MODELLING THE IMPACT OF HUMAN DEVELOPMENT AND WATER QUALITY ON HYPOXIA

by

Samantha Zeane Ramirez

M.Sc., The University of British Columbia, 2024

A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF
THE REQUIREMENTS FOR THE DEGREE IN

MASTER OF SCIENCE

in

The Faculty of Graduate and Postdoctoral Studies

(Oceans and Fisheries)

THE UNIVERSITY OF BRITISH COLUMBIA
(Vancouver)

November 2023

The following individuals certify that they have read, and recommend to the Faculty of Graduate and Postdoctoral Studies for acceptance, the thesis entitled:

Modelling the impact of human development and water quality on hypoxia

submitted by Samantha Zeane Ramirez in partial fulfillment of the requirements for the

degree of Master of Science

in Oceans and Fisheries

Examining Committee:

Jordan Rosenfeld, Adjunct Professor, Stream Ecology Scientist, B.C. Ministry of Water, Land, and Resource Stewardship
Supervisor

William Cheung, Director and Professor, Institute for the Oceans and Fisheries, UBC
Supervisory Committee Member

Emily Rubidge, Adjunct Professor, Forestry, UBC
Supervisory Committee Member

Abstract

Streams are subject to a variety of impacts as a consequence of human development which disrupt ecosystem processes and can lead to habitat change and species loss (Dos Reis Oliveira et al., 2019; Marques et al., 2019). Associated negative impacts include nutrient enrichment, increased light availability and water temperatures, and the alteration of channel structure and stream flow (Zhi et al., 2023; Mueller et al., 2005). Water quality is a good indicator of stream health, and was measured using various parameters, including nitrogen and phosphorus concentration, and DO concentrations. To understand the effects of nutrient enrichment (eutrophication) on stream metabolism and fish habitat, I measured key water quality parameters every month from May to August at 37 lower Fraser Valley stream sites. Overall patterns of water quality across the summer low-flow recession indicate increasing hypoxia associated with declining flow and water surface turbulence, high algal production and respiration associated with nutrient enrichment, and lack of canopy cover. One novel insight of this study is the limiting effect of hypoxia on aquatic plant and algal production; moderate increases in total P appear to stimulate plant and algal growth until moderate to severely hypoxic conditions occur (DO < 2 mg/L), causing total P to switch from a stimulating to inhibitory effect on algal and heterotroph production. Results showed that the likelihood of hypoxia is greater than 50% when total P exceeds ~0.06 mg/L, when discharge is less than ~0.05 $m^3 \cdot sec^{-1}$, when mean K is less than 4 ($m\ d^{-1}$), when total N is greater than 1 mg/L, and when water column depth exceeds 0.7 m. Conserving water quality is a particularly important issue in streams where *Species at Risk* and other sensitive species occur (i.e., salmonid species, and listed taxa like Salish Sucker (*Catostomus sp. cf. catostomus*), and Nooksack Dace (*Rhinichthys cataractae*)). It is necessary to better understand the interaction between human impacts and water quality to minimize further fish and fish habitat loss in a changing environment. The widespread hypoxia observed in lower Fraser Valley streams indicates a failure by responsible agencies to address this pivotal conservation issue.

Lay Summary

This research aims to highlight the stream characteristics that highly influence water quality and the amount of dissolved oxygen (DO) in the water available for fish. We hope that this research will direct conservation and management efforts towards streams that are at high risk of poor water quality and low levels of DO. This study can be used to cross-reference streams with similar stream characteristics to estimate the likelihood of an unsampled stream having poor water quality and low levels of DO. Management strategies that focus on conserving the most susceptible streams simultaneously help conserve the most sensitive habitats and fish populations including Salish sucker and juvenile salmonids.

Preface

Both chapters 2 and 3 are based on work by myself, Samantha Ramirez, as advised by Dr. Jordan Rosenfeld. This work was completed in Dr. Jordan Rosenfeld's lab in the Applied Freshwater Ecology Research Unit of the UBC Institute for Oceans and Fisheries. Chapter 2 will identify additive effects of light availability, water temperature, nutrients, gradient, conductivity, and flow on stream metabolism. More specifically, how these parameters influence the rate of gross primary productivity, ecosystem respiration, and dissolved oxygen concentration. Chapter 3 is based on work that will determine the influence of flow and the gas-water exchange coefficient (K) on hypoxia and help inform assessment of minimum flow thresholds for small streams.

I was responsible for site selection with help from Mike Pearson from Pearson Ecological and Dr. Jordan Rosenfeld (approximately 50% of the sites were independently chosen by myself). I was responsible, with assistance from my two field assistants Sydney Gass and Ariel Shatsky for the deployment and retrieval of the dissolved oxygen data loggers, stream habitat assessment (water temperature, canopy cover classification, discharge, sediment type classification, conductivity readings, gradient measurements, and landuse classification), and collection and partial processing of water samples (adding preservatives and filtering samples). ALS environmental was responsible for the testing of nitrogen and phosphorus concentrations in the water samples. Lastly, I was responsible for the processing and analysis of all data with Dr. Jordan Rosenfeld doing quality assurance.

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List of Abbreviations

DO – Dissolved oxygen

ER – Ecosystem respiration

GPP – Gross primary production

NPP – Net primary production

SM – Stream metabolism

Acknowledgements

I give my sincere gratitude to my advisor Dr. Jordan Rosenfeld for his well-balanced academic support, genuine understanding, and use of teachable moments throughout these two years. I want to thank my committee members Dr. William Cheung and Dr. Emily Rubidge for their valuable knowledge and time.

I would also like to thank Mike Pearson for his guidance during site selection, for sharing his knowledge on the streams in the lower Fraser Valley and for connecting me with private landowners and stewards in the area.

I owe a special thank you to the private land owners who both collaborated with me and welcomed myself and this research; A Rocha for taking the time to introduce me to the Campbell River sites and data sharing, Sherry Chrisholm (and her dog Jay) for always welcoming me with a warm smile and chat, and the community of Chawathil First Nation, specifically Art, who personally helped with the field work. We could not have pulled that canoe through the marshland without you!

Thank you to the grant support from the Department of Fisheries and Oceans Canada - Pacific Region Species at Risk branch for financially supporting my research goals and a special thanks to Thomas Smith, Pedro Gonzalez Espinosa, and Gauthier Monnet for taking the time and effort to troubleshoot R error messages with me and for helping me write my code.

Chapter 1: Introduction

1.1 General background and rationale:

Streams are subject to a variety of impacts as a consequence of human development that can disrupt ecosystem processes and can lead to habitat change and species loss (Dos Reis Oliveira et al., 2019). Urban and agricultural development has been of growing concern for stream health and will continue to be as human population numbers rise. Associated negative impacts include nutrient enrichment, increased light availability and water temperatures, and the alteration of channel structure and stream flow (Nelson et al., 2009). A good indicator of stream health is water quality, which can be measured using various parameters such as nitrogen and phosphorus concentration, turbidity, salinity, water temperature, and dissolved oxygen (DO) concentration. Conserving water quality is a particularly important issue in streams where *Species at Risk* and economically, culturally, and ecologically valuable taxa live. Current decline of habitat quality has resulted in an estimated a 2.4% extinction rate per decade for freshwater fish species in North America alone (Ricciardi & Rasmussen, 2001). Better understanding the role of human impacts to water quality and stream metabolism will help minimize further extinction and help guide species recovery in a changing environment.

1.2 What is stream metabolism?

Stream metabolism is an important indicator of water quality and incorporates both gross primary production (GPP) and ecosystem respiration (ER). GPP is the total carbon (energy) fixed by aquatic plants and algae during photosynthesis, and net primary productivity (NPP) is the daily average energy that is converted to plant biomass (Equation 1). During GPP, plants and algae use light energy from the sun to *consume* CO_2 and *produce* O_2 (Figure 1A). During daylight hours (approximately 8:00 – 18:00 depending on the season), there is typically a net positive DO concentration in the stream (Figure 1B).

