.13 and 0.20 g O$_2$ m^{-2} d^{-1}, for $\delta_D = 1$ mm, J_V over the range 0.02–0.30 g O$_2$ m^{-3} d^{-1}, and $\alpha(Z)$ over the range 0.2–1.0 m^2 m^{-3} (Fig. 4; Table 2). The average J_A decreases as J_V increases, by 0.007 to 0.058 g O$_2$ m^{-2} d^{-1} for a given value of $\alpha(Z)$, and, as $\alpha(Z)$ increases, by 0.003 to 0.041 for a given value of J_V.

The decrease in average J_A as $\alpha(Z)$ increases is not large (0.003–0.041 g O$_2$ m^{-2} d^{-1}) compared with the average value (0.13–0.20), but the effect of J_A not being constant over the hypolimnion does also lead to a further lowering of the field J_A when fitting a linear regression to the $J(Z)-\alpha(Z)$ results. This can be shown as follows: The change in average J_A with $\alpha(Z)$ for a given J_V value can be calculated from the results in Table 2; it is -0.05 g O$_2$ m^{-2} sediment d^{-1} (m^2 sediment m^{-3} water)$^{-1}$ for $J_V \leq 0.10$ g O$_2$ m^{-2} d^{-1}, and it can be used to alter the value of J_A in Eq. 1 as $\alpha(Z)$ varies from a constant value of 0.20 g O$_2$ m^{-2} d^{-1}. In this way, the $J(Z)-\alpha(Z)$ relationship that would be observed when J_A is not constant can be reproduced (Fig. 5). The slope of this relationship, ignoring that it is nonlinear, gives the J_A that would be derived by Eq. 1, the field value, and it is reduced from 0.20 to 0.095 g O$_2$ m^{-2} d^{-1}, if the regression uses $\alpha(Z) \leq 2.0$ m^2 m^{-3}, or to
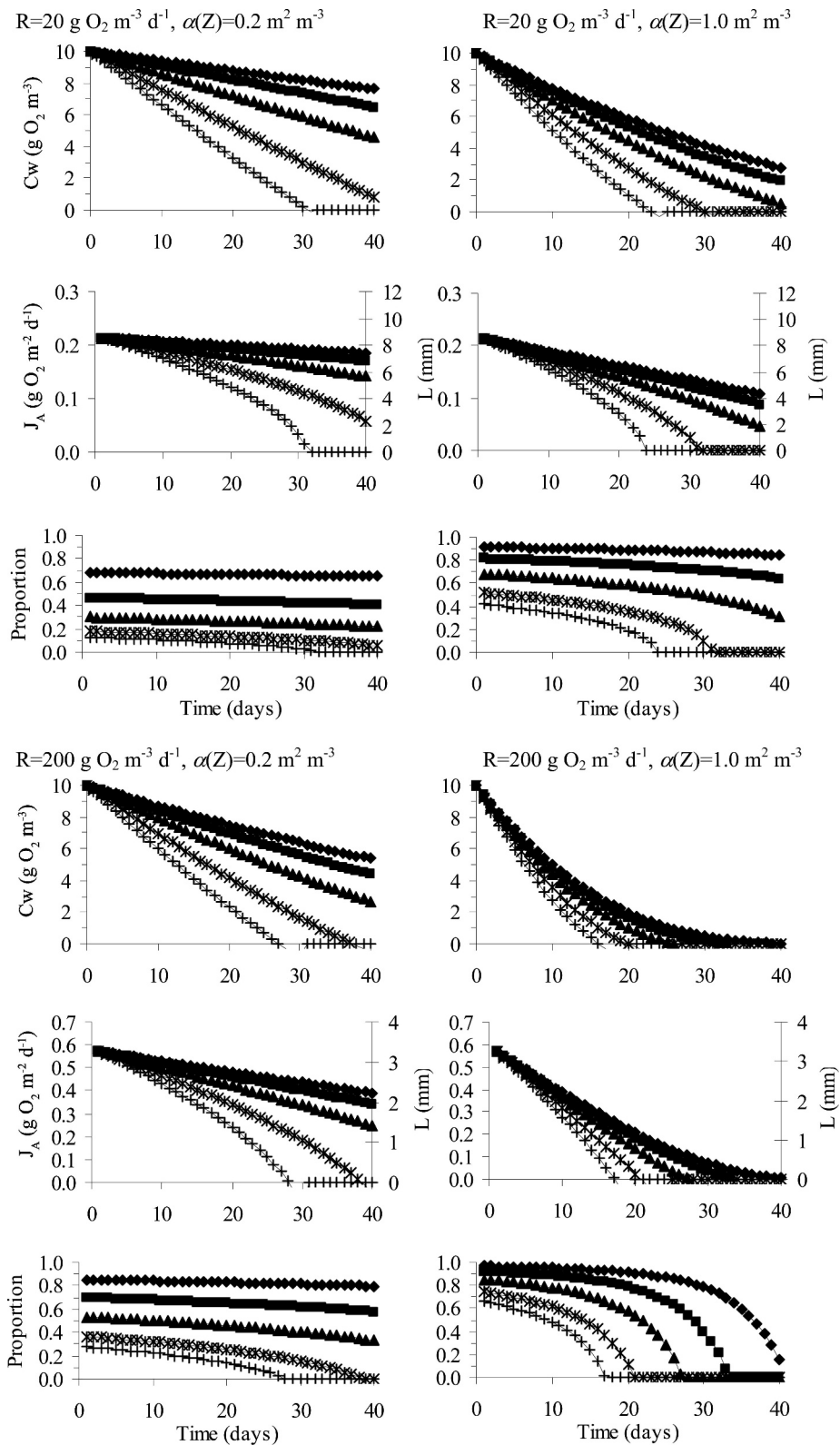
Fig. 4.   The variation of oxygen concentration in the water stratum, C_w; areal oxygen consumption rate, J_A; and consumption of oxygen in the sediment as a proportion of the total consumption in the water stratum with time during deoxygenation as predicted by the modified Livingstone and Imboden (1996) model for five values of the volumetric oxygen consumption rate (0.02, 0.05, 0.10, 0.20, and 0.30 g O_2 m^{-3} d^{-1}, corresponding to diamond, square, triangle, X, and +, respectively); two values of the sediment area to water volume ratio, $\alpha(Z)$; two values of the zero-order rate of oxygen consumption in the whole sediment, R; and a diffusive boundary layer thickness of 1 mm.

