UNIVERSITÉ DU QUÉBEC À MONTRÉAL

LARGE-SCALE PATTERNS OF HYPOLIMNETIC OXYGEN DEPLETION RATES USING A SINGLE VERTICAL PROFILE OF THE LAKES

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MODÈLES À GRANDE ÉCHELLE DE TAUX D'ÉPUISEMENT HYPOLIMNÉTIQUE EN OXYGÈNE À L'AIDE D'UN SEUL PROFIL VERTICAL DES LACS

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TABLE DES MATIERES

LISTE DES FIGURES

LISTE DES TABLEAUX

RÉSUMÉ

La transformation du carbone par minéralisation photochimique et biologique joue un rôle clé sous nos latitudes, principalement en été. Durant cette période, les eaux profondes des lacs stratifiés thermiquement sont isolées de l'oxygène atmosphérique, causant une diminution de l'oxygène hypolimnique dissous en raison de la respiration et de la dégradation microbienne. Cette diminution d'oxygène peut créer des hypolimnion hypoxique-anoxique au fil du temps, entraînant certains effets néfastes sur l'état des lacs. L'intensité de ces changements à travers le Canada ainsi que la façon dont les conditions trophiques et la morphologie contrôlent le métabolisme hypolimnétique reste mal connus. Bien que l'estimation du métabolisme des lacs (surface) ait été bien étudiée, les connaissances concernant le métabolisme hypolimnétique avec les modèles statistiques proposés pour quantifier les taux de perte d'oxygène sur la base d'observations de terrain sont limitées. Le projet Lake Pulse a échantillonné 664 lacs à travers le Canada pendant la période estivale. À l'aide d'un sous-ensemble de données Lake Pulse, nous avons développé un modèle empirique pour estimer les taux d'appauvrissement en oxygène (ODR) dans l'hypolimnion des lacs et pour expliquer les facteurs environnementaux affectant le métabolisme du lac. De plus, nous avons exploré l'importance relative des processus de la colonne d'eau et des sédiments de l'hypolimnion des lacs. Nos résultats suggèrent que l'ODR est dominé par la consommation d'oxygène dans la colonne d'eau et non dans les sédiments (médiane de 85 % produit dans la colonne d'eau) et avait lieu plus profond dans les lacs eutrophes que dans les lacs oligotrophes. La morphométrie du lac (en particulier, ZH) jumelé aux facteurs de productivité du lac (PT et COD) influencent fortement le métabolisme hypolimnétique. Cette étude améliore notre compréhension globale du rôle de la morphométrie du lac et des conditions trophiques sur l'ODR dans l'hypolimnion des lacs. De plus, l'utilisation de ce modèle permet de réduire l'effort d'échantillonnage et de produire le tout premier ensemble de données d'oxygène qui pourrait être utilisé pour obtenir des profils temporels de CH_4 ou de CO_2 au Canada.

Mots-clés : Métabolisme hypolimnétique, minéralisation de la matière organique, absorption d'oxygène dans les sédiments, minéralisation de la colonne d'eau, taux d'appauvrissement en oxygène (ODR), AHOD, morphométrie, statut trophique

GENERAL SUMMARY

Carbon processing via photochemical and biological mineralization plays a key role in our latitudes, mostly during summer. During this period, the deep water of thermally stratified lakes are isolated from oxygen sources, acting as a closed metabolic vessel, and hypolimnetic dissolved oxygen decrease due to respiration and microbial degradation. This potentially causes hypoxic-anoxic hypolimnion over time, thus leading to immediate adverse effects for the state of lakes. The extent of these changes across Canada is unclear, and there is a lack of information on how the trophic conditions and morphology control hypolimnetic metabolism. Although lake metabolism (surface) estimations were well studied, there are currently apparent knowledge gaps concerning hypolimnetic metabolism with the statistical models proposed to quantify oxygen loss rates based on limited field observations. This large-scale project (Lake Pulse) sampled 664 lakes once for each lake during summer across Canada. Therefore, we developed an empirical model to estimate oxygen depletion rates (ODRs) in lake hypolimnion using this Lake Pulse dataset and explained the potential environmental drivers affecting lake metabolism. Also, we explored the relative importance of water column and sediment processes in lake hypolimnia. Our results suggest that oxygen depletion is dominated by water column oxygen sink and not by sediments (median 85 % due to water column processes) and happens even more profoundly in the eutrophic lakes than in oligotrophic ones. The effect of lake morphometry (especially ZH) and lake productivity factors (TP and DOC) strongly influence hypolimnetic metabolism. The information provided by this study increases our overall understanding of the role of lake morphometry and trophic conditions in predicting ODRs in lake hypolimnion. Also, utilizing this study method proved to reduce field efforts and produced the first-ever dataset that could help develop models for CH_4 or CO_2 temporal profiles in Canada.

Keywords: Hypolimnetic Metabolism, Organic matter mineralization, Sediment oxygen Uptake, water column mineralization, Oxygen Depletion Rates, AHOD, Morphometry, Trophic Status

INTRODUCTION

Dissolved oxygen (DO) is a crucial parameter of ecosystem functioning and biogeochemical cycling and is considered to be of central importance for various investigations in lake ecosystems (Prasad *et al.*, 2014 ; Staehr *et al.*, 2010 ; Sudheesh *et al.*, 2022). Oxygen enters a lake via atmospheric (air-water) exchange, through primary production (photosynthesis), and also via streams and rivers inputs (Dick *et al.*, 2016 ; Gelda et Effler, 2002 ; Pace et Prairie, 2004). In temperate regions, lakes experience thermal stratification (creating a stable vertical density gradient) during summer, i.e., after spring turnover, where the lake separates into three distinct thermal layers. The surface layer of warmer waters is called the epilimnion. A thin middle layer, called the metalimnion, is often observed as a region of sharp change in water temperature that delineates an upper well-mixed region (epilimnion) from a relatively quiescent deep zone (hypolimnion) (Kirillin et Shatwell, 2016 ; Read *et al.*, 2011).

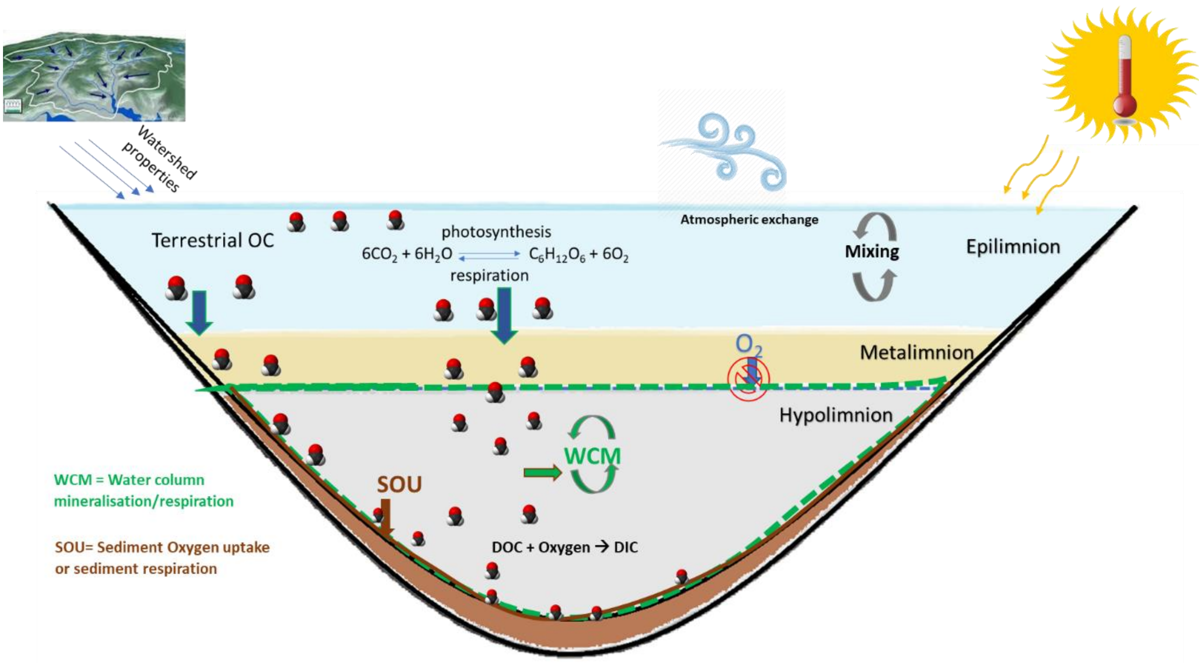

Fig. 0.1: Conceptual diagram showing the factors influencing lake metabolism in different layers of the lake.

Primary production is mainly restricted to epilimnion; metabolism in this layer can act as a net source and sink of oxygen, depending on the balance of gross primary production and respiration. Below the thermocline, hypolimnion waters are cut-off from the atmospheric exchange due to the stronger thermal condition, and dissolved oxygen decreases due to respiration and other microbial processes (Borowiak *et al.*, 2012 ; Charlton, 1980). This organic matter (OM) that sinks in lake hypolimnia from the productive surface zone, mineralization of OM generally occurs in different domains in the lake hypolimnia, they are in the water column and sediment surfaces (Livingstone et Imboden, 1996). The conceptual diagram explains the approximate process of lake metabolism (Fig. 0.1). In the hypolimnion, efficient organic matter mineralization may turn the hypolimnetic waters hypoxic or even anoxic (Rhodes *et al.*, 2017), thus leading to the production of reduced substances (NH_4^+, FE^{++}, SO_4^-) (Matzinger *et al.*, 2010). This severely affects biological processes and causes toxicity to fish and benthic organisms and drinking water sources. Also, it triggers the production of greenhouse gases (CO_2, CH_4, NO_2) from the anoxic sediment and then emit them into the atmosphere during lake mixing (Zimmermann *et al.*, 2019), contributing to global warming.

Quantifying lakes' metabolic rates provides essential information to understand how materials and energy cycle within these ecosystems and how lakes interact with their surrounding catchments (Pace et Prairie, 2004 ; Prairie *et al.*, 2002). Diurnal changes in dissolved oxygen concentration are widely used to examine ecosystem production and respiration in aquatic systems (Gelda et Effler, 2002 ; Howarth et Michaels, 2000 ; Staehr *et al.*, 2010, 2012). These studies have estimated the whole lake's metabolism. However, hypolimnetic metabolism requires the quantification of organic matter mineralization that occurs in lake hypolimnia, which could be from hypolimnion waters and sediment compartments (Livingstone et Imboden, 1996 ; Rippey et McSorley, 2009a). An alternative to the above methods is quantifying dissolved oxygen loss rates in the lake hypolimnion, which provides the relative estimation for hypolimnion respiration (Hutchinson, 1938). Temporal O_2 changes over depth and time can estimate oxygen depletion rates. The difference in oxygen at a given depth and time is referred to as oxygen deficit and then expressed at the rate of oxygen change per m^2 of the hypolimnetic surface (Lasenby, 1975 ; Wetzel et Likens, 2000). This is termed areal hypolimnetic oxygen deficit (AHOD), first developed by Strom (1931). These oxygen depletion processes can be quantified as volumetric or as an areal sink.

Researchers have explained the extent of hypolimnetic metabolism through interactions between the lake and its external drivers as well as internal processes, such as nutrient loading, climatic change, organic matter recycling, and lake morphometry. Many studies have attempted to explain the environmental factors that drive AHOD. Cornett and Rigler (1979) showed that lake phosphorus supply significantly influenced AHOD. Later they found that AHOD was explained by the paired effects of hypolimnion mean depth and productivity (Cornett and Rigler, 1980). Others explained that lake hypolimnion thickness (ZH) is an essential factor influencing AHOD but varies with lake productivity (Charlton, 1980 ; Müller *et al.*, 2012a). They suggested settling organic substances get enough opportunity for organic matter mineralization in the deeper hypolimnion than the shallower ones. Further, some other studies reported that lakes with thinner hypolimnia were strongly influenced by the sediment oxygen uptake relative to the water column sink (Bouffard *et al.*, 2013a ; Schwefel *et al.*, 2018). However, the extent of oxygen depletion rates behaved differently with the lake's trophic condition (Charlton, 1980 ; Steinsberger *et al.*, 2020) and showed depth independence for clearer lakes. Varying degrees of success may result from the methods used, and the research has been mainly regional.

In addition, most of the studies are from the European context and are lacking in the Canadian context. Exploring such studies is incredibly important for the Canadian context because Canada is one of the largest renewable freshwater resources (Sprague, 2007), and the drinking water supply mainly depends on them (based on Environment and Climate Change Canada reports). The observed continuous degradation of water quality in lakes can be due to many factors over the last 15 years (Rodell *et al.*, 2018) and simultaneously affects the bottom DO in the lakes. Recently, (Jane *et al.*, 2021) reported that the deep-water DO loss from temperate lakes over the world has increased by 18.6 % from 1980 to 2017, far greater than that observed in the ocean. This could alter natural biogeochemical processes (acting as sources and transformers of organic matter) and result in changes in CO_2 and CH_4 dynamics. Changes in nutrient inputs and transforming OM and the resultant C processes in lake hypolimnia are intimately linked to ecosystem metabolism. Therefore, this large spatial scale study was initiated to understand the potential environmental factors that affect hypolimnetic metabolism and to explain how it behaves in different environmental conditions in temperate climates.