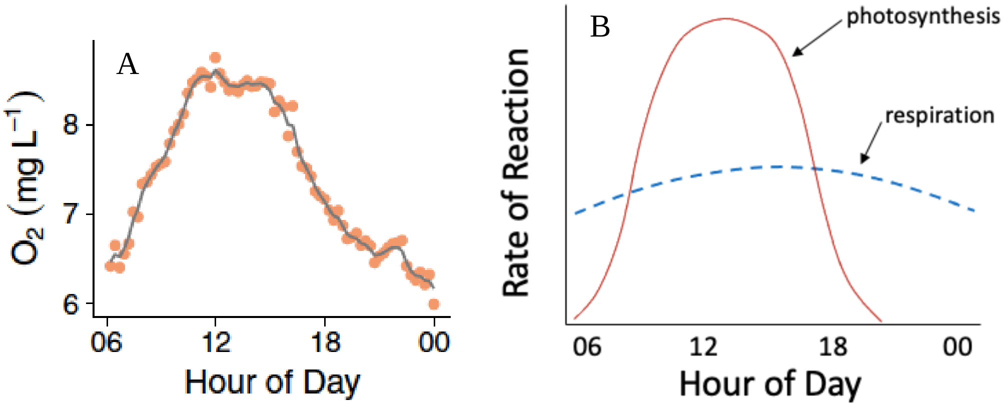


Figure 1 A) Daily change in oxygen concentrations in a reference stream (Appling et al., 2018) and B) Daily change in the rate of photosynthesis and respiration.

ER can be broken down into daily average autotrophic (R_a) respiration by plants and algae vs heterotrophic respiration (R_h) by fish, invertebrates, and microbes (Equation 2). During respiration, O_2 is *consumed* and converted to CO_2. Though autotrophic respiration is reduced at night, O_2 depletion is more prominent when photosynthesis stops at night (Figure 1B), and respiration is no longer offset by oxygen production, making the stream more susceptible to nocturnal hypoxia. Heterotrophic respiration, more specifically microbial respiration, is enhanced when plant and algae biomass begins to decompose via microbial or fungal decomposition, reducing the amount of O_2 in the water. In excess, ecosystem respiration can result in hypoxia (depression of DO below saturation) or anoxia (complete depletion of oxygen in the water column). These overall daily change in the amount of O_2 produced through GPP and consumed through ER can be described as stream metabolism (SM, Equation 3).

GPP and ER can be directly measured using light/dark bottles or C14 techniques, but these are comparatively labor intensive (Bender et al., 1984). Alternatively, both variables can be estimated using daily changes in DO concentration by making assumption about diffusion rates

(k) at the air-water interface (Equation 4; Bernot et al., 2010; Riley & Dodds, 2013). Below, Equation 4 can be used to calculate the change in DO concentrations over time where P_t is the GPP at time t, R_t is the ER at time t, and K_t (or $\Delta O_t/\Delta t$) is the rate of air-water oxygen exchange at time t.

Equation 1: $GPP = NPP + R_a$

Equation 2: $ER = R_a + R_h$

Equation 3: $SM = GPP + ER$

Equation 4: $\frac{\Delta O_t}{\Delta t} = P_t + R_t + K_t$

We must also consider that streams are constantly exchanging O_2 with the atmosphere at the water surface, which is an additional influence on DO concentrations in the water column. Accurate measurement of this gas exchange (K) is fundamental for quantifying stream ecosystem metabolism (Pennington et al., 2018). Oxygenation is influenced by many local geomorphological factors that affect turbulence at the water surface and enhance gas exchange, such as water velocity, depth, meandering, presence of riffles and pools etc. (Beaulieu et al., 2013).

1.3 Effects of Hypoxia on Fish

Studies have shown that hypoxia can increase O_2 consumption during exercise (Magnoni et al., 2018), damage gill structure (Araujo-Luna et al., 2018), reduce fish immunity to disease

(Colby et al., 1972), reduce fish appetite (Jobling, 1995), limit fish growth (Abdel-Tawwab et al., 2019; Rosenfeld and Lee 2022), induce fish migration (Breitburg et al., 2018), and inhibit natural reproduction (Colby et al., 1972). By addressing how current human development influences DO concentrations in streams, we can begin to predict how future human development and climate change may influence future productive capacity for fish. This should allow researchers and managers to better quantify the spatial and temporal impacts on specific fish species, particularly those at risk.

1.4 Natural & anthropogenic drivers of stream metabolism & water quality

Stream environments rely on a suite of naturally occurring drivers to regulate stream metabolism and water quality. These include shading, nutrient input, stream discharge, water temperature, and stream geomorphology (e,g., bank width, stream gradient, etc.). Previous research has identified strong positive and negative responses of GPP and ER to all of these factors – light (+), nutrients (+), temperature (+), flow (-) and sediment accumulation (-) (Bernhardt et al., 2018; Figure 2). Appropriate levels of these factors are essential for the production of prey and oxygen necessary for fish survival, and high flows are also critical for the creation of suitable spawning, rearing, and overwintering habitat. Altered levels of these factors as a result of human development may result in unfavourable fish habitat conditions and inadequate prey production and oxygen if the frequency of hypoxic events increases in a changing climate.

Natural fluctuations in flow and stream metabolism occur on daily, seasonal and annual time scales and are vital for some fish species (O’Connor 1967; Uehlinger 2006). For example, the increase in stream discharge following snow melt provides spawning flows for many species, while daily and seasonal input of allocthonous nutrients (i.e., leaves, woody debris, terrestrial invertebrates etc.) and dissolved organic carbon provide energy at the base of the stream food chain.

It is important to note that drivers of stream metabolism can be altered by human activities. Major anthropogenic impacts to water quality (stream metabolism) include flow regulation (dams and surface water withdrawals), landuse change, and global warming. Coupled natural and anthropogenic changes that jointly alter light, temperature, flow and nutrients may severely impact GPP, ER and DO, potentially increasing the risk of hypoxia, as described below (Figure 2). Landuse change is often the ultimate causation of changes to direct drivers of stream metabolism because of its impact on nutrients, channel structure, flow, light and temperature (Figure 2). Streams in urban and agricultural landscapes tend to be more hydrologically variable and have an increased supply of limiting nutrients that makes it more challenging to predict the cumulative impacts of these opposing stressors on stream metabolism (Blaszczak et al., 2019).

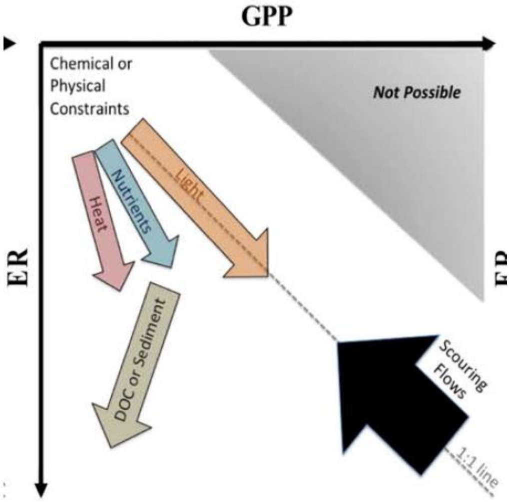


Figure 2 The relationship between various drivers of water quality (light, nutrients, heat, dissolved organic carbon or sediment, and scouring flows) and GPP and ER (Bernhardt et al., 2018).