Table 2. The areal oxygen consumption rate (J_A, g O_2 m^{-2} whole sediment d^{-1}) and consumption in the sediment as a proportion of the total consumption in the water stratum, as predicted by the modified Livingstone and Imboden (1996) model for five values of the volumetric oxygen consumption rate (J_V, g O_2 m^{-3} d^{-1}), three values of the sediment area to water volume ratio [$\alpha(Z)$, m^2 sediment m^{-3} water], two values of the zero-order rate of oxygen consumption in whole sediment (R, g O_2 m^{-3} whole sediment d^{-1}), and two values of the diffusive boundary layer thickness (δ_D).

J_V	J_A and consumption in sediment as proportion of total					
	$R = 20$ g O_2 m^{-3} d^{-1} and $\delta_D = 1$ mm for three $\alpha(Z)$					
	0.2		0.4		1.0	
0.02	0.199	0.67	0.190	0.79	0.161	0.89
0.05	0.192	0.43	0.182	0.59	0.152	0.74
0.10	0.179	0.26	0.168	0.40	0.136	0.56
0.20	0.147	0.13	0.136	0.20	0.132	0.37
0.30	0.141	0.08	0.138	0.15	0.135	0.29
	$R = 200$ g O_2 m^{-3} d^{-1} and $\delta_D = 1$ mm for three $\alpha(Z)$					
	0.2		0.4		1.0	
0.02	0.480	0.83	0.406	0.89	0.230	0.82
0.05	0.457	0.64	0.381	0.74	0.262	0.73
0.10	0.415	0.45	0.336	0.55	0.284	0.75
0.20	0.338	0.24	0.327	0.36	0.317	0.55
0.30	0.343	0.17	0.335	0.28	0.322	0.45
	$R = 20$ g O_2 m^{-3} d^{-1} and $\delta_D = 5$ mm for three $\alpha(Z)$					
	0.2		0.4		1.0	
0.02	0.147	0.59	0.140	0.74	0.122	0.86
0.05	0.140	0.36	0.134	0.52	0.115	0.69
0.10	0.129	0.20	0.122	0.33	0.103	0.49
0.20	0.102	0.09	0.095	0.15	0.089	0.28
0.30	0.094	0.05	0.094	0.10	0.091	0.22
	$R = 200$ g O_2 m^{-3} d^{-1} and $\delta_D = 5$ mm for three $\alpha(Z)$					
	0.2		0.4		1.0	
0.02	0.228	0.69	0.208	0.80	0.159	0.88
0.05	0.215	0.46	0.192	0.60	0.148	0.72
0.10	0.192	0.28	0.174	0.40	0.129	0.52
0.20	0.163	0.12	0.131	0.19	0.122	0.33
0.30	0.138	0.08	0.134	0.14	0.129	0.27