0.1 Literature review

0.1.1. Areal Hypolimnetic Oxygen Depletion (AHOD) dynamics.

The rate of loss of dissolved oxygen (DO) mass normalized to the surface area of the hypolimnion is expressed as the areal hypolimnetic oxygen deficit (AHOD). This concept, first introduced by Thienemann (1928), was extensively developed in a series of papers to describe hypolimnion behavior (Strom, 1930,1931 & 1932). Hutchinson (1938) used these methods to classify lakes, and later focused on relating AHOD measures of lake trophic state, considering the influence of lake morphometry and other environmental properties (Hutchinson, 1957). AHOD has been widely used as an index of metabolism in stratified lakes, particularly for inter-lake comparisons. Several studies have used these concepts and approaches to better understand, predict, and explain hypolimnion oxygen deficit with respect to various environmental factors.

Lasenby (1975) indirectly determined hypolimnetic deficit by comparing it with the summer average of the dry weight of seston and Secchi depth. Cornett & Rigler (1979) developed an alternative model based on (Lasenby, 1975) to predict AHOD rates based on temperature, phosphorus, and hypolimnion thickness (ZH). Their model implied lakes with thicker hypolimnia had higher AHOD than lakes with thinner ones, as AHOD increased with increasing ZH. This relationship suggests that settling organic matter has more time to decompose in the water column of deeper lakes. Some studies showed that AHOD is poorly correlated with seston biomass and trophic factors (Cornett et Rigler, 1979 ; 1980). However, others showed that AHOD was strongly associated with surface plankton biomass and trophic factors (Borowiak *et al.*, 2012 ; Steinsberger *et al.*, 2020). Furthermore, a statistical modeled study emphasized the importance of hypolimnetic thickness in oxygen depletion rates, particularly for eutrophic lakes (Müller *et al.*, 2012a). This study demonstrated that the contribution of reduced substances to total areal hypolimnetic mineralization (AHM) was higher in lakes with shallower eutrophic hypolimnia. AHM represents the sum of all O_2 consumption processes within the entire hypolimnion, including AHOD and reduced substances from the sediments. However, this model's applicability may be limited to eutrophic state lakes, and its application to mesotrophic or oligotrophic lake conditions may not be appropriate.

0.1.2. Oxygen depletion rates (ODRs) in different domains (volumetric water column and surface sediment) of hypolimnion.

The mineralization of organic matter (OM) in the hypolimnion of lakes (Carstens *et al.*, 2012) occurs in two distinct domains (Charlton, 1980 ; Livingstone et Imboden, 1996 ; Rippey et McSorley, 2009a). Oxygen sinks that occurs in water column and sediment are referred to as water column mineralization (WCM) and sediment oxygen uptake (SOU), respectively (Steinsberger *et al.*, 2020). Livingstone and Imboden (1996) proposed a simple modeling approach to estimate the relative contributions of benthic and water column metabolism to the total oxygen consumption of hypolimnion. They related the rate of oxygen decline at a given depth to the sediment surface area-to-water volume ratio at that particular depth. Reports suggest that sediment respiration contributes nearly 48 % of total respiration in lake hypolimnia (Rippey et McSorley, 2009b). Müller et al. (2012) noted that sediment serves as the primary O_2 sink for shallower hypolimnia in eutrophic lakes. However, (Schwefel *et al.*, 2018) reported that approximately about 70 % of ODRs occur in the water column.

Interestingly, (Steinsberger *et al.*, 2020)) reported that the water column mineralization represents a significant proportion of ODRs in larger hypolimnion lakes. This finding can be explained by lake depth and productivity. However, these studies mainly reported deeper lakes, where their thickness of hypolimnion is greater than 50 m. However, these studies primarily focused on deeper lakes with hypolimnion thickness greater than 50 m. There is a dearth of studies explaining WCM contributions to ODRs in shallower lakes with different trophic conditions. Investigating mineralization dynamics in shallower hypolimnion lakes is highly necessary.

0.1.3. Mineralization dynamics of DOC in the hypolimnion water column.

Dissolved organic carbon (DOC) is a significant organic carbon (C) pool in aquatic ecosystems, consisting of a heterogeneous mixture of different C compounds (McDowell, W. H., & Likens, 1998 ; Stackpoole *et al.*, 2014 ; Xenopoulos *et al.*, 2003). It regulates the structure and function of lake ecosystems. It can be mineralized through microbial degradation (heterotrophic respiration) and photochemical breakdown, removed via flocculation, and generated in-lake via primary production and heterotrophic processing of particulate organic carbon (Attermeyer *et al.*, 2014 ; Tranvik *et al.*, 2009), whereas microbial respiration accounts for the majority of the mineralization of organic matter.

The DOC pool in the lake is supplied mainly from terrestrial inputs, i.e., from surrounding watershed catchments to lakes through fluvial networks (McDowell, W. H., & Likens, 1998 ; Sobek *et al.*, 2007). During summer, increasing temperatures lead to lake stratification, which may segregate different DOC pools in freshwater lakes. Primary production is mainly restricted to epilimnion, while the hypolimnion hosts more degraded organic substances from the sediments or inorganic substrates from the upper water column. Studies have shown that under the effects of a physical process (mixing events), the two DOC pools mix vertically and thus influence aquatic carbon cycling and food web dynamics (Lambert et Perga, 2019). Heterotrophic bacteria play a key role in the biological processing of terrestrial DOC. Additionally, fractions of DOC are transported downward to the hypolimnion and buried in the sediments. The transported DOC can then be mineralized when nutrients and a heterotrophic bacterial community are exposed to the oxic condition. The lability of this DOC can be explored by the contribution of oxygen utilization by heterotrophic microbial communities in the aquatic systems (Calleja *et al.*, 2019). Studies have revealed that the degradation dynamics of terrestrial and algal DOC pools vary significantly across lakes and are influenced, in part, by interactions with nutrients and lake trophic status (Guillemette *et al.*, 2013). The potential for degradation also depends on the available metabolic substrates in the subsurface water column and, thus, varies with deep oxygen availability (Lau et Del Giorgio, 2020). The organic material decomposition in the hypolimnion affects the availability of metabolic end-products (CO_2, CH_4, and nutrients) to the lake ecosystem and the atmosphere. However, there is a need to explore the role of nutrients in processing the DOC pool under the oxic and anoxic states in lake hypolimnion.

0.2 Problem Statement

The rate of dissolved oxygen (DO) loss, normalized to the surface area of the hypolimnion, is described as the areal hypolimnetic oxygen deficit (AHOD). Traditionally, hypolimnion oxygen consumption rates have been estimated by monitoring temporal changes in oxygen concentration over depth and time (Lehman, 1988). However, such time-series measurements are resource-intensive, making the assessment of lake metabolism challenging for larger-scale studies. Surprisingly, there is a lack of large-scale studies elucidating hypolimnetic metabolism on a global scale.

Previous research has attempted to predict AHOD rates based on environmental variables, including lake productivity, temperature, and morphology (Charlton, 1980 ; Cornett, R. J. & Rigler, 1979 ; Ladwig *et al.*, 2021 ; Nakhaei *et al.*, 2021). Nevertheless, the characterization of AHOD rates across different lake trophic conditions and depths has remained limited (Borowiak *et al.*, 2012 ; Cornett, 1989 ; Müller *et al.*, 2012a ; Nakhaei *et al.*, 2021). Notably, AHOD rates are significantly higher in eutrophic lakes compared to oligotrophic ones, and they also exhibit a strong correlation with lake depth and size (Rippey et McSorley, 2009a ; Steinsberger *et al.*, 2020). While most studies emphasize the strong relationship between AHOD and hypolimnion thickness (ZH), this dependence is not always consistent (Charlton 1980; Steinsberger et al. 2020). Additionally, observations have shown that AHOD levels decrease with increased lake hypolimnetic thickness (Müller *et al.*, 2012b).

Furthermore, Steinsberger et al. (2020) reported that Areal Hypolimnetic Mineralization (AHM) rates in large-sized lakes can be confounding when related solely to productivity. For instance, eutrophic Lake Geneva exhibits an AHOD only three times greater than oligotrophic Lake Brienz, despite Lake Brienz having 40 times more total phosphorus (TP) and a nearly equivalent hypolimnion thickness. Conversely, Baldegg Lake, although having a lower ZH, displays higher AHM rates than expected. However, it's evident that the relationship between ZH and AHM varies depending on lake trophic conditions, highlighting the independence of ZH on AHM. Consequently, there's a lack of comprehension regarding the influence of ZH on AHOD in lakes with differing trophic statuses. Moreover, the mineralization of organic matter (OM) has been examined by partitioning oxygen depletion rates in various domains within the lake hypolimnion. Understanding the relative importance of these processes (water column and sediment) in the hypolimnion offers insights into how it behaves based on productivity, coupled with lake morphometry and potential influencing factors.

Simultaneously, freshwater lakes face various pressures, such as increasing eutrophication in agricultural regions and elevated contaminant levels from diverse sources. Changes in land use and climate have altered landscapes, impacting lake metabolism. The extent of these changes across Canada remains unclear, and there's a paucity of information regarding how land use changes and watershed properties regulate AHOD. Previous research on this topic has primarily been regional, making it challenging to develop models that can be applied to lakes with markedly distinct characteristics. Consequently, significant knowledge gaps persist concerning hypolimnetic respiration rates, O_2 metabolic rates, and their local variability across Canada, accounting for varying environmental conditions and regions.

0.3 Thesis Objectives

To address the aforementioned problem, this study will utilize one-time observational data collected through the pan-Canadian Lake Pulse project, which sampled 664 lakes during the summers of 2017-2019, encompassing diverse ecozones, catchment properties, human impact levels, and lake sizes. The primary objectives of this research are as follows:

a. Create an empirical model based on one-time observational data to quantify oxygen depletion rates in the hypolimnion of lakes across Canada.
b. Investigate AHOD rates across various ecozones in Canada to understand regional differences and the impact of stressors on lake functioning and biogeochemistry.
c. Predict AHOD rates using different environmental variables, including lake morphometry, temperature, and productivity factors.
d. Explore the relative importance of water column mineralization and sediment oxygen uptake processes in the hypolimnion of lakes.
e. Determine which environmental variables have the strongest influence on AHOD rates in lakes with different trophic statuses.

CHAPTER-1

LARGE-SCALE PATTERNS OF HYPOLIMNETIC OXYGEN DEPLETION RATES USING A SINGLE VERTICAL PROFILE OF THE LAKES

1.1 Abstract

Severe hypolimnetic oxygen depletion, a recurring phenomenon during summer stratification in most temperate lakes, has been studied extensively. Existing models have identified mean hypolimnetic thickness (ZH), temperature, and trophic status as essential determinants of Areal Hypolimnetic Oxygen Deficit (AHOD). However, these studies have typically been region-specific, and there is a notable absence of large-scale spatial investigations spanning diverse environmental conditions. Traditional methods rely on temporal profiles of lakes to estimate hypolimnetic metabolism, which can be challenging for broader-scale studies. To address this challenge, we have developed an empirical model that utilizes a single vertical oxygen profile of lakes to estimate oxygen depletion rates in lake hypolimnia. Our novel approach revealed that hypolimnion thickness (ZH), dissolved organic carbon (DOC), and total phosphorus (TP) were identified as important drivers, with ZH alone explaining a significant portion of the variability. This suggests that lakes with thicker hypolimnia experience more efficient decomposition of settling organic matter and increased respiratory efficiency, particularly under higher trophic conditions. Furthermore, our study delves into the mineralization of organic matter (OM) in the water column during the settling of organic particles and sediment surfaces subject to intensive remineralization. Our findings showed that water column mineralization (WCM) made a substantial contribution to total hypolimnion respiration, accounting for a median of 85%. DOC and TP, in conjunction with ZH, were identified as the most influential variables for WCM. This suggests that organic particles settling in lake hypolimnia, originating from productive surface waters, have a greater opportunity for oxidation in the volumetric water column than in the sediments. Moreover, our study also sheds light on the impact of lake ZH on AHOD and its modulation of the relative contribution of sediment vs. water column processes. This modulation is particularly pronounced in lakes with shallow hypolimnia. In conclusion, this study introduces a novel and efficient approach for estimating lake hypolimnetic metabolism using minimal datasets. Our large-scale investigation provides essential baseline data for exploring lake hypolimnetic metabolism across diverse ecozones in Canada, shedding light on the intricate interplay of factors influencing oxygen depletion rates in lake ecosystems.

1.2 Introduction

Hypolimnetic oxygen levels are a critical metabolic parameter in lake systems, with severe depletion occurring during summer thermal stratification (Hutchinson, 1938 ; Lasenby, 1975 ; Pace et Prairie, 2004). The loss of dissolved oxygen (DO) in the hypolimnion is primarily attributed to the mineralization of both particulate and dissolved organic matter during these particle settle (Cornett et Rigler, 1987 ; Houser *et al.*, 2003 ; Rippey et McSorley, 2009b). The loss of dissolved oxygen (DO) in the hypolimnion is primarily attributed to the mineralization of particulate and dissolved organic matter during particle settling (Matzinger *et al.*, 2010 ; Steinsberger *et al.*, 2017). Global studies have drawn attention to the increasing deep-water DO loss from temperate lakes, emphasizing the need for a more profound understanding of the factors influencing hypolimnetic oxygen depletion rates (Jane *et al.*, 2021).