1.4.1 Flow

Flow is impacted by humans through the construction of dams and water diversions or through the isolation of rivers from their floodplains that normally modulates the natural high and low water events that are essential for fish productivity. Ludlam and Roy (2020) found that dammed streams were on average 5.6°C warmer than streams without dams as a result of flow reduction. Similarly, Marcarelli et al. (2010) observed that intensive irrigation causing a 70% reduction in river discharge and significantly increased GPP and ER in the river. Other studies have found that *extreme* high flows can also be problematic because plant biomass from NPP is excessively scoured as a result of high flows, reducing both food availability and suitable habitat for fish and invertebrate species (Bernhardt et al., 2018).

Extreme low flow has been shown to reduce DO concentrations in stream and river environments (Bernhardt et al., 2018; Carter et al., 2021). A study by Blaszczak et al. (2019), showed that approximately 97% of DO conditions below 50% saturation occurred when flow conditions were less than 0.15 mm/hour. This study also provided evidence of reaeration of streamwater approaching anoxia following a storm event (Blaszczak et al., 2019; Figure 11), highlighting the sensitivity of hypoxia to flow regulation.

1.4.2 Landuse Change and the importance of riparian buffers

Changing land from pristine forested landscapes to agricultural or urban ones can have severe impacts on flow, temperature, light availability, and nutrient enrichment. Land use has been shown to be scale-dependent, where upstream land use has a greater impact in larger streams and local landuse close to the stream is more influential in smaller streams (Buck, Niyogi, & Townsend, 2019).

Understanding the influence of flow on stream metabolism and DO concentrations requires consideration of the role of geomorphology (Peckarsky et al., 2014). Previous studies show that shallow gradient streams have the most drastic decline in median percent saturated DO throughout the winter (December-February) and summer (June-August; Blaszczak et al., 2019), because turbulence is positively correlated with stream gradient. Variability in DO concentrations is also much higher in developed landscapes (Dos Reis Oliveira et al., 2019; Griffiths et al., 2013).

Riparian zones are examples of landuse in close proximity to the stream that has a significant influence on water quality. When humans remove riparian forest, they reduce allochthonous inputs to streams, a key energy source for the base of the aquatic food chain. The removal of riparian vegetation and associated reduction of canopy also results in increasing light availability and water temperature, which contribute to increase GPP and ER, potentially elevating hypoxia to levels threatening the persistence of aquatic life (Bernhardt et al., 2018; Mulholland et al., 2001; Griffiths et al., 2013; Stets et al., 2020).

Land development also results in increased nutrient enrichment from diffuse runoff and direct sewage and stormwater inputs. Excess nutrients will stimulate GPP and indirectly increase ER and oxygen uptake by microbial respiration. The importance of riparian zones also relates to nutrient enrichment, because riparian vegetation acts as a filter for nutrients and contaminants coming from upslope runoff (Lind et al., 2019). Riparian zones 9-11 m wide have been shown to remove at least 75% of sediment and nutrients, and a minimum 21 m riparian zone is required to generate stable water temperatures (Lind et al., 2019), depending on the site potential vegetation height of the native vegetation. With inadequate riparian zones in most agricultural and urban streams, increased light availability, higher water temperatures and reduced runoff filtering, we have severe current and future impacts on water quality.

1.4.3 Water temperature

For every 1°C increase in air temperature, stream water temperatures rises about 0.6-0.8°C (Morrill, Bales, & Conlkin, 2004). Even though rising water temperature is evident across all landscapes, the most rapid increase in water temperature is in urban landscapes (Kaushal et al., 2012), where streams are subject to the removal of riparian zones and the "Urban heat island" effect, where the high albedo of asphalt and concrete can increase the surface temperature of the landscape (Brazel et al., 2000). Previous studies on the effects of global warming on stream productivity found that a 1°C increase in water temperature may lead to streams becoming 23.6% more heterotrophic (Song et al., 2018).

Temperature strongly influences dissolved oxygen concentration, with high water temperatures associated with low DO and cool temperatures corresponding with high DO (Rajwa-Kuligiewicz et al., 2015). Water temperature also directly affects fish physiology (i.e., metabolic rates and growth), behaviour (i.e., spatial and temporal migration patterns) and overall population productivity (i.e., egg development, larval viability, etc.). DO solubility decreases with temperature, which can further limit metabolic rates of fish (Mandic et al., 2009). Hypoxia and elevated metabolism may directly reduce fish growth, and alter habitat selection and population productivity (Breitburg et al., 2018; Abdel-Tawwab et al., 2019). However, fish responses to increasing water temperatures is species-dependent; for instance, cold-water and stenothermal species (i.e., salmonids) may be more temperature-sensitive (Rosenfeld and Lee 2022), and thus more susceptible to stress from elevated water temperatures compared to species with larger thermal ranges (i.e., centrarchids).

There is also a strong interaction between river discharge and water temperature that can indirectly alter DO. Modelled maximum water temperatures are higher when discharge is reduced, leading to flow-and temperature-dependent depression of DO (Vliet et al., 2011). This highlights the impact that altered discharge and future flow regulation may have on reducing water quality.

1.5 Study Area

The Fraser Valley in the province of British Columbia is Canada's number one agricultural region and has a population growth rate of 6.6% every year (FVRD, 2016). The Fraser Valley Regional District population growth is higher than that of Metro Vancouver and the provincial average (FVRD, 2016). Domination of urban and agricultural landuse coupled with rapid urban growth are predicted to degrade habitat quality and increase hypoxia, which could threaten local aquatic and at risk species (Figure 3).

The most susceptible streams to these human impacts tend to be those with high variability and low flows (Reynolds et al., 2015). Stream vulnerability to climate change and rising water temperature is also dependent on stream size, where smaller streams have been shown to be more highly impacted (O'Driscoll & DeWalle, 2006).

Streams in the lower Fraser Valley are generally small (i.e. wetted width), and characterized by low gradient and velocity, making them suitable habitat for *Species at Risk* such as the Salish Sucker (*Catostomus sp. cf. catostomus*) and economically valuable salmonids like Coho salmon (*Oncorhynchus kisutch*). Since both species prefer habitats more susceptible to hypoxia (low velocity and gradient) and exhibit sensitivities to low DO, this makes them key indicator species for water quality impairment.