Fig. 5. The variation of oxygen depletion rate, $J(Z)$, at water depth Z with the sediment area to water volume ratio, $\alpha(Z)$, for a constant value of the areal oxygen consumption rate, J_A (0.20 g O_2 m^{-2} d^{-1}) and for J_A varying with $\alpha(Z)$ at a rate of -0.05 g O_2 m^{-2} sediment d^{-1} (m^2 sediment m^{-3} water)$^{-1}$. The Livingstone and Imboden (1996) model was used to calculate $J(Z)$ with the varying J_A values and a volumetric oxygen consumption rate of 0.10 g O_2 m^{-3} d^{-1}. The linear regression between $J(Z)$ and $\alpha(Z)$ that would be obtained with varying J_A, but assuming a linear relationship, is also shown. (a) The behavior if an $\alpha(Z)$ range of 2.0 m^2 m^{-3} is used and (b) if 1.0 m^2 m^{-3} is used.

0.145 if ≤ 1.0 m^2 m^{-3} is used. This is a considerable reduction in the average value of J_A estimated from field results, especially if the larger $\alpha(Z)$ range is used, and it could be the main reason why the field J_A is less than the sediment cores value if R is low and it is assumed that the sediment core value is an estimate of J_A at some time during the earlier part of the deoxygenation period (Fig. 4). The nonlinear $J(Z)-\alpha(Z)$ behavior when the $\alpha(Z)$ range is large might explain why the strong linear increase of $J(Z)$ with $\alpha(Z)$ in five lakes in Quebec and one in central Ontario did not continue to the highest $\alpha(Z)$ value (Lovering, Stukely, Lyster, Orford, North Memphremagog, and Solitaire; Figs. 1, 5).

The value of J_A is not constant but decreases during deoxygenation (Fig. 4), especially during the latter stages, and the proportion of the total oxygen consumption that occurs in the sediment is also not constant, becoming smaller as deoxygenation progresses, particularly at high J_V and low $\alpha(Z)$ (Fig. 4; Table 2).
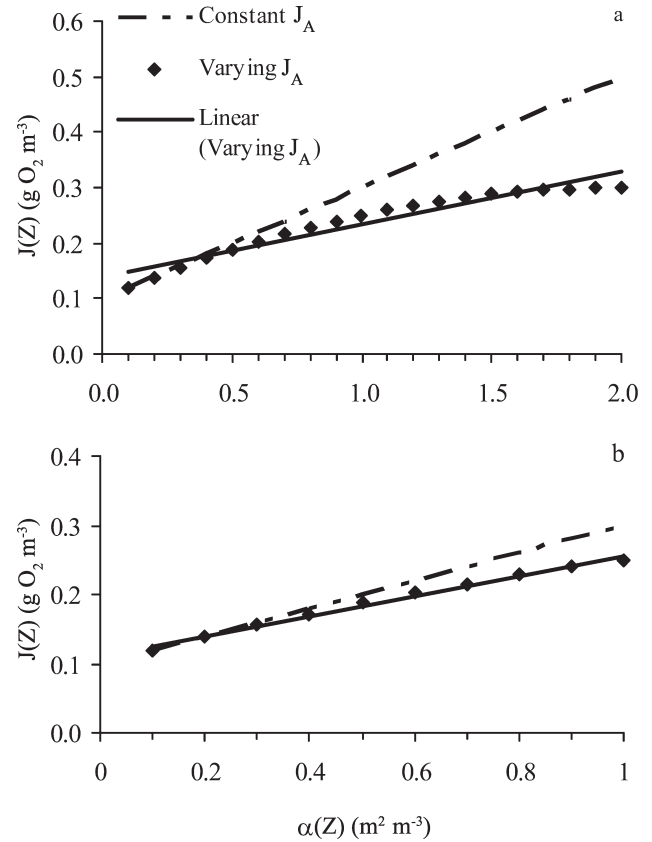
The reduction in the average J_A at higher values of J_V and $\alpha(Z)$ is greater when R is higher (200 g O_2 m^{-3} whole sediment d^{-1}); the average J_A decreases by -0.092 to 0.142 g O_2 m^{-2} d^{-1} at the higher values of J_V for a given value of $\alpha(Z)$ and by 0.008 to 0.250 at the higher values of $\alpha(Z)$ for a given value of J_V (Fig. 4; Table 2). This could be one reason for the low field J_A compared with the sediment core value if R is high and the sediment core value applies to a point earlier in the deoxygenation. The effect of J_A not being constant as $\alpha(Z)$ increases is also greater when R is larger (Table 2); the slope of the $J_A-\alpha(Z)$ relationship for a given value of J_V is around -0.20 g O_2 m^{-2} sediment d^{-1} (m^2 sediment m^{-3} water)$^{-1}$ for $J_V \leq 0.10$ gO_2 m^{-3} d^{-1}, and so the linear $J(Z)-\alpha(Z)$ relationship when J_A is not constant leads to a reduced estimate of the average J_A from 0.48 to 0.060 g O_2 m^{-2} d^{-1} if the regression uses $\alpha(Z) \leq$ 2.0 m^2 m^{-3} or to 0.260 if $\alpha(Z) \leq 1.0$ m^2 m^{-3} is used. The behavior is similar to that in Fig. 5, but the reduction in average J_A is greater with the higher R values. This could be a second reason for the lower field J_A values if R is high.