The magnitude and spatial extent of oxygen depletion generally result from intricate interactions between the lake and its external environmental drivers. These drivers include the input of anthropogenic effluents, land-use changes, climatic phenomena, and in-lake processes such as organic matter recycling. Given the vital importance of DO for lake biota, several studies have aimed to develop models that predict rates of areal and volumetric hypolimnetic oxygen depletion (AHOD and VHOD, respectively) for inter-lake comparisons (Cornett & Rigler, 1979 ; Hutchinson, 1938 ; Matthews et Effler, 2006). AHOD rates can be estimated by temporal oxygen (O_2) changes over depth and time in the hypolimnion (Lehman, 1988). The difference in oxygen at a given depth and time is referred to as oxygen deficit, which represents the rate of oxygen change per m^2 of the hypolimnetic surface (Wetzel et Likens, 2000). It’s essential to note that if the difference is negative, it signifies a decrease in oxygen concentration over time and depth, indicating a decline in oxygen levels. Methodologically, this approach requires temporal variations in O_2 or total deficits between two periods, combined with lake morphometry information such as lake volume or area for different strata (Cornett et Rigler, 1980 ; Lasenby, 1975 ; Matthews et Effler, 2006).

While lake morphometry, temperature, and productivity have been identified as important factors affecting hypolimnetic oxygen depletion rates (Borowiak *et al.*, 2012 ; Cornett et Rigler, 1979 ; Lasenby, 1975), the influence of lake morphometry on the areal hypolimnetic mineralization (AHM; AHOD and reduced substances from the sediments) exhibits variation, especially in lakes with deeper hypolimnia and varying productivity levels (Müller *et al.*, 2012a ; Steinsberger *et al.*, 2020).

The sink for oxygen in the lake hypolimnion occurs in different domains, namely the water column and sediment surface (Charlton, 1980; Cornett et Rigler, 1987; Livingstone et Imboden, 1996). While sediment is often considered the primary sink for DO (Rippey et McSorley, 2009a ; Steinsberger *et al.*, 2020), recent studies have reported that a significant proportion of oxygen depletion rates (ODRs) occur in the water column, accounting for about 70 % of oxygen depletion rates (ODRs) occur in the water column, while the remaining 30% occur in the sediment surface. Moreover, the relative contributions of water column mineralization and sediment oxygen uptake in hypolimnetic mineralization vary with lake size and depth (Steinsberger *et al.*, 2020). Nevertheless, the factors driving oxygen consumption in both domains, especially when considering lake morphometry and productivity, remain poorly understood. However, the factors driving oxygen consumption in both domains, particularly considering lake morphometry and productivity, remain poorly understood. Therefore, it is imperative to investigate the factors that control hypolimnetic oxygen depletion rates and their interrelationships in lakes of varied sizes and trophic statuses.

In this study, our primary objectives are to develop empirical models that estimate AHOD rates based on single oxygen profiles from lakes obtained during the summer. We explore how AHOD rates vary across Canadian ecozones and assess whether these rates are influenced by lake size. Additionally, we examine the effects of temperature, hypolimnion thickness (ZH), dissolved organic carbon (DOC), and trophic status on AHOD rates. Lastly, we investigate the relative importance of water column mineralization and sediment oxygen uptake processes in understanding lake hypolimnetic metabolism.

1.3 Materials and Methods

1.3.1 Study Area

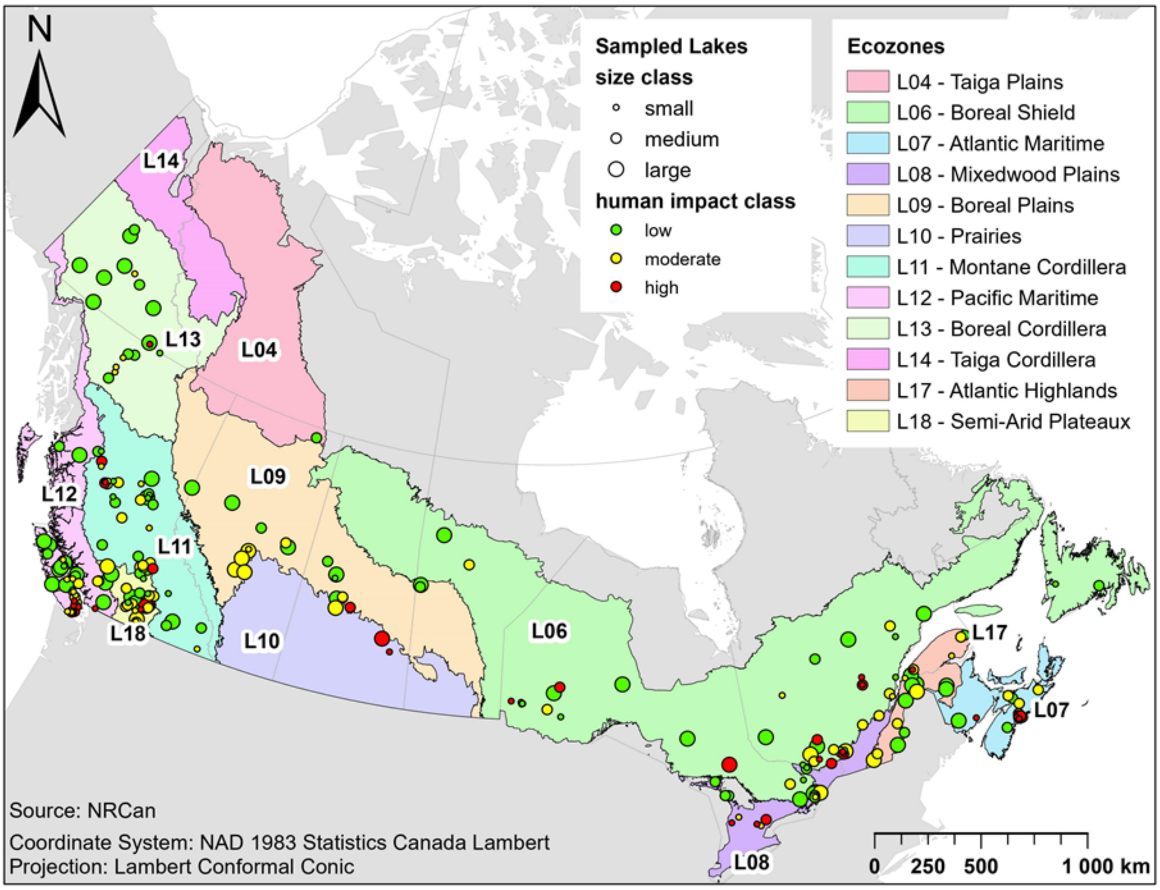

Fig. 1.1. Map of Sampling Lakes Across Canadian Ecozones.

The study area for this research project encompassed 242 lakes selected from a larger dataset of 664 lakes surveyed across Canada over a three-year period (2017-2019) as part of the pan-Canadian Lake Pulse project (Huot *et al.*, 2019). The selection of the 242 lakes was based on specific criteria, including the identification of the top of the hypolimnion for each lake (Fig.1.1). The detailed description to derive the top of the hypolimnion and specific criteria for the selection of 242 hypolimnetic lakes out of 664 lakes are explained in the section below (2.3). These lakes were distributed across 12 eco-regions, which are regions characterized by similar ecological, geological, and climatic properties. This selection ensured representation of lakes with varied sizes, ranging from ≥0.1 to 0.5 km^2, ≥0.5 to 5 km^2, and ≥5 to ≤100 km^2, as well as different levels of human impact (low, medium, and high). Among the selected lakes, there were 68 large, 93 medium, and 81 small-sized lakes, with 46 classified as high-impacted, 109 as low-impacted, and 87 as moderate-impacted lakes. Additionally, accessibility was considered, and lakes located within a maximum distance of 1 km from a road were included in the study. The human impact index for each lake was calculated based on an evaluation of land use patterns in their respective watersheds, utilizing remote sensing datasets with a resolution of 30 meters (Huot *et al.,* 2019a provides detailed information on the land use data).

1.3.2. Collection of samples

Sampling of water and other parameters was conducted during maximum thermal stratification, typically from July to the beginning of September, during mid-morning to early afternoon hours. The sampling program involved visiting each lake in Lake Pulse selected lakes only once. Epilimnion samples were consistently taken at the deepest point of the lake. In cases where bathymetry was unavailable, we utilized a motorboat to traverse the lake or a specific bay while continuously monitoring the depth. The region of potential maximum depth was identified through orthogonal transects, and sampling was conducted in that area using a coordinate system (Huot et al. 2019b).

Vertical profiles of various water quality parameters, including temperature, dissolved oxygen, pH, salinity, conductivity, and chlorophyll-*a* were taken throughout the water column using an RBR Maestro multi-parameter water quality probe (RBR Ltd. Ottawa, Canada). Meteorological parameters, including air temperature, relative humidity, wind speed, atmospheric pressure, precipitation, and sky conditions (cloudiness), were measured at each site using a Kestrel 5500 weather meter.

Epilimnion water samples were collected using an acid-washed 2-m tube sampler and transferred to the mobile lab on the lake's shore for further processing. Hypolimnion water samples were collected from Van Dorn bottles above the bottom sediment without disturbing it. Surface samples were collected for various analyses, including dissolved organic carbon (DOC), dissolved inorganic carbon (DIC), chlorophyll-a, nutrients (total phosphorus [TP], total nitrogen [TN], soluble reactive phosphorus [SRP], ammonium [NHX], nitrate/nitrite [NOX]), greenhouse gases (CH_4, CO_2, N_2O), and total suspended solids (TSS). Deep water samples only included chlorophyll-a and nutrient analysis. Standard protocols were followed during the field campaign for sample collection and analysis (field protocols described in NSERC Canadian Lake Pulse Network, 2021). Depending on the sample type and analysis requirements, samples were stored in portable freezers at -20°C, 4°C freezers, or at room temperature and were shipped to the corresponding laboratories on a weekly basis.

The lake water clarity and indirect measure of lake productivity were also determined using the Secchi disk appearance/disappearance metric. The Secchi disk was vertically deployed from the lake surface, and the disappearance metric, represented by the mean value of "Secchi disk disappearance in meters," was used to assess the lake's trophic status. Lakes with a mean disappearance metric greater than 5 were classified as oligotrophic, those with a mean value less than 2.5 were classified as eutrophic, and lakes with a mean value between 2.5 and 5 were classified as mesotrophic (Istva, 2020).

1.3.3. Estimating areal hypolimnetic oxygen depletion rates (AHOD)

Stratification in the lakes during summer is driven by the density of water varying with temperature and creates a stable vertical density gradient of the surface waters, which can be used to define the hypolimnetic boundaries. Hypolimnetic boundaries, specifically the top of hypolimnion, was defined using the LakeAnalyzer R package with a density gradient threshold of 0.1 kg m^{-3} (Read *et al.*, 2011).

Traditionally, the approach to estimating oxygen depletion rates in the lake hypolimnion involves analyzing changes in O_2 concentration profiles over time, in combination with the hypsographic profile. However, it's essential to acknowledge that neither of these conditions could be directly applied to the lakes within the Lake Pulse project due to the limitations of a single field visit and the unavailability of detailed bathymetry data for most lakes. As such, we employed a pragmatic approach to estimate the relative lake area or volume at depth, based on the generic hypsometric description proposed by Imboden and Joller (1984):

$$A_Z = A_0 \left(1 - \frac{z}{z_{max}}\right)^q \tag{1}$$

Here, A_Z represents the planar area at depth z, A_0 corresponds to the lake surface area, z_{max} is the maximum lake depth, and q is a non-dimensional exponent that typically hovers around 2. This formulation is versatile, accommodating h larger q values indicative of generally flat lakes but with small deep holes, as well as lower q values reflecting cup-shaped lake profiles.

For this study, a q value of 2 was assumed, corresponding to a perfect cone shape (unpublished Prairie data).

To estimate lake volume, we approximated the lake's shape as a cone and determined the volume of an infinitely thin water layer (0.1 m) at each depth by multiplying the surface area at that specific depth by its depth stratum. The total lake volume was subsequently computed by summing the surface areas at specific depths.

$$Vol_i = A_Z . z_i \tag{2}$$

Having obtained the relative lake area at specific depths, we proceeded to estimate areal hypolimnetic oxygen depletion (AHOD) rates. This estimation commenced with the assumption of a dissolved oxygen (DO) profile at the onset of stratification, which typically occurs after the spring turnover and ice-out. We assumed the entire lake profile was initially at 100% oxygen saturation and maintained a constant temperature of 4°C. For simplicity, we set the onset of stratification on May 1st for all lakes. It's important to note that we assumed a consistent date for the onset of stratification (May 1st) for all lakes across Canada for the sake of model simplicity. While this assumption simplifies the model, it's essential to acknowledge that the actual evolution of stratification and hypolimnion depth during the summer may vary due to differences in latitude and longitude. Additionally, we acknowledge that the depth of the hypolimnion can vary considerably during the season, which may influence the patterns observed in our study. However, due to limitations of a single field visit and the unavailability of detailed bathymetry data for most lakes, we had to make certain assumptions about the lake’s relative area or volume at specific depths.