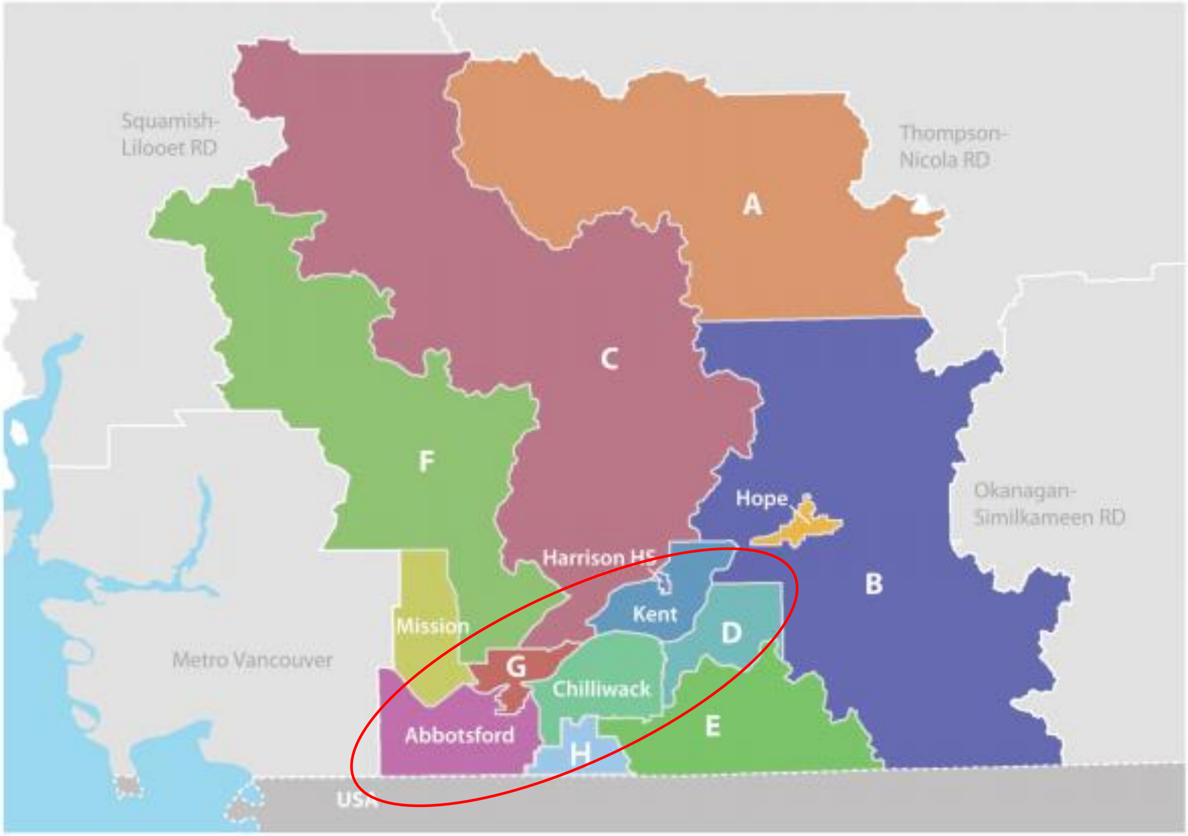


Figure 3 Map of the Lower Fraser Valley Regional District showing municipalities in various colours (Statistics Canada, Census Population 2016). Red ellipse indicates the lower Fraser Valley region downstream of Hope with the highest density of low gradient salmonid streams and the highest impacts of agriculture and urbanization.

1.5.1 Species inhabiting the study streams

Important species that inhabit the slower moving waters of the lower Fraser Valley tributary streams include Salish sucker and salmonids such as coho salmon, cutthroat trout, rainbow trout (steelhead), and to a lesser degree Chinook salmon. The Salish sucker is a Threatened species under the *Species at Risk* Act and is endemic to only 11 watersheds in the Fraser Valley and 4 others in Washington, USA (DFO, 2020). The major threats to sucker include hypoxia, seasonal lack of water, and habitat destruction (DFO, 2020). On the other hand, Coho salmon and other salmonids support culturally and economically important sport and commercial fisheries. The major threats to salmonids in lower Fraser valley streams also include habitat degradation, reduced flows, and hypoxia.

Lower Fraser Valley streams with low DO have been shown to exhibit decreased abundance of sensitive taxa such as Salish sucker and Coho salmon (Scott et al. 2016; Waite et al., 2019; Rosenfeld et al. 2021). By relating spatial patterns of GPP to distributions of juvenile salmonids, researchers found that salmonids were most abundant in cool stream sections where rates of GPP were low (Kaylor et al., 2019). More specifically, hypoxia has been shown to significantly decrease food consumption and growth rates of juvenile coho salmon and reduce habitat use (Zinn et al., 2021). When investigating the effects of hypoxia on Salish sucker in field experiments, growth rates were not significantly affected by hypoxia when well-oxygenated waters were present, but use of hypoxic habitat appeared to decline (Zinn et al., 2021). To help conserve these economically and ecologically important species, studies that can better predict the future impact of human development on hypoxia in these streams will help anticipate the long-term prognosis for species persistence and recovery.

1.6 Anticipated Research Significance

This study will estimate the current effect of human impacts on water quality throughout representative reaches of salmonid rearing habitat and Salish sucker critical habitat, and provide a foundation for predicting the effects of future human impacts on water quality parameters; specifically, DO, GPP, ER and temperature. My research also supports the estimation of parameters to populate a three-parameter metabolism model to estimate GPP, ER and K in unsampled smaller, lower gradient streams, as well as empirical (regression) models relating water quality to site attributes (i.e., flow, gradient, landuse). It also provides an assessment of the cumulative and interactive effects of nutrients, channel structure, flow, light, and temperature on these water quality parameters by contrasting agricultural, urban, and forested streams. By analyzing which streams are most susceptible to low water quality, this information will help inform management strategies, and focus conservation efforts on streams most at risk based on shared physical and biotic factors. Management strategies focused on conserving the most susceptible streams simultaneously conserve the most sensitive habitats and fish populations, including Salish sucker and juvenile salmonids.

Chapter 2: Drivers of Stream Metabolism

2.1 Summary

There are many naturally occurring drivers of stream metabolism (GPP and ER), which are heightened by anthropogenic impacts, including rising air and water temperatures associated with global warming and nutrient enrichment from surrounding agricultural and urban land. The pathways of effect impacting stream metabolism are complex, and this study highlights the linkages among drivers and their influence on stream metabolism. I used streamMetabolizer (Appling et al., 2018) to estimate GPP and ER, and Generalized Linear Mixed Models to identify the most influential environmental drivers of GPP and ER. Deeper pond habitats had roughly double the primary production as stream habitat, largely because of the greater depth integrated rate of GPP. Light availability as mediated by canopy cover had the strongest influence on primary production, but this light effect was not noticeably enhanced in nutrient enriched agricultural streams as expected. However, there was a cascading effect of light and nutrients on DO, with hypoxia being significantly worse at meso and eutrophic open-canopy sites than at similarly high nutrient forested sites, particularly under N enrichment. Surprisingly, there was a significant negative relationship between primary production and phosphorus concentration, rather than the positive relationships originally hypothesized. However, this negative relationship was only evident at hypoxic sites, indicating that hypoxia from nutrient enrichment may be limiting both primary production and respiration. Overall, there were fewer interactions among drivers GPP and ER than hypothesized, suggesting that main effects of nutrients, light, and flow explain most of the significant variation in metabolism.   StreamMetabolizer generated insightful estimates of stream metabolism, although the program was unable to resolve GPP and ER at extremely hypoxic sites with lots of data noise and some reference sites with minimal daily

changes in DO (26 out of 125 logger deployments). For future studies, continuous logger deployments (rather than weekly) may improve model fit, preventing loss of data at key reference and impact sites. Simple light-dark chamber incubations may also provide ground-truthing of GPP and ER estimates at selected low productivity sites.

2.2 Introduction

Stream metabolism (SM), also referred to as aquatic ecosystem metabolism or net ecosystem production, represents how energy is created and used in aquatic environments. Stream metabolism has two compartments: gross primary production (GPP) and ecosystem respiration (ER). GPP is the total carbon (energy) fixed by aquatic plants and algae through photosynthesis, and net primary productivity (NPP) is the residual energy that is converted to plant biomass (Equation 1, Chapter 1). Photosynthesis consumes CO_2 and generates O_2; respiration is the mirror image of photosynthesis, consuming O_2 and creating CO_2. ER can be separated into autotrophic respiration (R_a) associated with algae and aquatic plants and heterotrophic respiration (R_h) from microorganisms, fungi, and fish respire.

Aquatic metabolism is challenging to measure, but can give considerable insight into water quality and fish habitat dynamics. Fortunately, the generation and consumption of O_2 on a diel cycle, expressed as temporal changes in DO, provides a well-established avenue for estimating aquatic metabolism (Odum, 1956). Oxygen production occurs during daylight hours when plants photosynthesize, and typically peaks just after solar noon. At night, photosynthesis ceases and ER dominates, resulting in declining oxygen concentration in the water column. Although GPP and ER can be directly measured using light/dark bottles or C14 techniques, these approaches are relatively labor intensive (Bender et al., 1987). Alternatively, metabolism can be estimated using daily changes in DO concentration (Equation 4, Chapter 1; Bernot et al., 2010; Riley & Dodds, 2013) and models that solve simultaneously for oxygen consumption, (i.e., ER), production (GPP) and oxygen diffusion rate at the air-water interface (Appling et al. 2018).