Table 3.　The zero-order rate of oxygen consumption in whole sediment (R, g O_2 m^{-3} whole sediment d^{-1}) in lakes available in the literature or derived by Eq. 5 from results in the literature, along with the observed values of the depth of oxygen penetration in the sediment (L), oxygen concentration at the sediment–water interface [$C(0)$] and the ratio of $C(0)$ to the oxygen concentration in the water stratum above the diffusive boundary layer (C_w). The method used and the spatial resolution of the measurements are also given.

Reference	Lake	Site	Method	Resolution (μm)	Date	R (g O_2 m^{-3} d^{-1})	L (mm)	$C(0)$ (g O_2 m^{-3})	$C(0):C_w$
Muller et al. (2002)	Alpnach	Profundal	in situ	50	24 Mar 98	99	3.7	9.9	0.89
				50	21 Apr 98	147	2.9	9.8	0.86
				50	27 May 98	384	1.7	7.3	0.81
				50	14 Jul 98	458	1.3	5.4	0.74
					25 Aug 98	205	1.3	2.3	0.79
Lorke et al. (2003)	Alpnach	Profundal	in situ	50	14–15 Aug 02	168	0.41		
Sweerts et al. (1986)	L302S (fig. 2)	Littoral	core	200	Summer 83	16	12.6	7.7	0.90
Sweerts and Cappenberg (1988)	Kievitsbuurt (fig. 1)	Littoral	core	200	1986	329	3.2	9.6	0.79
	L305 (fig. 2)	Littoral	core	250	Jun 86	283	2.25	6.9	0.90
	L302S (fig. 3)	Littoral	in situ	250	Jun 86	152	4.5	11.2	1.21
Danielopol and Niederreiter (1990)	Mondsee (fig. 6)	Profundal, 20 m	core	1000	Apr 88	249	5	16.5	0.92
	Mondsee (fig. 7)	Profundal, 6 m	core	1000	Feb 88	22	10	10.0	0.63
Martin et al. (1993)	Baikal (fig. 2)	Profundal, 22 m	core	500	Aug 91	47	5.5	5.4	
Huttunen et al. (2006)	Soiviojarvi	Profundal, 9.8 m	core	1000	Aug 94	23	6		
	Postilampi	Profundal, 32.5 m	core	1000	Aug 95	13	5		
	Lokka	Profundal, 8.8 m	core	1000	Aug 95	6.6	4		
	Tuusulanjarvi	Profundal, 7.8 m	core	1000	Aug 95	14	3		

Note. R was estimated by Müller et al. (2002) by fitting in situ oxygen microprofile results for the profundal of Lake Alpnach to Eq. 5. The mean in situ value for a 25-h period during 14–15 August 2002 in the same lake was measured by Lorke et al. (2003) and B. Müller (pers. comm.). Further values for R were derived by fitting Eq. 5 to published microprofile results and adjusting the value of R to minimize the variance between observed and predicted concentrations. No porosity values were given, so a value of 0.98 was assumed for the sediment surface between 0.4 and 15 mm depth.

An example would be the low field J_A values in the three eutrophic Irish lakes, in that the maximum $\alpha(Z)$ value is >1.0 m^2 m^{-3} (1.40–3.40 m^2 m^{-3}; Table 1).

An increase in δ_D to 5 mm when R is high causes a further and considerable decrease in the mean value of J_A and, assuming J_A does not vary with $\alpha(Z)$, reduces the value even further (results not shown). The effect of this higher δ_D value on reducing the average J_A value is less when R is low.