The rate of change of dissolved oxygen (DO) in the hypolimnion over time was estimated by comparing the measured DO profiles with the assumed initial profile. This difference between the measured and assumed DO concentrations at each depth provided the apparent oxygen utilization/consumption (AOU) over a specific time period. The total mass loss of oxygen over time was calculated by summing the volume-weighted oxygen loss in each depth stratum, starting from the top of the hypolimnion to the maximum depth of the lake, using the relative lake area at each specific depth. This summation represented the total mass loss of oxygen in the hypolimnion.

$$\Delta\, O_2\, mass_{t-t_0} = \sum_{strat(i)}^{z_{max}} \frac{Vol_i \cdot \Delta[O_2]_i}{t - t_0} \tag{3}$$

where, $\Delta\ \mathrm{O_2\ mass_{t-t_0}}$ is total mass oxygen loss, $\mathrm{strat(i)}$ is hypolimnion depth stratum (m), $\mathrm{Vol_i}$ is stratum volume (m^3), $\Delta[\mathrm{O_2}]_\mathrm{i}$ is stratum change in O_2 (g O_2 m^{-3}), $\mathrm{t - t_0}$ is the change in the time between the observed and assumed date.

Lastly, we normalized the rate of DO mass loss to the upper surface area of the hypolimnion, yielding the AHOD.

$$\mathrm{AHOD} = \frac{\Delta\, O_2\, mass_{t-t_0}}{area\, upper\, surface\, hypolimion} \tag{4}$$

Additionally, we estimated the mean hypolimnion thickness by dividing the hypolimnion volume by the area at the estimated top of the hypolimnion.

$$Z_H = (V_H / A_H) \tag{5}$$

While this modeling approach provides valuable insights into AHOD rates, it is important to acknowledge the limitations. Regarding anoxia and partly anoxic conditions in the lakes, we considered these factors in our analysis. Lakes with anoxic layers or partly anoxic hypolimnia depths were not accounted for or removed in our calculations, and these conditions were taken into consideration when estimating AHOD rates.

Lastly, in clear lakes with relatively thin epilimnia, light penetration beyond the thermocline can influence O_2 dynamics within the hypolimnion through photosynthesis. While our study focused on a specific subset of lakes, we did account for these potential effects when analyzing the data and interpreting the results. However, it's important to note that the significance of this effect may vary among the lakes in our study.

1.3.4. Estimating oxygen sink for water column and surface sediment

Livingstone and Imboden (1996) developed a statistical model to estimate the relative contribution of sediment and water column oxygen depletion to the total oxygen depletion in the lake hypolimnion by using the linear regression between oxygen depletion rates at a given depth (ODR_Z) to the ratio of sediment surface to water volume at that particular depth (α_z).

$$\alpha_z = \frac{q}{z_{max} - z} \tag{6}$$

Application of this method to a vertical profile of oxygen, the intercept $(J_V)_z$ and slope $(J_A)_z$ represent volumetric water column consumption rates and surface sediment respiration rates, respectively.

$$ODR_Z(mg/L/d) = (J_V)_z + (J_A)_z * \alpha_z \tag{7}$$

1.4. Statistical Analysis

In the statistical analysis, various methods were employed to gain insights into the data. Distribution plots were used to visualize and obtain the central tendency of AHOD rates, providing an overview of their distribution. The relationship between AHOD and ZH rates was examined through a linear analysis, revealing significant variations in ZH in response to AHOD rates. Box and whisker plots were utilized to visually explore AHOD patterns across different ecozones in Canada, enabling the identification of potential differences. To assess the statistical significance of inter-system differences, several tests were conducted, including All Pairs, Tukey HSD, and one-way ANOVA. Furthermore, standard least squares regression analysis was performed to evaluate the impact of environmental variables on predicting AHOD rates and to identify the most influential predictors. Standard least squares are the exceptional cases of partial least squares where y variables are predicted, and model leverage plots show all the other input variables that contributed significantly to the model performance. The effect leverage emphasis divides the repository into those that relate to the whole model and those that relate to individual model effects. Skewed variables were appropriately log-transformed to ensure a more normal distribution. The statistical analyses were carried out using JMP Pro 14.0, a software tool for predictive analysis provided by SAS.

1.5. Results

1.5. General characteristics of lakes across Canada.

Table 1.1: Basic information on lake physicochemical characteristics and morphological data for the studied ecozones, including averages and standard deviations. The parameter estimates are depicted with mean and standard deviation. Parameter abbreviations are as follows: Hypolimnion (Hypo.), Temperature (Temp.), and Watershed (Wshed.). The table also indicates the total number of lakes considered in our study.

Ecozones	Atlantic Highlands	Atlantic Maritime	Boreal Cordillera	Boreal Plains	Boreal Shield	Mixedwood Plains	Montane Cordillera	Pacific Maritime	Prairies	Semi-Arid Plateaux
No. of lakes	19	14	19	19	46	20	35	41	3	25
Surface Temp. (°C)	19.5 ± 2.96	20.8 ± 2.77	16.1 ± 3.29	19.06 ± 2.94	19.9 ± 5.1	20.4 ± 4.17	16.19 ± 3.8	18.22 ± 2.8	19.5 ± 4.96	21.19 ± 4.7
Hypo. Temp. (°C)	8.9 ± 4.7	11.2 ± 5.6	6.9 ± 4.3	12 ± 6.1	7.34 ± 2.55	8.62 ± 3.89	7.9 ± 2.8	7.25 ± 1.69	5.31 ± 2.74	6.12 ± 1.3
pH	7.2 ± 0.58	4.29 ± 1.75	4.2 ± 3.3	7.98 ± 0.5	6.76 ± 0.83	7.51 ± 0.22	6.51 ± 2.05	6.95 ± 0.85	8.3 ± 0.38	7.14 ± 1.96
Hypo. Chl-a ($\mu g\ L^{-1}$)	3.74 ± 3.72	2.27 ± 3.19	2.71 ± 2.31	3.53 ± 2.08	7.21 ± 24.8	9.31 ± 29.65	3.26 ± 2.76	2.64 ± 2.9	5.18 ± 3.29	2.3 ± 1.44
ZH (m)	5 ± 5.1	3.2 ± 2.33	8.08 ± 7.04	2.35 ± 2.11	3.89 ± 3.68	3.56 ± 2.87	3.75 ± 3.49	5.34 ± 5.13	1.97 ± 1.21	6.37 ± 4.05
Max. Depth (m)	22.6 ± 17.6	17.4 ± 9.2	31.3 ± 23.1	12.9 ± 7.9	18.6 ± 11.5	17.2 ± 9.19	16.7 ± 10.86	23.6 ± 17.2	14.3 ± 6.9	26.5 ± 14.4
Wshed. Area (km^2)	250 ± 592	47 ± 100	502 ± 1028	171 ± 248	270 ± 861	173 ± 509	295 ± 874	237 ± 742	539 ± 629	785 ± 1903
TSS ($mg\ L^{-1}$)	20.4 ± 60.1	1.06 ± 0.8	1.02 ± 0.62	3.79 ± 6.07	1.49 ± 1.06	5.64 ± 9.42	2.3 ± 2.74	1.42 ± 2.37	5.15 ± 1.2	1.62 ± 0.87
DOC ($mg\ L^{-1}$)	10.13 ± 10.4	4 ± 1.92	4.46 ± 3.42	18.9 ± 11.1	6.53 ± 3.92	7.13 ± 2.3	10.6 ± 6.3	4.1 ± 3.02	23.05 ± 7.03	9.02 ± 6.33
Hypo. TN ($\mu g\ L^{-1}$)	0.81 ± 2.6	0.3 ± 0.21	0.63 ± 1.09	1.09 ± 1.64	0.23 ± 0.18	0.39 ± 0.29	0.34 ± 0.30	0.267 ± 0.42	1.20 ± 0.81	0.395 ± 0.346
Hypo. TP ($\mu g\ L^{-1}$)	NA	16.3 ± 6.5	191.8 ± 450	197.6 ± 252.3	42.6 ± 38.7	NA	190.8 ± 224.4	76 ± 164.4	92.03 ± 45	85.9 ± 86.5

The lakes included in our study exhibited significant variations in their average physicochemical and morphological factors across different ecozones (Table 1.1). Hypolimnetic water temperatures varied significantly among the ecozones, with the highest average temperatures observed in the shallowest ecozones, such as Boreal Plains and Atlantic Maritime. These temperature variations showed strong correlations with two key morphological factors: lake ZH ($r^2 = 0.48$, $p < 0.0001$, $n = 33$) and maximum depth ($r^2 = 0.42$, $p < 0.0001$, $n = 33$). Conversely, deeper ecozone lakes, like Semi-Arid Plateaux and Boreal Cordillera, displayed the lowest average hypolimnion temperatures, with less significant relationships with ZH and maximum depth.

Furthermore, we examined trophic factors, namely dissolved organic carbon (DOC), hypolimnion total phosphorus (TP), and bottom chlorophyll-a (Chl-a), to understand their spatial variations across Canada. Our analysis revealed significant variations only in DOC values across the ecozones. Notably, there was a close relationship between lake DOC and hypolimnion TP, with higher average values observed in the Boreal Plains and Prairies ecozones, and lower values in the Atlantic Maritime ecozone. We observed a considerable association between average DOC content and lake ZH (Fig.S1.1), where ZH increased as DOC content decreased. Similarly, a statistically significant log-log relationship was found between average hypolimnion TP and ZH. These trends were more pronounced in lakes with shallower hypolimnia compared to deeper ones.

1.5.2. Distribution of AHOD rates across Canada

The frequency distribution of AHOD rates of 242 lakes across Canada widely varied from 0.016 to 1.59 g O_2 m^{-2} d^{-1}, with a mean of 0.3 ± 0.23 g O_2 m^{-2} d^{-1} (Fig. 1.2.). Approximately 80% of the lakes, AHOD rates were between 0.01 and 0.4 g O_2 m^{-2} d^{-1}, consistent with previously studies conducted in Canada (Cornett and Rigler 1980; Lasenby 1975b). These findings underscore the potential of our estimation approach in investigating hypolimnetic metabolism at a broader scale, supporting its relevance and applicability.

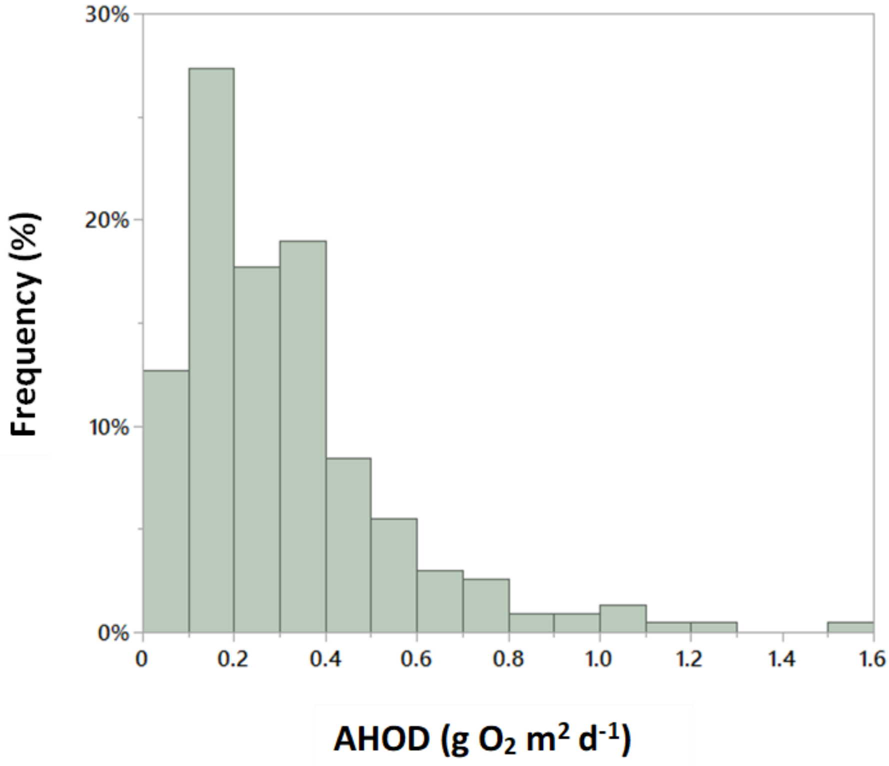

Fig. 1.2. Histogram of the mean AHOD rates in the 242 lakes across Canada.

1.5.3. Inter-ecozone variability of AHOD rates across Canada

We organized the lakes into different ecozones and conducted a series of statistical analyses to examine the variations in Areal Hypolimnetic Oxygen Depletion (AHOD) rates. The results of the one-way ANOVA and subsequent Tukey HSD tests revealed that, in general, there was no substantial and statistically significant variability in AHOD rates between the different ecozones, as illustrated in Fig. 1.3. However, it's noteworthy that the Semi-Arid Plateaux ecozone exhibited a notable exception to this trend. The AHOD rates in the Semi-Arid Plateaux ecozone were significantly different from those in all other ecozones, with particularly high significance when compared to the Boreal Shield ($p<0.0001$) and Pacific Maritime ($p=0.0032$) ecozones.