Accurate estimation of the gas exchange (i.e., re-aeration) rate (K) is fundamental to accurate measurement of GPP and ER (Pennington et al., 2018). Reaeration is influenced by discharge, gradient, and local geomorphological factors that affect surface turbulence such as water velocity, depth, gradient, presence of riffles and pools, etc. (Beaulieu et al., 2013).

In addition to instream habitat structure, the daily cycle of GPP and ER is influenced by other environmental factors including water temperature, flow, nutrients, and light availability. These represent key drivers of stream metabolism in natural landscapes, but their influence is often exacerbated by anthropogenic effects. For example, rising air temperatures as a result of climate change is warming waters above historic norms, while land development continues to increase light availability to streams while removing the cooling benefits of riparian shade, resulting in excess algal production. Similarly, water diversion for irrigation coupled with climate change-induced drought reduces flow and therefore surface turbulence and re-aeration. Excess nutrient enrichment from agricultural and urban landscapes stimulates excess algal production that eventually decomposes and consumes the oxygen that fish require to survive. This complex network of cumulative effects continues to challenge our understanding of the most detrimental threats to fish persistence under climate change.

The aim of my thesis is to address this problem by determining the influence of key environmental drivers on water quality and metabolism in the highly developed lower Fraser Valley of British Columbia, Canada, where urban and agricultural landscapes dominate and human population growth creates a trajectory of habitat loss (Rosenfeld et al 2021). Streams in the lower Fraser Valley are characterized by relatively low gradient pool-riffle habitat, making them suitable for *Species at Risk* such as the Salish Sucker (*Catostomus sp. cf. catostomus*) and economically valuable salmonids like Coho salmon (*Oncorhynchus kisutch*), which are threatened by ongoing habitat degradation (DFO, 2020).

To quantify the drivers of aquatic metabolism across a representative subset of streams, I placed continuously recording DO loggers at 37 reference and impact sites to generate diel DO data; these DO times series were used both as a direct measure of water quality impairment, and to estimate GPP and ER using StreamMetabolizer. To better understand environmental drivers of metabolism and DO, I also measured water temperature, depth, discharge, conductivity, stream gradient, total phosphorus (P), total nitrogen (N), and light availability (canopy cover) at all sites.

Specific objectives were i) to determine the roles of light, nutrients, water temperature, discharge, and gradient in limiting GPP and ER; ii) to determine the extent to which metabolism differs between reference and agriculturally-impacted sites; and iii) to test for the presence of key interactions driven by nutrient enrichment. My expectations were that sites in agriculturally-dominated watersheds would exhibit enhanced primary production and respiration leading to hypoxia, and that interactions between nutrient loading and canopy cover would cause eutrophication to be worse at open-canopied sites, and exacerbate the negative impacts of reduced flows on respiration. The ultimate goal of my thesis is to use insights into metabolic causation to prioritize management actions. For instance, if light availability is the dominant driver of primary production, then restoring riparian forest may be a useful interim measure to mitigate water quality while agencies grapple with nutrient reduction at a landscape scale.

2.3 Methods

2.3.1 Study sites

I used stratified sampling to select 37 representative stream sites across a broad range of site attributes (landuse, gradient, flow, light, water temperature & nutrients) representative of the range of conditions present in small streams in the lower Fraser Valley, ranging from open-canopied eutrophic agricultural sites to oligotrophic forested sites (Figure 4). First, I selected sites across 20 different tributaries (10 ponds and 27 streams) with the help of Lower Fraser Valley knowledge holders including Jordan Rosenfeld and Mike Pearson of Pearson Ecological, along with satellite image investigation by myself. Following this, I measured site attributes at each site to ensure I captured sites across an environmental gradient. Daily changes in DO were recorded monthly using MiniDot data loggers for 5-7 day continuous intervals from May to early late August of 2021, and sites with different combinations of potential environmental drivers were selected to increase the likelihood of detecting the most consequential interactions. The study design aimed to include approximately 30% low nutrient reference sites, 40% high nutrient impacted sites, and 30% moderately impacted sites. Final trophic classifications based on water chemistry sampling were 37% oligotrophic, 26% ~~mesotrophic,~~ and 37% eutrophic based on nutrient thresholds identified by Dodds et al. (1998; oligo/meso/eutrophic thresholds for nitrogen: 0.7<, 0.7-1.5, > 1.5, respectively; for phosphorous: 0.025<; 0.025-0.075; > 0.075). Stream habitat characteristics measured at each site included canopy type (open, partial, forested), water temperature, discharge, conductivity, gradient, total nitrogen, total phosphorus, average depth, algal cover, landuse (reference or agricultural), and sediment type. On average, agricultural sites had 5-10X higher concentrations of nitrogen and phosphorus, respectively, in comparison to reference sites (Figure 5). The proportion of sites for each categorical variable can be found in Table 5 in the Appendix. Note, two urban streams were included in the study and incorporated under the agriculturally impacted category as agriculturally impacted streams were also impacted by urban development at some sites.

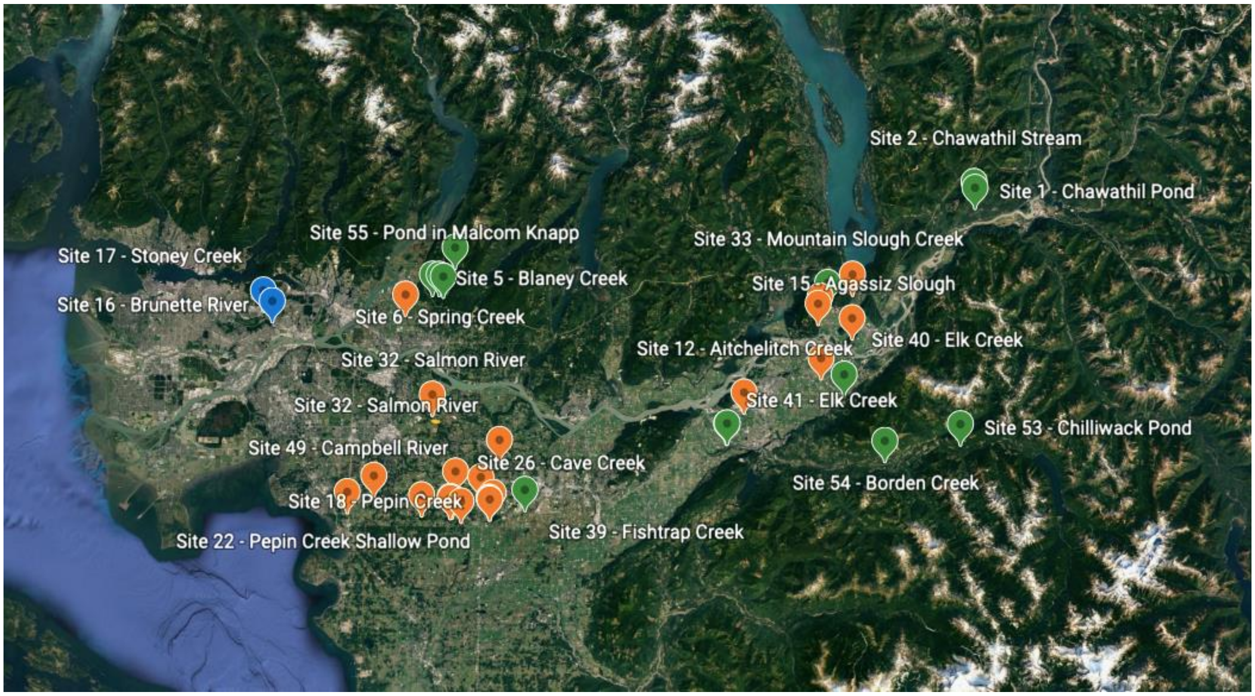


Figure 4 Map of representative sites across the Lower Fraser Valley. Blue pins are urban sites, orange pins are agricultural sites and green pins are reference sites. Note that only a subset of site names are evident on this map.