The use of the modified model, in which J_A is not constant with depth and time, has shown that consumption of oxygen in a water stratum, as represented by J_V, and consumption in the sediment, as represented by $\alpha(Z)J_A$, causes consumption in the sediment to decrease as J_V and $\alpha(Z)$ increase. The effect of consumption is to reduce $C(0)$, and as $C(0)$ decreases, so does J_A (Eq. 2). J_A should be proportional to $C(0)^{0.5}$, and this has been observed in sediment cores by Provini (1975). Furthermore, the effect of J_A decreasing with $\alpha(Z)$ also leads to a lower average J_A value derived from a linear relationship between $J(Z)$ and $\alpha(Z)$. These two reasons are likely to be responsible for the field J_A values being lower than those estimated from sediment cores; it could be that the second is more important if R is low and that both are involved if R is high. Although further analysis of the extrapolation of a sediment core value to the whole period of deoxygenation is needed, at this stage, the field J_A value appears more relevant in the context of modeling deoxygenation in lake hypolimnia. It integrates consumption over the sediment in the hypolimnion and over the period of deoxygenation. Single field values for J_A and J_V in a lake and the condensed linear model described by Eq. 1 do generally reproduce the observed variation of $J(Z)$ with $\alpha(Z)$ in the 32 lakes well (Fig. 1). We have identified the limitations of the model and they are not due to the difference between the field and sediment core J_A values but to the occasional bias estimating $J(V)$ with nonlinear $J(V)-\alpha(Z)$ behavior in lakes with a high $\alpha(Z)$ range.

Oxygen consumption rate in the whole sediment—Because the oxygen consumption rate in the whole sediment (R) is an important variable in the modified Livingstone and Imboden (1996) model, it is useful to know its value in lake sediment (Table 3). R varies from 7 to 460 g O$_2$ m^{-3} whole sediment d^{-1}, and a histogram of the 17 values from the 10 lakes shows that they are generally around 20 or 200–300 g O$_2$ m^{-3} whole sediment d^{-1}; 20 and 200 were used in the application of the modified model. The depth of oxygen penetration in the sediment (L) varies from 0.41 to 12.6 mm (mean = 4.3, median = 3.7). With 11 values of the $C(0)$:C_w ratio, the mean = 0.82, with all values >0.62. As is expected from Eq. 3, the relationship is strong between L and $[C(0)/R]^{0.5}$ ($R^2 = 0.86$, $p < 0.001$, 14 df), whereas that between L and $R^{0.5}$ is much weaker ($R^2 = 0.25$, $p = 0.043$, 16 df).

There is some evidence that the value of R changes seasonally. It increased from 99 to 458 g O$_2$ m^{-3} d^{-1} from March to July 1998 in the profundal of Lake Alpnach and then decreased; the higher values lasted for approximately 2 months (Table 3). The evidence is stronger for seasonal changes in R in coastal sediment. Glud et al. (2003) showed directly that R varied seasonally in the sediment of Aarhus Bay during 1990–1992, from a low of 80 to highs of 480 and 960 g O$_2$ m^{-3} d^{-1}, during periods of intensified sedimentation; the higher values lasted 2 to 3 months. This evidence suggests that R does vary seasonally because of the sedimentation of fresh organic matter and variations in sediment temperature. The effect of fresh organic matter in the sediment resulted in higher R values for around 2 months in Lake Alpnach and 2 to 3 months in Aarhus Bay. Because R seems to vary, it might be as difficult as it was with the sediment core J_A to characterize the consumption rate of oxygen in sediment for the period of deoxygenation with a single value.

The use of the Livingstone and Imboden (1996) model has produced field values for the volumetric oxygen consumption rate (J_V) and areal oxygen consumption rate (J_A) that apply to the deoxygenation period in the hypolimnia of 32 lakes. Analysis of a modified model showed that J_A is not constant with depth and time in the hypolimnion, and it was suggested that the field J_A value integrates the areal consumption over the hypolimnion and over the deoxygenation period. If it is taken that the field J_A value integrates oxygen consumption in the hypolimnion and that $J(Z)$ varies linearly with $\alpha(Z)$, then the Livingstone and Imboden model is a general condensed model for oxygen depletion in lake hypolimnia. It can be used to predict the changing oxygen concentration–water depth profiles during deoxygenation in thermally stratified lakes with the use of a constant value for J_A (0.0816 ± 0.0150 g O$_2$ m^{-2} whole sediment d^{-1}) and the relationship between J_V and lake trophic state (Fig. 3b,c) to predict how $J(Z)$ varies with $\alpha(Z)$ in a lake according to Eq. 1. There is some empiricism in this approach, in the use of the relationships in Fig. 3, and so it is similar in some ways to the model of Molot et al. (1992).

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