Further analysis by categorizing the lakes based on their size (large, medium, and small-sized lakes) revealed intriguing patterns in AHOD rates. Specifically, the mean AHOD rates were found to vary with lake size, measuring 0.317 g O_2 m^{-2} d^{-1} for larger lakes, 0.337 g O_2 m^{-2} d^{-1} for medium-sized lakes, and 0.25 g O_2 m^{-2} d^{-1} for smaller lakes. The lakes with higher mean AHOD rates were predominantly associated with larger and deeper lakes, primarily situated in the Semi-Arid Plateaux and Montane Cordillera ecozones, located in the western and northwest regions. These higher AHOD rates were influenced by morphometric factors such as watershed area. The relationship between log-log AHOD and the watershed area for larger lakes was statistically significant ($r^2 = 0.12$, $p<0.0001$, $n= 67$). Conversely, the lower mean AHOD rates were observed in the ecozones of Boreal Shield and Prairies and were associated with smaller-sized lakes. The rates of AHOD on these ecozones were showed a strong relationship with both lake hypolimnion thickness ($r^2 = 0.7$, $p<0.0001$, $n= 46$) and hypolimnion mean temperature ($r^2 = 0.2$, $p = 0.0021$, $n= 46$), highlighting the significant influence of lake morphometry and temperature on smaller lakes.

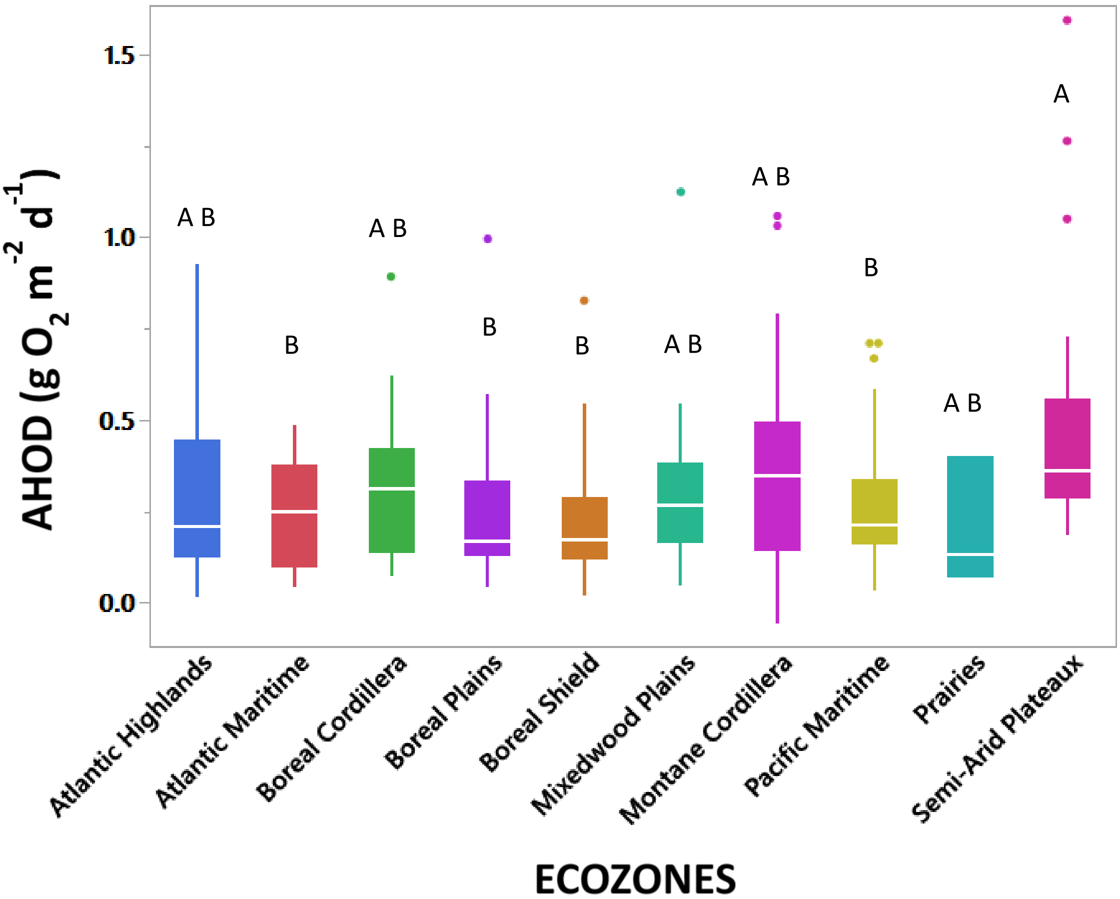

Fig. 1.3. AHOD variation in various ecozones across Canada. Box and whisker plots are outlier box plots used to visualize the pattern. The line at the median is shown by white space. The ends of the box represent the 25th (1st quartiles) and 75th quantiles (3rd quartiles), respectively. AHOD rates are on the Y axis and ecozones on the X axis across Canada. Letters A and B indicate statistical variation at the significance level (Tukey's HSD). The different colors represent the various ecozones.

1.5.4. Relationship between mean AHOD rates and ZH of all the lakes across Canada

A strong and highly significant positive log-log relationship was observed between the mean AHOD rates and ZH (r^2 = 0.54, p<0.0001, n= 240) (Fig. 1.4) with a slope of 0.64, indicating that as ZH increased, AHOD rates also increased. Similar trends were observed when examining the relationship in different lake size categories, with strong and highly significant relationships found in large-sized lakes (r^2 = 0.45, p < 0.0001, n = 67), medium-sized (r^2 = 0.52, p<0.0001, n = 90), and small-sized lakes (r^2 = 0.59, p<0.0001, n = 80), (Fig.S1.2). However, the slope of the AHOD and ZH relationship decreased with increasing lake sizes, indicating that the increase in AHOD rates is less pronounced with increasing ZH in larger lakes compared to smaller lakes.

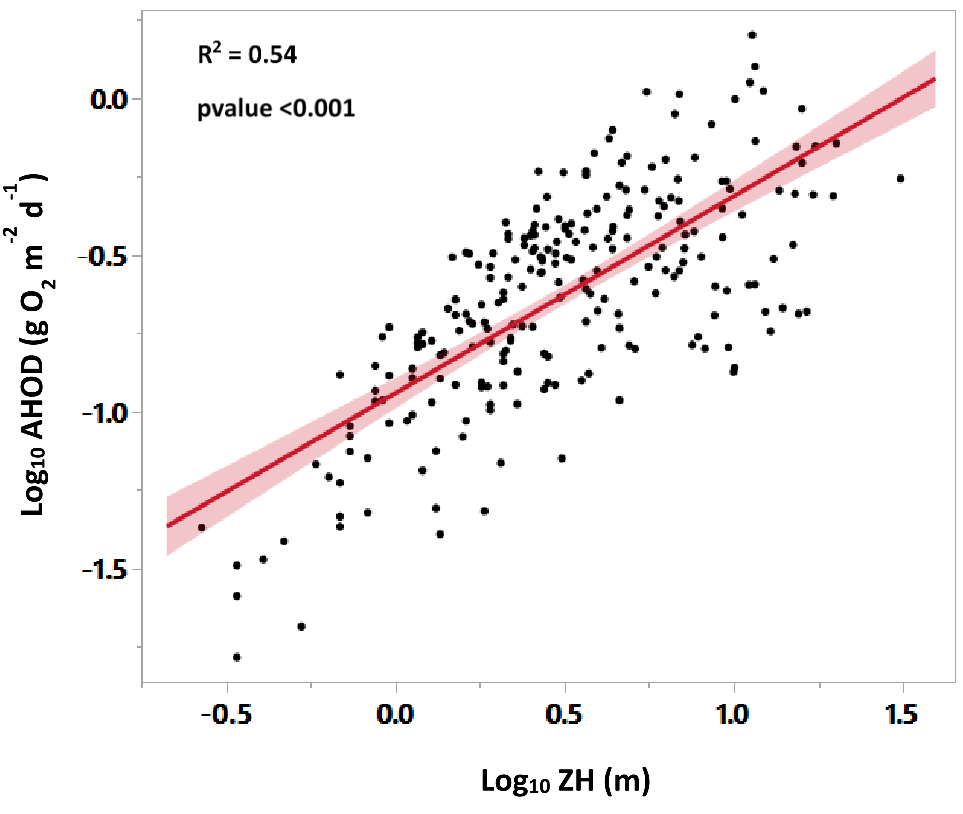

Fig. 1.4. Rates of $\log_{10}$ Areal Hypolimnion Oxygen Depletion (AHOD) linearly plotted against $\log_{10}$ Hypolimnion Thickness (ZH) in 242 lakes across Canada.

To assess the consistency of our estimates with literature, we combined our eutrophic lake data with the data from Muller et al. (2012) grouping them into ZH classes (our lakes were binned them into ZH classes) (Fig. 1.5). The analysis revealed that all the data followed the same general pattern, with a positive relationship between AHOD rates and hypolimnetic thickness. Importantly, the Canadian data extended this relationship to much smaller lakes, providing valuable insights into AHOD dynamics across a broader range of lake sizes.

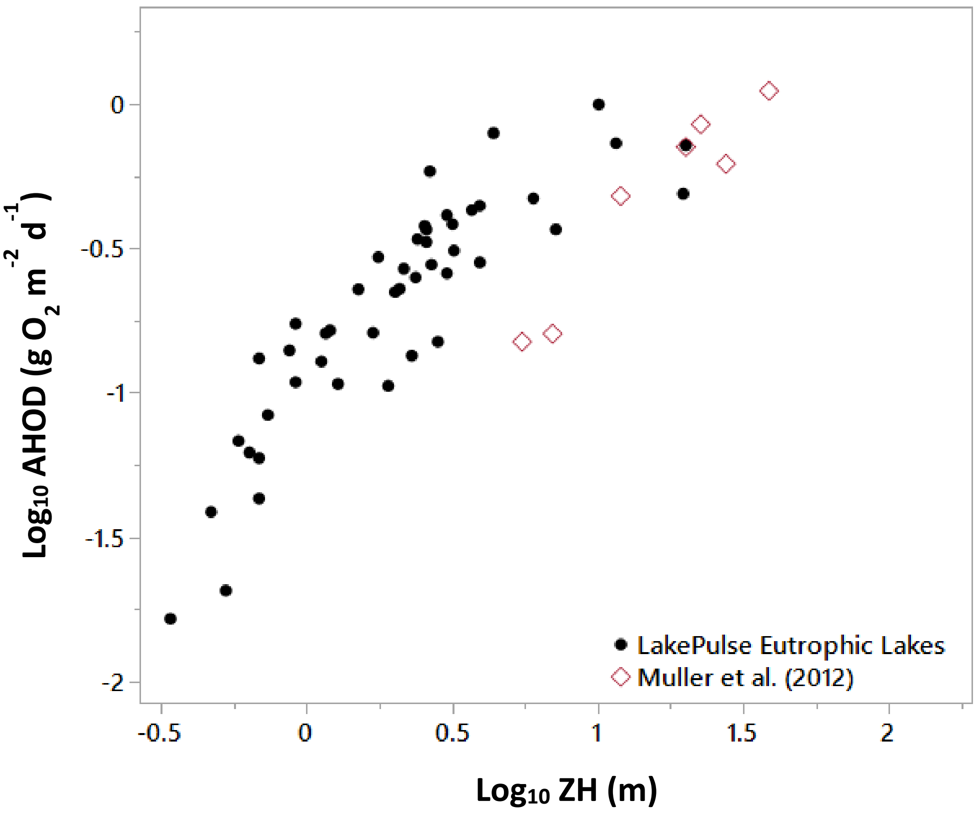

Fig. 1.5. Relationship between $\log_{10}$ AHOD and $\log_{10}$ ZH of Lake Pulse lakes and Swiss lakes of similar productivity

1.5.5. Variation of AHOD rates under the different trophic status of lakes

Next, we examined the variation in AHOD rates under different trophic statuses of lakes. Initially, a test comparing the means between AHOD rates and lake trophic status did not show any significant differences (Fig. S1.3). However, when accounting for the effect of ZH in a mixed model, both trophic status and its interaction with ZH were found to be significant. This suggests that the relationship between AHOD and ZH varied among lake trophic statuses (Fig. 1.6). Specifically, mesotrophic and eutrophic lakes exhibited similar effects in predicting AHOD rates, while oligotrophic lakes showed a distinct pattern. Overall, these results highlight the importance of considering both trophic status and ZH in understanding AHOD rates in different lake types. It is noteworthy that in lakes with shallow hypolimnions, the AHOD rates were comparable regardless of trophic status.