2.3.2 Stream Metabolism Measurements

I used the single station method to measure stream metabolism, which assumes homogeneity of gradient, channel structure, and canopy type in the upstream reach above the DO logger. Assessment of homogeneity of canopy cover, stream geomorphology, and land use was conducted using a visual assessment of Google Earth satellite imagery and a field site visit.

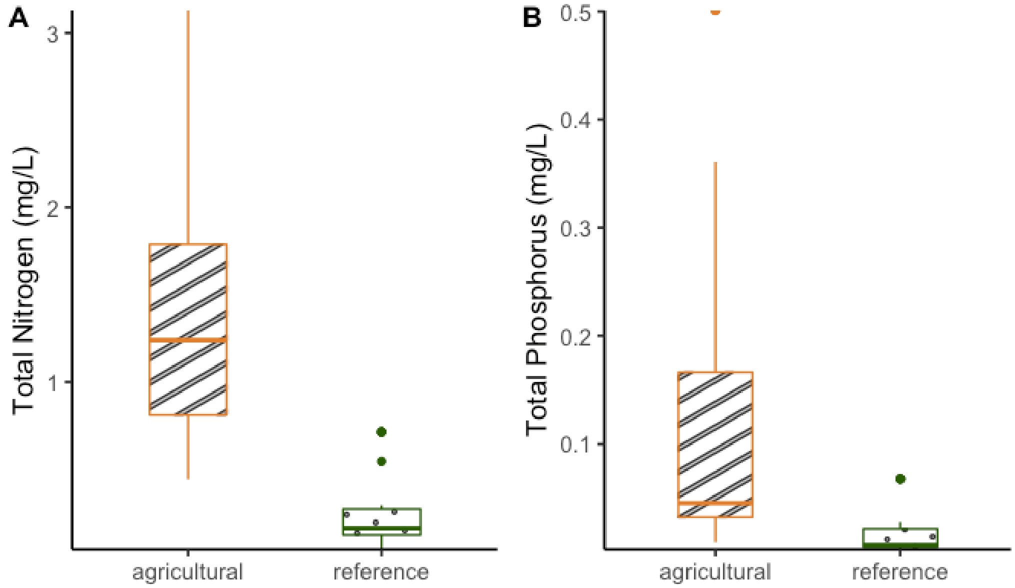


Figure 5 Total nitrogen (A) and total phosphorus (B) in agricultural (n=69) and reference (n=30) sites.

2.3.3 DO Logger placement

Loggers were installed at each site in a location that was broadly representative of the reach, with sufficient velocity to ensure that the water column was well mixed (i.e., not in a channel margin or side pool with stagnant water). The DO data logger was attached to a metal rod at 50% of total water column depth, with the sensor oriented downstream to avoid debris affecting DO measurements.

Two DO loggers were deployed at the majority of pond sites (n= 10) to account for vertical stratification in DO, with one logger installed 10-15 cm below the surface and a second 10-15 cm above the bottom substrate. A single DO logger was placed at 50% depth in the 2 pond sites that lacked temperature stratification within the water column. Loggers recorded DO, time, and water temperature at 10 minute intervals. A limited number of available loggers precluded simultaneous measurement at all 37 sites; instead, logger deployments were rotated among sites to obtain a minimum of 5 days of continuous data each month between May and August, which exceeds the recommended 3-day duration for an integrated metabolism measurement (Staehr et al., 2010).

2.3.4 Collection of environmental covariates

At every site I visually estimated percent canopy cover up to 100 m upstream of the logger location, (open/partial/forested canopy thresholds: 0-25%, 25-75%, 75-100%), average channel depth, gradient, conductivity, DO concentration at the time of logger placement and retrieval (measured using a handheld YSI meter), water velocity at the logger location, percent cover of algae and macrophytes, and discharge using standard velocity depth transects (Table 1). All sampling took place in 2021 with the exception of water quality samples to classify sites by nutrient status (Dodds et al., 2000), which were collected at each site in mid-August 2022 and analyzed for total nitrogen and phosphorus.

Table 1 The mean value and range of each continuous stream variable collected in this study.

Stream Characteristic	**Mean**	**Range**
Average channel depth (m)	0.67	0.04 – 2.06
Gradient (%)	0.62	0 – 15
Conductivity (µs/s)	209	14 – 680
Min. DO concentration (mg/L)	4.29	0.01 – 10.53
Mean DO concentration (mg/L)	6.08	0.04 – 12.54
Mean GPP (g O_2/m^2/day)	2.57	0.002 – 9.55
Mean ER (g O_2/m^2/day)	-7.88	-0.1 – -27.28
Discharge (m^3/s)	0.11	0 – 0.99
Total Nitrogen (mg/L)	1.04	0.04 – 3.13
Total Phosphorus (mg/L)	0.09	0.003 – 0.5

2.3.5 Modelling Stream Metabolism

A three-parameter inverse modelling software (streamMetabolizer) was used to estimate GPP, ER, and K by modelling the best fit between predicted and observed changes in DO (Appling et al., 2018). StreamMetabolizer simultatneously estimates daily average GPP, ER, and a daily value of K600, the gas exchange coefficient, where K600 is standardized to the Schmidt number (Sc) 600 (corresponding to O_2 at 17.5C; Jahne and HauBecker, 1998). StreamMetabolizer requires six input variables: average water depth in the reach upstream of the DO logger, and a time series of observed DO, saturated DO, water temperature, light, and solar time. Observed DO, water temperature, and time were recorded using DO loggers. An estimate of depth is also required to ensure reliable GPP and ER estimates, and was measured at 5 transects upstream of the DO logger. Local time was converted to solar time using the calc_solar_time() function (all required functions are integrated into the streamMetabolizer R package). Saturated DO was calculated using the calc_DO_sat() function using water temperature, air pressure, and water salinity. Light was calculated using the calc_light() function, which uses longitude and latitude to estimate light availability.

The mm_name() function was used to specify a Bayesian metabolism model (*type* = 'bayes'); *pool_K600* was set to 'normal' for specifying how the model pools information among days to maximize consistency in daily estimates for K600. Additional model specifications included *err_obs_iid* = TRUE to configure observation error, *err_proc_iid* = TRUE to include processing error autocorrelation, and lastly, *GPP_fun* was set to 'linlight', assuming that GPP is a linear function of light with 0 intercept and a slope that varies among days. In some cases, using 'satlight' fit a better estimate of modelled DO against the observed DO data, where 'satlight' assumes GPP is a saturating function of light availability.

Arguments for the specs() function and revise() function varied for each site. Within the revise() function, *burnin_steps*= 1000, *saved_steps*= 500, and n*_cores*= 4 were held constant for all models at the default values used by Appling et al. (2018), while *GPP_daily_mu* and *ER_daily_mu* (the means of the density function of the normal distribution for daily GPP and ER, respectively) varied across sites, as did *GPP_daily_sigma* and *ER_daily_sigma* (the standard deviations of the density function of the normal distribution for daily GPP and ER). The *predict_DO*() and *predict_metab*() functions were used to extract the modelled DO, GPP, ER, and K estimates for each site.