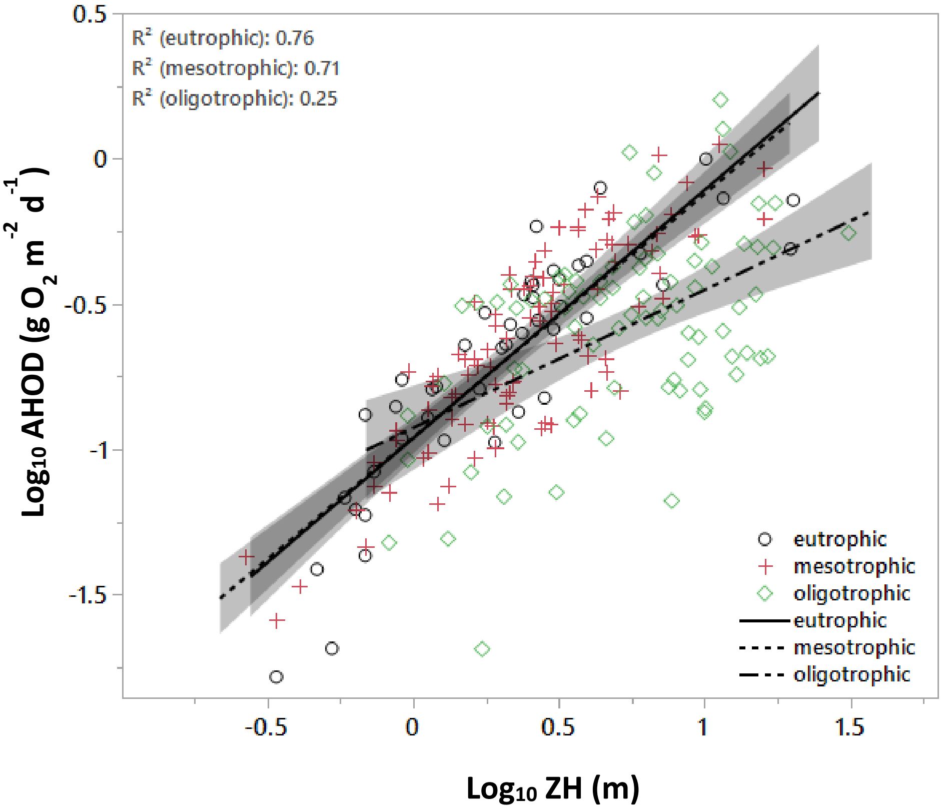

Fig. 1.6. Effects of $\log_{10}$ ZH on $\log_{10}$ AHOD in various trophic status lakes across Canada.

1.5.6. Effects of environmental variables in predicting AHOD rates

We further evaluated the key environmental factors influencing AHOD rates, multiple regression analysis was performed, incorporating various environmental variables. The variables included total nitrogen (TN), total phosphorus (TP), dissolved organic carbon (DOC), bottom chlorophyll-a (Chl-a), hypolimnion mean temperature, and ZH. Among these variables, only ZH, hypolimnion TP, and DOC were found to be significant predictors of AHOD rates. The resulting multiple regression model explained approximately 64% of the variations in AHOD (Fig. 1.7). The equation of the model indicates that log transformed AHOD (Log_{10} AHOD) can be predicted using the following equation:

$$Log_{10}\,AHOD = -1.422 + 0.727 * Log_{10}\,ZH + 0.18 * Log_{10}\,TP + 0.22 * Log_{10}\,DOC \quad (8)$$

Interestingly, ZH emerged as the most important variable, while TP and DOC had lower but similar explanatory power. Overall, these findings underscore the importance of hypolimnetic thickness (ZH) as a primary driver of AHOD rate variability across lakes. Additionally, the trophic status of lakes and specific environmental factors, such as hypolimnion TP and DOC, contribute to the complex dynamics of AHOD.

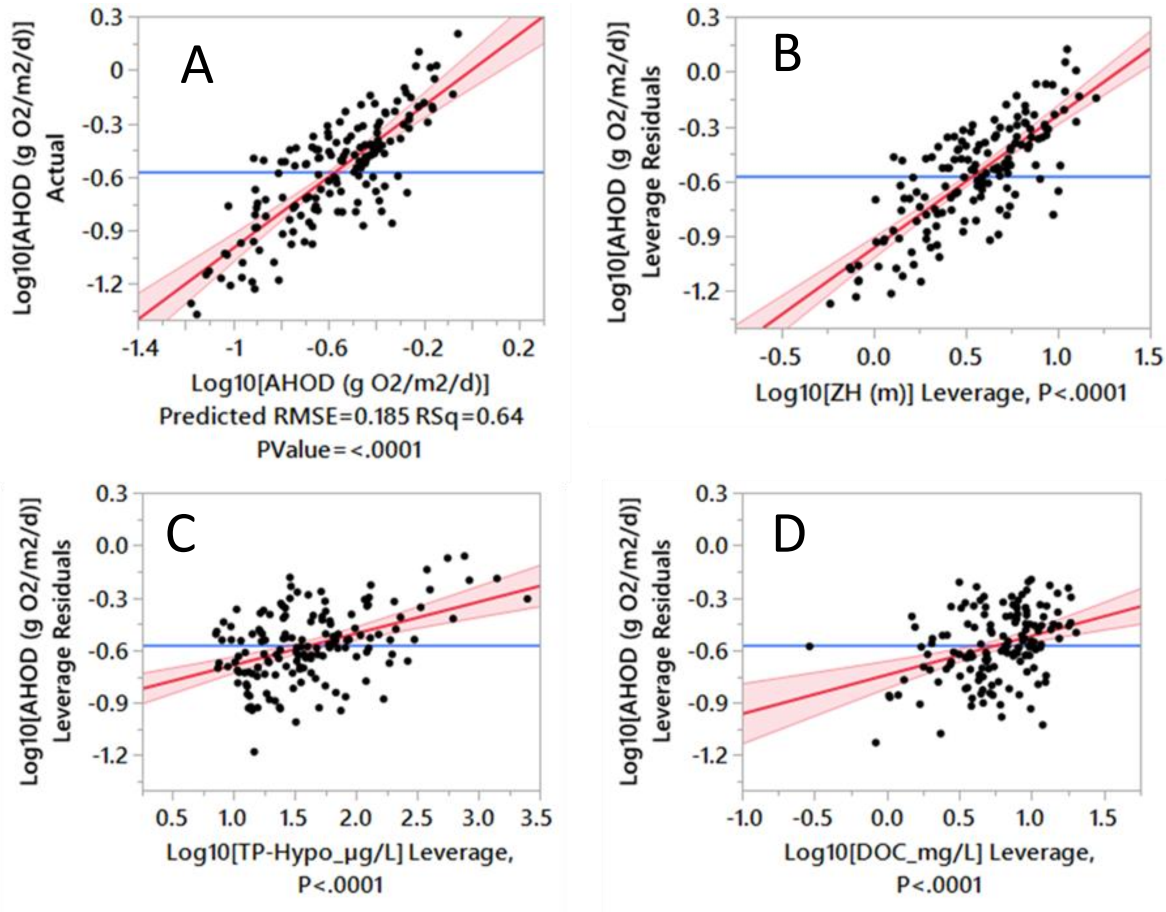

Fig. 1.7: Effects of Log_{10} ZH, Log_{10} TP and Log_{10} DOC in predicting the rates of AHOD. (A) Measured by the predicted plot of the model of the rates of Log10 AHOD using Log_{10} ZH (m), Log_{10} TP (µg/L) and Log_{10} DOC (mg/L) as predictors. (B) Linear regression between Log_{10} ZH and the residuals of the model of the rates of Log_{10} AHOD. (C) Linear regression between Log_{10} TP and the residuals of the model of the rates of Log_{10} AHOD. (D) Linear regression between Log_{10} DOC and the residuals of the model of the rates of Log_{10} AHOD.

1.5.7. Sinks for dissolved oxygen in the water column and surface sediments in lake hypolimnion.

Using the approach developed by Livingstone and Imboden (1996), we partitioned the whole hypolimnetic O_2 consumption into its water column (J_V) and sediment (J_A) respiration components. The J_V and J_A median rates of all lakes were found to be 0.06 g O_2 m^{-3} d^{-1} and 0.02 g O_2 m^{-2} $d^{-1,}$ respectively. Our analysis highlights the significant contribution of the water column as a major sink for hypolimnetic oxygen consumption, accounting for a median of 85% of the total. The proportion of water column respiration relative to the overall respiration in lake hypolimnion varied with lake depth. Shallow lakes exhibited a lower fraction of water column respiration, whereas deeper lakes demonstrated a higher reliance on the water column for oxygen consumption. This observation emphasizes the influence of lake depth on the relative importance of the water column in driving hypolimnetic oxygen dynamics. Using a logit transformation, we developed a simple model predicting the contribution of the water column to total respiration from ZH and trophic status. This model (Fig. 1.8) shows that for the same hypolimnetic thickness, the contribution of water column respiration to total metabolism increases with richer trophic status.

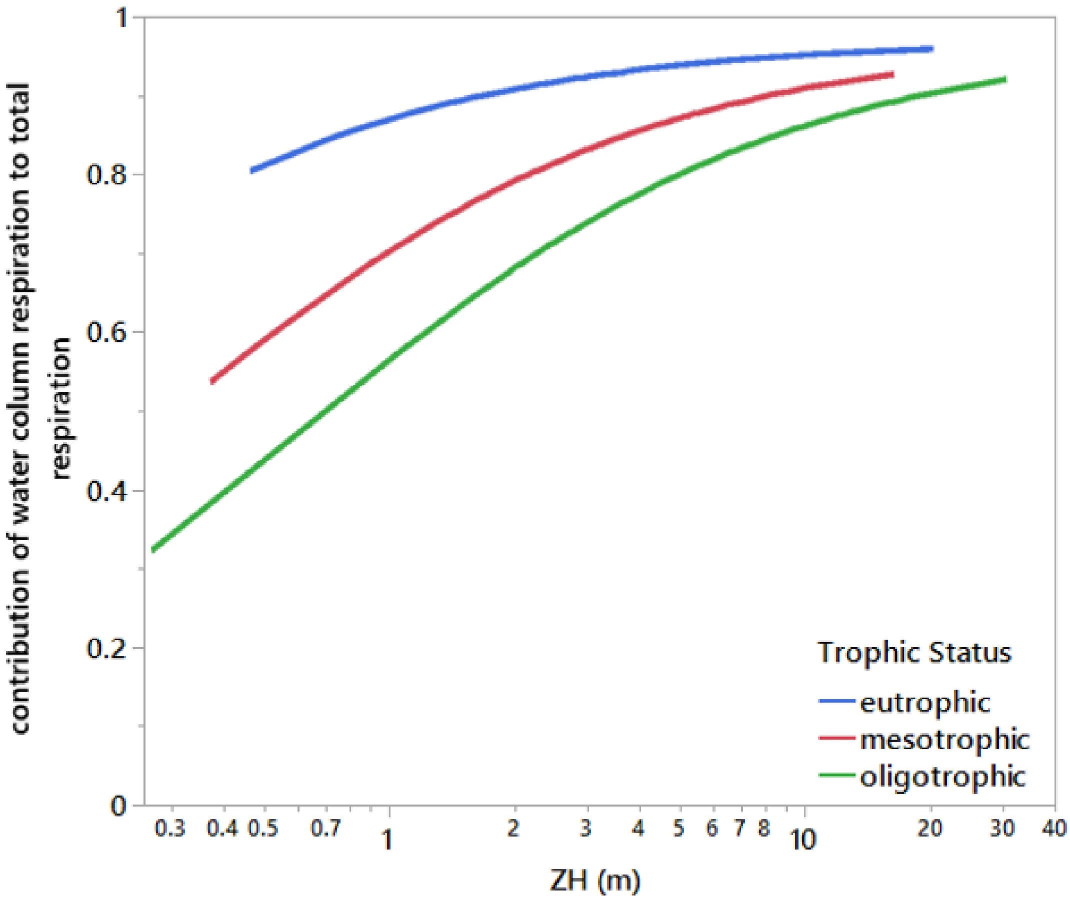

Fig. 1.8: Relationship between the contribution of water column respiration to total respiration and ZH in the lake hypolimnion under various trophic conditions.

1.6. Discussion

1.6.1. Comparison of AHOD rates across lakes and validation of the modeled study.

We compare the AHOD rates obtained in our study with those reported in existing literature and validate the robustness of our modeled approach. Our analysis includes lakes from 12 ecoregions across Canada, encompassing a wide range of morphometry and trophic states. AHOD rates were estimated based on the assumption of full oxygenation of the hypolimnion after spring water column mixing, and the difference between this time point and our summer sampling campaigns.

Validation of our AHOD estimates is crucial to establish the reliability and generalizability of our findings. Our estimated AHOD rates fall within the reported range for Canadian and global lakes, providing confidence in the accuracy of our modeled approach (Table 1.2). Specifically, the AHOD rates observed in lakes of Quebec (AHOD; 0.06 – 0.41 g O_2 m^{-2} d^{-1}) and Ontario (AHOD; 0.048 – 0.43 g O_2 m^{-2} d^{-1}) closely align with previous studies conducted in the same regions, demonstrating consistency in the reported values (Cornett et Rigler, 1984 ; Lasenby, 1975). However, we note that the mean AHOD rates in our study were lower than the average values reported in European studies, which can be attributed to morphological differences between continents, with European lakes generally being larger and having deeper hypolimnia.

Table 1.2: Summary of literature reporting AHOD rates and lake trophic conditions worldwide.

Study Region	**No. of Lakes**	**Mean AHOD**	**Trophic Conditions**	**Reference study**
Across Canada	242	0.30	Mixed Trophic	This Study
Ontario, Canada	6	0.62	Oligo-Mesotrophic	Charlton (1980)
Quebec, Canada	12	0.39	Mixed Trophic	Cornett et Rigler (1987)
Ontario, Canada	14	0.30	Eutrophic	Lasenby (1975)
Switzerland and France	11	0.58	Eutrophic	Muller *et al.,* (2012)
Switzerland	11	0.67	Oligo-Mesotrophic	Stenisberger *et al.,* (2020)
Poland	5	0.52	Mesotrophic	Borowaik *et al.,* (2012)

To further validate our modeled approach, we observed a strong qualitative and quantitative relationship between AHOD and hypolimnion thickness, as depicted in Fig. 1.4. This finding is consistent with similar relationships reported in the literature (Müller *et al.,* 2012), strengthening the reliability of our AHOD estimates derived from detailed oxygen and temperature profiles. This convergence of results suggests that AHOD can be reliably estimated from detailed oxygen and temperature profiles, affirming the robustness of the simplifying assumptions employed in deriving AHOD estimates. By comparing our results with previous studies and validating our modeled approach, we establish the credibility of our investigation. Our comprehensive dataset obtained from the Lake Pulse campaigns in Canada provides a solid foundation for further understanding the drivers of AHOD variability in lake ecosystems.