The threshold criteria used to assess quality of model fit in streamMetabolizer (Table 2) followed those outlined in Appling et al. (2018). The scores were weighted by adding up the sum of the points for each criteria to determine the confidence. Visual Inspection criteria 1 determines how well the modelled DO data fits the observed DO data, Visual Inspection criteria 2 determines if the predicted GPP and ER values make sense (e.g., GPP should be positive, ER should be negative), K600 range evaluates whether K600 estimates are reasonable and realistic given site conditions like gradient, % GPP negative is the percentage of incorrect negative values of GPP and conversely % ER positive is the percentage of incorrect positive values of ER. Lastly, root mean square error (RMSE) is the standard deviation of the difference between the predicted DO and modelled DO, and r-squared is the proportion of variance in the observed DO that can be explained by the modelled DO. Two general contexts emerged where GPP and ER estimates were considered to have low confidence: 1) reference forested sites where the daily change in DO was minimal (i.e., cyclic oxygen dynamics were not detectable); and 2) ponds where both primary production and respiration were high with extreme variability in daily DO without distinct diurnal cycles. This lack of daily trend reduced the power of the software to solve for all three parameters with accuracy, often resulting in negative GPP and positive ER estimates. Consequently, sites with both negative GPP and positive ER estimates (26 out of 125 observations across 37 sites) were excluded from the final analysis.

Table 2 Criteria used to determine low, medium, or high confidence that the stream metabolism model provided a good fit. The points are added up as a sum for each criteria to determine the confidence.

	Confidence		
Criteria	**Low**	**Medium**	**High**
Visual Inspection 1: How well does the modelled DO data fit the observed DO data? 1. Is the general daily DO pattern apparent? 2. Do the peaks of the modelled data line up with the peaks of the observed data? 3. Do the troughs of the modelled data lines up with the troughs of the observed data? No = 0 points, Somewhat = 1, Yes = 2 points 4. How much variability is apparent in the observed data around the modelled data? significant variability = 0 points, moderate variability = 1 point, minimal variability = 2 points, and minimal to no variability = 3 points	1-4	4-6	6-10
Visual Inspection 2: Do the predicted GPP and ER values make sense? 1. Do GPP estimates appropriately correspond to the canopy cover type for that site? (e.g., very high GPP at a heavily shaded low-nutrient site would be suspect) 2. Do ER estimates appropriately correspond to the canopy cover type for that site? No = 0 points, Somewhat = 1, Moderately = 2 points, Yes = 3 points 3. Are GPP estimates consistent with the observed algal biomass and site photos portraying abundance of algae? 4. Does GPP and ER appropriately match the corresponding land use? No = 0 points, Somewhat = 1, Yes = 2 points	1-4	4-6	6-10

If photos are not available then add 0.5 to each point category for sub criteria 1 and 2.			
K600 range (m d $^{-1}$)	>50	15-50	<15
% GPP negative	>0.5	0.25-0.5	<0.25
% ER positive	>0.5	0.25-0.5	<0.25
RMSE values	>0.5	N/A	<0.5
R-squared values	<0.6	N/A	>0.6

2.3.6 The Final Decision: To keep or discard metabolism estimates based on the 7 criterion

Metabolism estimates were retained if negative GPP and positive ER estimates were infrequent (‘medium’ or ‘high’ confidence; Table 2) and were paired with an r-squared value of 0.6 or higher for model fits between observed and predicted DO. Data were discarded if either negative GPP and positive ER occurrences were frequent (‘low’ confidence) and/or if the visual inspection of GPP and ER had ‘low’ confidence due to unrealistic values given site characteristics. In other words, some site-month combinations were excluded because of poor data.

2.3.7 Data Analysis

To identify the primary drivers of metabolism and hypoxia, the response variable GPP, maximum GPP, ER, and maximum ER were modelled as a linear function of canopy type (open, partial, forested), water temperature, discharge, channel depth upstream of the DO logger, conductivity, gradient, mean K, total N and P, and month using a Generalized Additive Model (GAM) in R (Version 4.2.2; Wood, 2017; Table 3). Stream identify was included as a random effect to account for differences among sites that were not captured by independent covariates. Maximum site GPP and ER were modelled in addition to mean values because the extremes of metabolism and variation in DO can have disproportionately large impacts on system state. I used model selection (dredge function in MuMin; *Dredge Function - RDocumentation*, n.d.) to rank the likelihood of candidate models and their constituent variables using AIC (Symonds and Moussalli, 2011; Akaike, 1987). Selected interactions were included among the drivers where ecological expectations suggested they were realistic (e.g., an interaction between canopy type and N or P, with the expected effects of nutrients on aquatic plant biomass being greater when light availability is not limiting).

Model averaging was performed on the full model for each response variable, including interactions as well as month as a class variable (May, June, July, August). Because many of the environmental drivers were strongly correlated with month (i.e., discharge, temperature), a reduced model was also included with month dropped as an explanatory variable. Reduced models were also included that retained only statistically significant variables, and a model with only easily measured explanatory variables was also included (i.e., excluding ER and GPP as predictors).

As a coarse correction for potential non-linear spatial autocorrelation among sites, latitude and longitude were included in all GAM models as non-linear covariates. All other drivers were modelled as linear (barring log-transformation of the response variable) because i) variability in the data reduced sensitivity to detect non-linear effects, ii) there was no clear expectation for non-linear relationships among most responses and drivers, and iii) to simplify the analysis.

To minimize multi-collinearity, paired correlations among independent variables were assessed, and only one variable of a pair was included in regression when a correlation exceeded 0.7 ($R^2 > 0.49$) (Figure 21 in Appendix). I ran the full ER and GPP model with latitude and longitude as a non-linear relationship and tested for normality. The output was not normally distributed so I square root or inverse square root transformed the GPP and ER data and re-ran the model using the transformed data and latitude and longitude as non-linear.

GAM regressions were fit in R (version 4.2.2) using the ‘gam’ function from the ‘mgcv’ package. Since most response variables did not have a clear best model (multiple models were within 2ΔAIC of the top model), model averaging was used to derive average model coefficients (Dormann et al., 2018).

Models were removed from the model averaging process when **1)** models were below the cumulative Akaike weight threshold of 0.95 (Symonds and Moussalli, 2011), **2)** ΔAIC exceeded 7 (Burnham et al., 2011; Symonds and Moussalli, 2011), and **3)** novel variables were introduced between ΔAIC 5 and 7 with low coefficients that contribute minimally to predictions, and the cumulative weight of models including the new variables was less than 0.05 (Symonds and Moussalli, 2011).

Assumptions of normality were evaluated by testing the normality of residuals using the Shapiro-Wilk statistic from the ‘stats’ package. If residuals were not normally distributed the response variable was transformed to improve normality (typically log or square root transformation). Homogeneity of variance was assessed by regressing residuals against predicted values. Model assumptions were tested using the full model, which was assumed to be a worst case scenario for violating assumptions.

Transformations varied based on the severity and direction of skew in the distribution of residuals, ranging from a square root transformation for moderately positively skewed data, to log base 10 transformation, and inverse transformation for severely positively skewed data (Anatomise Biostats, 2017). Response variables with negatively skewed residuals were first reflected then transformed as described above (Anatomise Biostats, 2017).

In addition to the GAM models, simple linear analysis of covariance and 2-way ANOVAs were also used for a posteriori tests and to test ancillary patterns in the data. This included calculation of the ratio of ER to GPP to compare with previous findings that suggest the ratio will be larger in streams as a result of allochthonous input. I used a 2-way ANOVA to explore the influence of canopy type on average GPP throughout the spring and summer. The effect of P on GPP and ER in different DO classes (0-2, 2-4, 4-6, >6 mg/L) was modelled as a simple linear analysis of covariance. Differences in GPP and ER between streams and ponds was assessed using GAM, simple linear regression, and a t-test. The effect of canopy type (open, partial, and forested) on GPP in reference and impacted sites was also modelled as a simple linear analysis of covariance. Finally, I explored the effect of N and P levels (N: 0-0.7,0.7-1.5, 1.5-3.5 mg/L; P: 0-0.025, 0.025-0.075, 0.075-0.6 mg/L) on DO in different canopy types (open, partial, and forested), which was also modelled as a simple linear analysis of covariance.