1.6.2. Variability and drivers of AHOD rates across Canadian lakes: Insights into Stratification, Temperature, and Organic Content.

Stratification is a fundamental factor influencing oxygen dynamics in lakes, plays a crucial role in determining AHOD rates across Canadian lakes (Ladwig *et al.,* 2021). Deeper lakes located in ecozones characterized by warm climatic conditions, such as the Semi-Arid Plateaux, Montane Cordillera, and Boreal Cordillera, exhibit stronger thermal stratification. Surface water temperatures in these deeper lakes ranged from 16°C to 21°C, while hypolimnion temperatures averaged between 6°C to 8°C. Limited mixing events, evident by the lack of a significant relationship between surface and hypolimnion temperatures ($p=0.9919$), restricted the supply of oxygen-rich surface waters to deeper regions. Consequently, hypolimnion regions experienced elevated oxygen depletion, leading to increased AHOD rates in these lakes. Conversely, shallower lakes in ecozones like the Boreal Plains and Atlantic Maritime displayed weaker stratification, resulting in higher surface (averaging nearly 19°C) and hypolimnion temperatures (averaging nearly 12°C). This facilitated enhanced oxygen transport through mixing processes, contributing to comparatively lower AHOD rates in these shallower lakes.

Another notable facet of our investigation was the relationship between organic content and AHOD rates across lakes. Shallower lakes exhibited higher levels of organic content, as indicated by total phosphorus (TP) and dissolved organic carbon (DOC) concentrations (Cornett et Rigler, 1979; Rippey et McSorley, 2009). However, within the context of similar hypolimnion thickness, no significant relationship was observed between AHOD rates and DOC ($p=0.42$). This implies that settling particles in shallower lakes may directly deposit into the benthic sediment, effectively restricting hypolimnetic respiration primarily to the sediment compartment. The sediment area relative to water volume increases with lake depth, contributing to efficient hypolimnetic respiration in the sediment compartment of small lakes (Baxa *et al.*, 2021 ; Bouffard *et al.*, 2013b). Nevertheless, the quantitatively lower hypolimnetic respiration rates in shallower lakes can be attributed to variations in lake hypolimnion thickness. Conversely, deeper lakes displayed lower organic content, but a strong positive relationship emerged between organic content and AHOD rates ($p<0.0001$). This indicated a higher rate of decomposition for settling organic substances and subsequent oxygen demand in the hypolimnion. In contrast, deeper lakes exhibit lower organic content, and a strong positive relationship is observed between organic content and AHOD rates

($p<0.0001$). This indicates a higher decomposition rate of settling organic substances and subsequent oxygen demand in the hypolimnion of these lakes. Furthermore, deeper lakes may facilitate the release of organic content from sediments, contributing to further oxygen depletion in the hypolimnion (Matthews et Effler, 2006; Imboden, 1974; Molot *et al.*, 1992; Müller *et al.*, 2019). While various mechanisms for sediment DOC release, such as diffusion, physical disturbance, and Fe-mediated release, are known, their relative prominence in deep lakes remains a topic for further investigation.

Our study also explored the responsiveness of AHOD rates to changes in nutrient loadings, shedding light on potential management strategies. Deeper lakes displayed greater sensitivity to variations in nutrient inputs, suggesting that efforts targeting nutrient reduction could have a more pronounced effect on AHOD rates in these lakes. Conversely, shallower lakes exhibited a lower degree of responsiveness, indicating that factors beyond nutrient inputs may exert a stronger influence on their AHOD rates.

1.6.3. Environmental factors influencing hypolimnetic oxygen depletion rates in lake ecosystems.

The influence of various factors on the rates of hypolimnetic oxygen depletion (AHOD) in lake ecosystems has been extensively studied. Among these factors, the morphometric characteristic of hypolimnetic thickness (ZH) has been found to play a significant role in driving AHOD rates (Charlton, 1980; Cornett et Rigler 1980; Müller *et al.*, 2012; Nakhaei *et al.*, 2021). Our analysis of Canadian lakes aligns with these findings, demonstrating that ZH explains a substantial portion of the observed variability in AHOD rates (Fig. 1.4).

As an areal metric, AHOD integrates the whole hypolimnetic water column, and it is therefore not entirely surprising that the thicker the hypolimnion, the larger the integrated O_2 consumption. Although the relationship is linear on a log-log scale, its slope was significantly lower than unity (slope = 0.64, prob (slope =1) <0.0001), indicating that the relationship is not directly proportional. In other words, a doubling in hypolimnetic thickness resulted in less than a doubling in O_2 consumption. This suggests that factors other than ZH also contribute to AHOD rates.

The relationship between ZH and AHOD can provide insights into the primary source material of oxygen consumption in the hypolimnion (Charlton, 1980). If the primary material of hypolimnetic decomposition is particulate organic matter settling towards the sediment surface, the hypolimnetic thickness can be construed as a proxy for the residence time of particles in the water column. Thus, our findings (Fig. 1.4) suggest that lakes with thicker hypolimnia experience more complete decomposition of settling organic matter, but the rate of mineralization slows down with exposure time. On the other hand, if the primary source material of O_2 consumption was in the dissolved form (DOC), one would not have necessarily expected a relationship with time or hypolimnetic thickness because the hypolimnetic water residence time is determined by the duration of stratification. Thus, the form of the AHOD-ZH relationship suggests that particulate matter settling is likely an important source component of O_2 depletion. Nevertheless, the contribution of DOC cannot be completely ruled out since larger and deeper lakes typically have longer water residence times. According to the reactivity continuum, lakes with longer residence time have lower DOC degradation rates (Vachon *et al.*, 2017). Thus, the lability of the DOC trapped at the onset of stratification is likely lower in lakes with thicker hypolimnion, consistent with the significant negative curvilinear relationship between DOC and ZH we found (Fig. S1.1) further supports its role in influencing AHOD rates.

To delve deeper into this hypothesis, it would be valuable to examine existing literature on organic matter sedimentation rates. For example, a study by Freland *et al.*, (2013) measured particulate organic carbon (POC) sedimentation rates in oligotrophic boreal lakes, reporting an overall average of approximately 68 mg m^{-2} d^{-1} or 5.7 mmol C m^{-2} d^{-1}. If we assume complete mineralization (though it rarely occurs), this organic matter could support a hypolimnetic respiration rate of around 0.09 g m^{-2} d^{-1}. In eutrophic lakes with higher sedimentation rates, this contribution to observed AHOD might be even more significant.

In addition to ZH, other environmental factors, such as total phosphorus (TP), dissolved organic carbon (DOC), and temperature, also influence AHOD rates (Fig. 1.7). TP has consistently been identified as a primary driver of AHOD rates in previous studies (Borowiak *et al.*, 2012; Cornett, 1989; Steinsberger *et al.*, 2020), emphasizing the importance of available phosphorus as a source of organic matter for AHOD. Muller et al. (2019) recently investigated the relationship between AHM (Areal Hypolimnetic Oxygen Depletion) and annual phosphorus supply (APS), demonstrating that AHM rates tend to increase with rising APS until they reach a certain level of oxidation. Beyond that point, AHM rates decline as lake depth increases. Our own study aligns with these findings, emphasizing the role of TP as a fundamental determinant of AHOD rates, although its influence varies with lake depth.

Temperature is often associated with AHOD rates due to its relationship with oxygen consumption processes. Our research highlights a strong connection between AHOD, lake productivity, and hypolimnion temperature. This connection is rooted in the impact of temperature on various biological processes within the lake ecosystem. We propose that lakes with elevated surface productivity can significantly influence vertical mixing and stratification dynamics. As a result, the entire hypolimnion benefits from lower temperatures. This, in turn, fosters increased organic matter mineralization due to the presence of readily available substrates in those strata. However, it's essential to note that this effect tends to diminish as lake depth increases. While temperature exhibits a significant relationship with AHOD rates when analyzed individually ($r^2 = 0.16$, $p<0.001$, $n=238$), its inclusion in multiple regression models (Table. 1.3) did not improve the model's performance. This suggests that the contribution of temperature to AHOD rates may be influenced by other factors, such as the availability of organic matter.

Suppose that during summer stratification, the lake's hypolimnion remains oxygenated, preventing the oxidation of reduced substances from the sediments. In such conditions, the degradation of settling organic substances is reduced. In oligotrophic lakes with deeper water columns, the hypolimnion is thicker, which enhances the efficient mineralization of organic matter. As a result, there is a decrease in the amount of available organic matter for sediment oxygen uptake. This phenomenon can lead to the rates of AHOD in oligotrophic lakes appearing to be depth independent. In essence, the reduced flux of substances from the sediment or sediment respiration has a minimal impact on the AHOD of oligotrophic lakes under these circumstances. The protective effect of an oxygenated hypolimnion plays a crucial role in this depth-independent pattern.

Overall, these factors interact in complex ways, influencing the efficiency of organic matter decomposition and oxygen consumption. Using model comparison statistics (AICc and BIC criteria), we found that the best model only included ZH, TP, and DOC as independent variables Table 1.3). The understanding of these interrelationships is crucial for predicting and managing AHOD rates, ultimately contributing to improved water quality and effective conservation strategies in lake ecosystems. Further research is needed to explore the intricate relationships between hypolimnetic thickness, nutrient availability, organic matter supply, temperature, and other environmental variables. This will enhance our understanding of AHOD processes and their implications for water quality, providing valuable insights for effective management and conservation efforts in lake ecosystems.

Table: 1.3. Summary of statistical models evaluated. The response variable and all explanatory variables describe the models. The explanatory variables include mean hypolimnion thickness (ZH), average hypolimnion phosphorus (TPhypo), dissolved organic carbon (DOC), average hypolimnion chlorophyll (HypoChl-a), and average hypolimnion temperature (HypoTemp).

No.	Model	AICc	BIC	R^2
1	AHOD ~ ZH	-5.816	4.444	0.54
2	AHOD ~ ZH + TPhypo	-62.18	-50.47	0.61
3	AHOD ~ ZH + TPhypo+ DOC	-74.517	-59.99	0.65
4	AHOD ~ ZH + TPhypo+ DOC + HypoChl-a	-74.24	-56.993	0.65
5	AHOD ~ ZH + TPhypo+ DOC + HypoChl-a+ HypoTemp	-72.94	-52.92	0.65

1.6.4. Effects of ZH explaining AHOD rates in lakes with various trophic status.

Moreover, the influence of ZH on AHOD rates is modulated by the trophic status of the lake, highlighting the importance of organic matter supply in shaping AHOD (Fig. 1.6.). The non-proportional effect of ZH on AHOD is even more pronounced in eutrophic lakes (Fig 1.5). In eutrophic lakes, the relationship between ZH and AHOD exhibited a clear non-linear pattern, with a more than two-fold increase in hypolimnetic metabolism for a doubling in ZH within a certain size range. In other words, there appears to be an enhancement in the efficiency of oxygen utilization with increasing ZH. However, it’s essential to note that this effect undergoes a complete reversal in lakes with thick hypolimnia. In these cases, even a substantial increase in hypolimnetic thickness has a minimal impact on hypolimnetic respiration. The rate essentially plateaus for lakes with hypolimnia exceeding 100 meters in thickness (Rhodes *et al.*, 2017 ; Schwefel *et al.*, 2018). In oligotrophic lakes, the relationship was less significant, indicating a lower impact of ZH on AHOD rates (Fig. 1.6). Additionally, the role of hypolimnetic sediment respiration was evident in richer trophic lakes, where AHOD rates showed larger slopes with thinner ZH, suggesting its contribution to hypolimnetic oxygen consumption in lakes with higher trophic states. Comparison of AHOD-

ZH relationships across lakes of various trophic statuses from literature sources worldwide revealed significantly lower AHOD for the same ZH in oligotrophic sites, while meso- and eutrophic lakes showed similar AHOD-ZH relationships, indicating comparable variability in AHOD rates despite differences in trophic status (Charlton, 1980; Cornett et Rigler, 1980; Müller *et al.*, 2012; Steinsberger *et al.*, 2020).

1.6.5. Organic matter mineralization in different domains (water column and surface sediment) of lakes.

Livingstone and Imboden's (1996) model were used to describe the oxygen depletion rates in lake hypolimnion. Using this model in our data allowed us to estimate the relative importance of sediment oxygen uptake and water column mineralization, separating the oxygen consumption rates associated with water column (J_V) and surface sediments (J_A) in the hypolimnion. Our study estimated rates for J_A and J_V were similar to those of other studies (Nakhaei *et al.*, 2021 ; Rippey et McSorley, 2009b). The implication of this model in our study revealed that the contribution of water column depletion to total depletion in lake hypolimnion explained a major fraction (85 % of total depletion). Cornett and Rigler (1987) reported that about 15-66 % of the total oxygen consumption occurred in the water column of the hypolimnion in Canadian lakes. Similarly, Lasenby (1975) found that almost 70% of hypolimnion respiration was associated with the water column. However, others have reported that sediment respiration (>50%) is the major sink for dissolved oxygen for shallower hypolimnion lakes (Rippey et McSorley, 2009b ; Steinsberger *et al.*, 2020).

The proportion of respiration that occurs in the sediments vs water column depends on morphometry, i.e., by the sediment area to water volume ratio (α) (Livingstone et Imboden, 1996 ; Rhodes *et al.*, 2017 ; Schwefel *et al.*, 2018). Conceptually, ZH is the sediment area to volume ratio of the whole hypolimnion, and a smaller ZH corresponds to a larger sediment contribution to AHOD (and a smaller contribution to water column processes. In our lakes, Jv was significantly related to epilimnion TP ($r^2 = 0.17$, $p<0.0001$, n=224) and DOC ($r^2= 0.21$, $p<0.0001$, n=224), suggesting again that the organic particles that fall in lake hypolimnion originated from the productive epilimnion waters, sinks for dissolved oxygen in the volumetric water column have a greater opportunity to oxidize most of these settling substances (Borowiak *et al.*, 2012 ; Steinsberger *et al.*, 2020). The extent of organic matter degradation in a larger hypolimnion decreases with lake depth and is important for hypolimnetic metabolism.

Our study confirmed the positive relationship between the contribution of water column respiration to total respiration and the mean thickness of hypolimnia. However, we showed that for a given ZH, the contribution of water column processes followed the trophic status gradient (Fig 1.8), with AHOD in eutrophic lakes being most determined by water column processes. This suggests that J_A and J_V do not follow the same trend with productivity, or at least not to the same extent. It may also be that in eutrophic lakes, regions of the hypolimnion are already anoxic, and therefore, the sediments do not contribute to the consumption of O_2 directly. While reduced substances liberated by sediments can be oxidized when they reach an oxygenated portion of the water column, their rate is usually lower. Regardless of the exact mechanism, ZH's influence on the relative contribution of sediment vs water column processes is strongly modulated by the trophic status of lakes, particularly in lakes with shallow hypolimnia.

Conversely, the dependency of deeper hypolimnion lakes on the availability of organic matter quality (labile or refractory organic substances) that mineralizes in the water column is evident. This suggests that when seston particles (readily available organic matter) are exported from the productive surface zone to the hypolimnion, the degradation of these sinking particles intensifies oxygen depletion in the deeper layers before reaching the sediment.

Moreover, it is well-documented in the literature that deep lakes are likely to remain in an oxic state throughout the entire water column and sediments, regardless of their trophic condition (Baxa *et al.*, 2021 ; Bouffard *et al.*, 2013b ; Muller *et al.*, 2003 ; Maerki *et al.*, 2006). As a result, these lakes predominantly favor oxic respiration for organic matter mineralization in the surface sediment of the lake hypolimnion. The rate of sediment respiration is slower due to the limited availability of labile organic substances for biological oxidation in these oxic conditions. Consequently, the contribution of sediment respiration to the total respiration in the hypolimnion is smaller in thinner hypolimnia compared to thicker ones. However, it's worth noting that the magnitude of the sink for dissolved oxygen in the lake sediment surface is likely to increase when the lake experiences minimal water column vertical mixing. In such cases, longer water residence times can lead to the transformation of refractory organic substances into labile forms, making them more accessible for bacterial oxidation.

1.7. CONCLUSION

This study presents a groundbreaking approach to estimate lake hypolimnetic metabolism, offering a novel and efficient method that requires only a single vertical profile of dissolved oxygen and temperature, measured at any point during the summer stratification period. While recognizing the inherent limitations of our estimation method, our findings consistently align with previous studies, demonstrating the validity and applicability of our approach for investigating hypolimnetic metabolism on a broader scale.

This study represents the first extensive examination encompassing approximately 242 lakes across diverse environmental regions in Canada, providing crucial baseline data for comprehending lake hypolimnetic metabolism. Notably, while AHOD rates exhibit variation across different ecozones, our analysis reveals that the variability is not significantly pronounced across Canada. The pivotal discovery in our study underscores the substantial influence of lake morphometry on hypolimnetic metabolism, with hypolimnion thickness (ZH) emerging as a predominant predictor of AHOD rates. This underscores the concept that lakes with thicker hypolimnia facilitate a more efficient decomposition of settling organic matter, particularly evident in lakes with higher trophic conditions. Furthermore, the synergy of ZH with hypolimnion total phosphorus (TP) and dissolved organic carbon (DOC) content plays a substantial role in predicting AHOD rates, accounting for an even greater portion of the overall variability. Our investigation reveals that the effect of ZH on AHOD rates is more pronounced in lakes with richer trophic conditions, indicating an enhanced respiratory efficiency with increasing hypolimnion thickness. In contrast, ZH exerts the least influence on AHOD rates in oligotrophic lakes, suggesting that the limited organic matter production in these systems is effectively oxidized within their upper hypolimnia.

While both water column and sediment processes contribute to the mineralization of organic matter in lake hypolimnia, our study highlights that the primary oxygen consumption in our sampled lakes predominantly stems from water column-related processes rather than sediment-based oxygen sinks. This delicate balance between respiration in sediments and the water column is intricately linked to lake morphometry. Intriguingly, our findings demonstrate that the contribution of water column processes aligns with the trophic status gradient for a given hypolimnion thickness (ZH). In eutrophic lakes, water column processes overwhelmingly dictate AHOD, implying that sediments in these lakes tend to remain consistently anoxic, regardless of stratification and morphometric factors, contributing to their relatively lower AHOD via sediment-based processes.

Finally, the implementation of this study's method for estimating lake AHOD rates using a single vertical profile of dissolved oxygen and temperature streamlines field efforts, making it a valuable tool for exploring hypolimnetic conditions, particularly in the context of eutrophication and extended stratification periods resulting from climate change. Moreover, the study's large spatial scale opens avenues for understanding the fate of methane in Canadian lakes, encompassing its storage, processing, and emissions. By utilizing AHOD rates from both water column and sediment compartments in lake hypolimnia, models can be developed to elucidate the temporal profiles of methane or carbon dioxide in lakes, thereby enhancing our understanding of these critical processes and their implications for Canadian lake ecosystems.

ANNEXE A- SUPPLEMENTARY INFORMATION

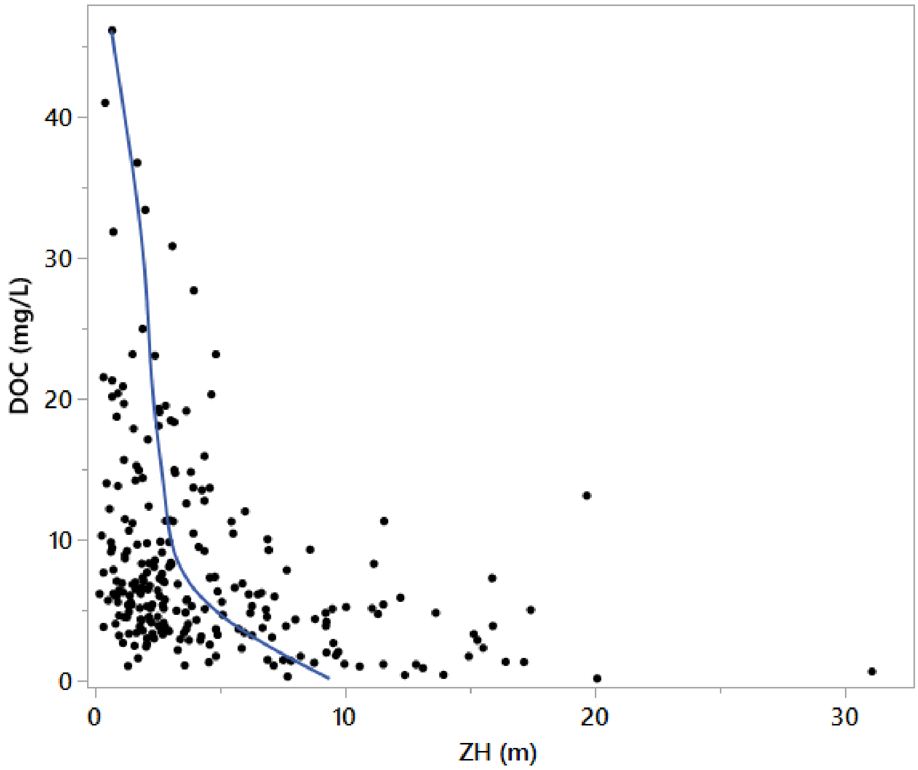

Fig S1.1. Polynomial relationship between the average DOC (mg/L) and ZH (m) of studied lakes.

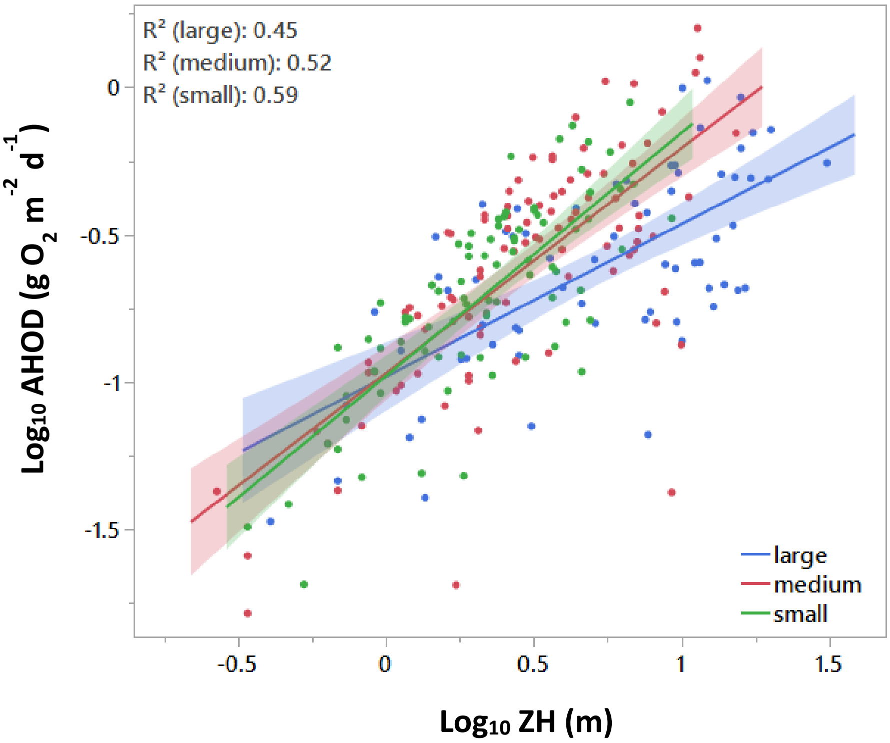

Fig. S1.2. The linear relationship between Log10 AHOD and Log10 ZH for different sizes (small, medium, and large) of lakes.

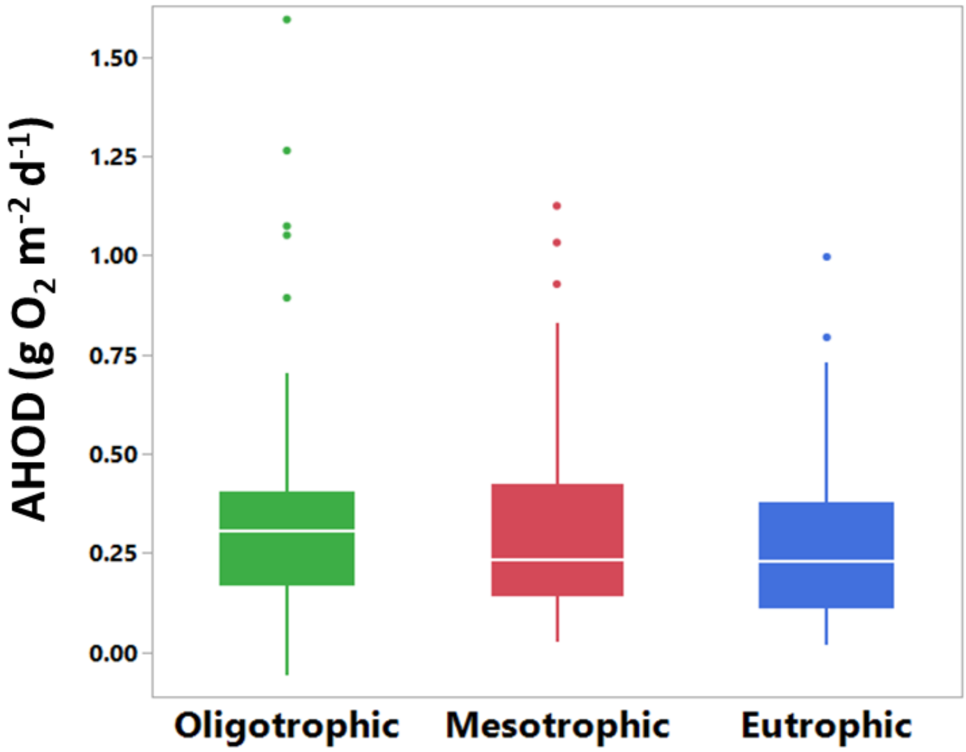

Fig S1.3. AHOD variation in various trophic status lakes across Canada. Box and whisker plots are used to visualize the distribution patterns.

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