2.4 Results

2.4.1 Most Influential Drivers of Stream Metabolism

Generalized Additive Models of metabolism showed that GPP and Respiration have both shared and unique drivers. Canopy type, depth, and phosphorous were consistently identified as the primary significant drivers of both mean and maximum GPP (Table 3). As expected, primary production was significantly lower at forested sites compared to sites with partial or no canopy cover (Fig. 7; mean GPP: **t_{35} = 2.4, P <0.01**; maximum GPP: **t_{35} = 2.6, P = 0.02**); however, primary production at partial and open canopy sites were not significantly different (mean GPP: **$t_{34\ (partial)}$ = 2.6, $t_{34\ (open)}$ = 2.7, P = 0.99**; maximum GPP: **$t_{37\ (partial)}$ = 2.1, $t_{37\ (open)}$ = 2.8, P = 0.99**; Figure 7). Depth was also a consistently positive predictor of mean and maximum GPP, while total phosphorous appeared to be negatively associated with both metrics of primary production (Table 3), in contrast with expectation.

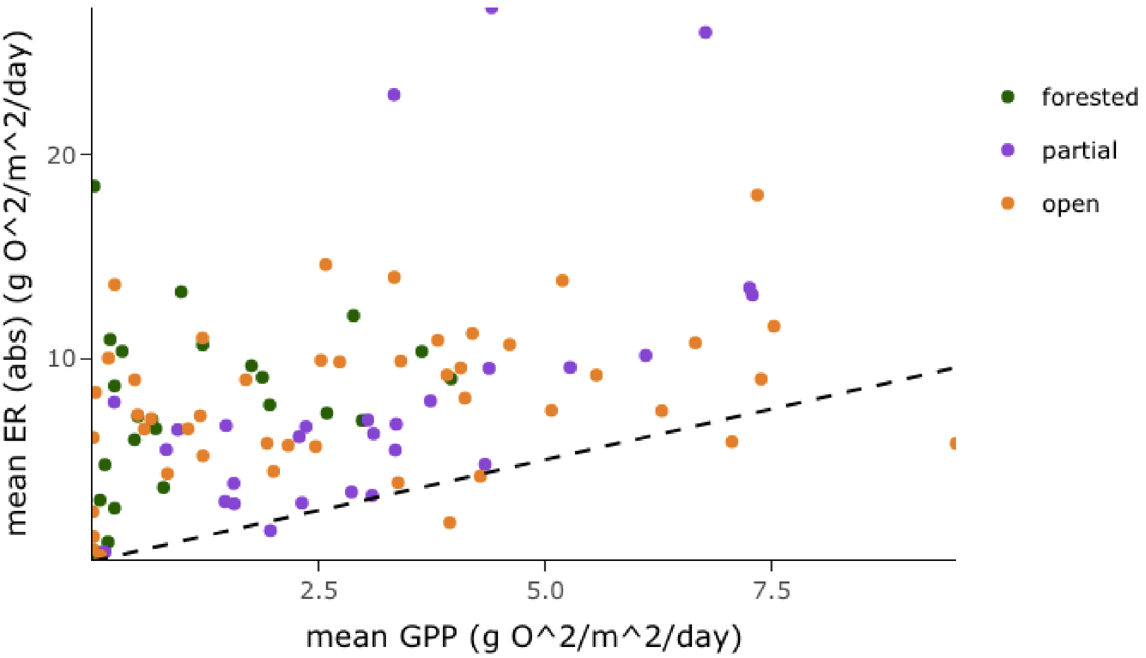


Figure 6 Ratio of ER to GPP along a productivity gradient. Broken line represents ER = GPP; ER almost always exceeds GPP, indicating the presence of allochthonous subsidies that elevate ER (forested n=25; partial n=28; open n=46).

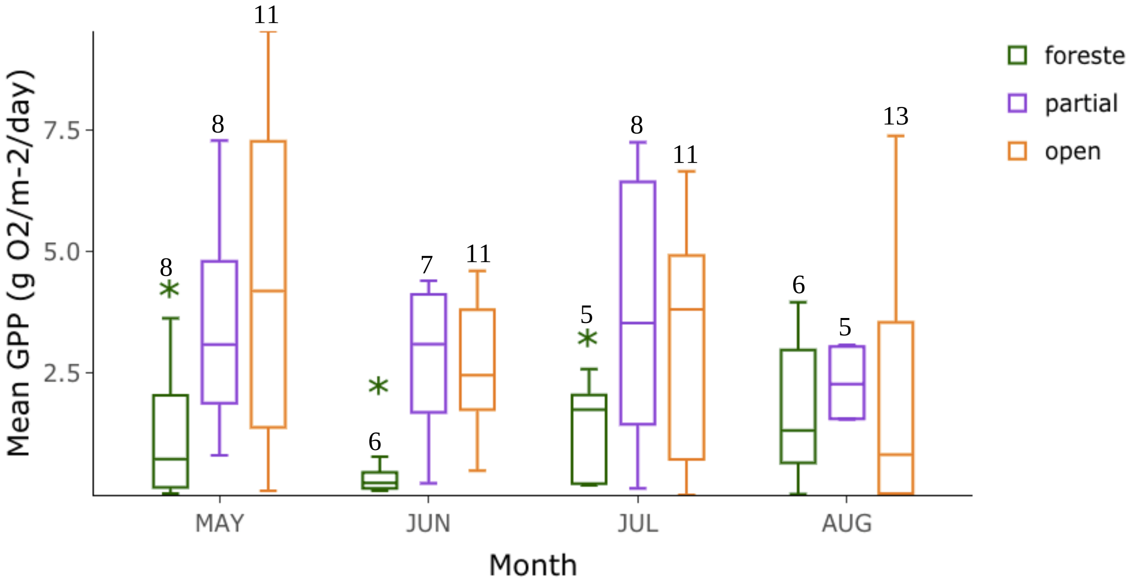


Figure 7 Monthly changes in mean GPP by canopy type (orange= open, purple= partial, and green= forested). GPP is significantly lower at forested sites compared to partial and open canopy sites. Asterisk denotes $p < 0.05$ for differences among canopy types within a month. Numbers above boxplots indicate the sample size.

Total phosphorous and depth also emerged as key predictors of mean and maximum ecosystem respiration (Table 3). Similar to GPP, increasing depth also generally increased the magnitude of total respiration (note that the negative coefficient for depth in Table 3 corresponds with higher ER because respiration is expressed as a negative rate of change in dissolved oxygen). Surprisingly, but similar to results for GPP, increasing phosphorous also reduced the absolute magnitude of respiration rates.

The negative relationship between both mean and maximum gross primary production and P was unexpected, since P is expected to release primary producers from nutrient limitation and stimulate photosynthesis. However, this negative relationship appears to be driven in large part by low dissolved oxygen at high phosphorous levels (Figure 8), suggesting that hypoxia induced under nutrient enrichment may be limiting primary production. The statistically significant negative effect of high P on GPP for the complete data set is removed when sites are stratified by hypoxia level (0-2, 2-4, 4-6, and >6 mg/l; **$F_{3,91} = 2.8$, $P = 0.54$**, Figure 8), and the slope of the GPP vs. P relationship becomes non-significantly positive in the highest mean DO class. Although this relationship is not significant, it is consistent with the inference that respiration of primary producers, like heterotrophs, can be limited by severe hypoxia. This inference is further supported by the observation that average GPP is significantly lower at dissolved oxygen levels below 2 mg/l (**$t_{95\,(2\text{-}4)} = 2.8$, $P_{2\text{-}4}<0.01$, $t_{95\,(4\text{-}6)} = 2.5$, $P_{4\text{-}6}=0.02$, $t_{95\,(6+)} = 3.8$, $P_{6+}<0.01$**, Figure 8).

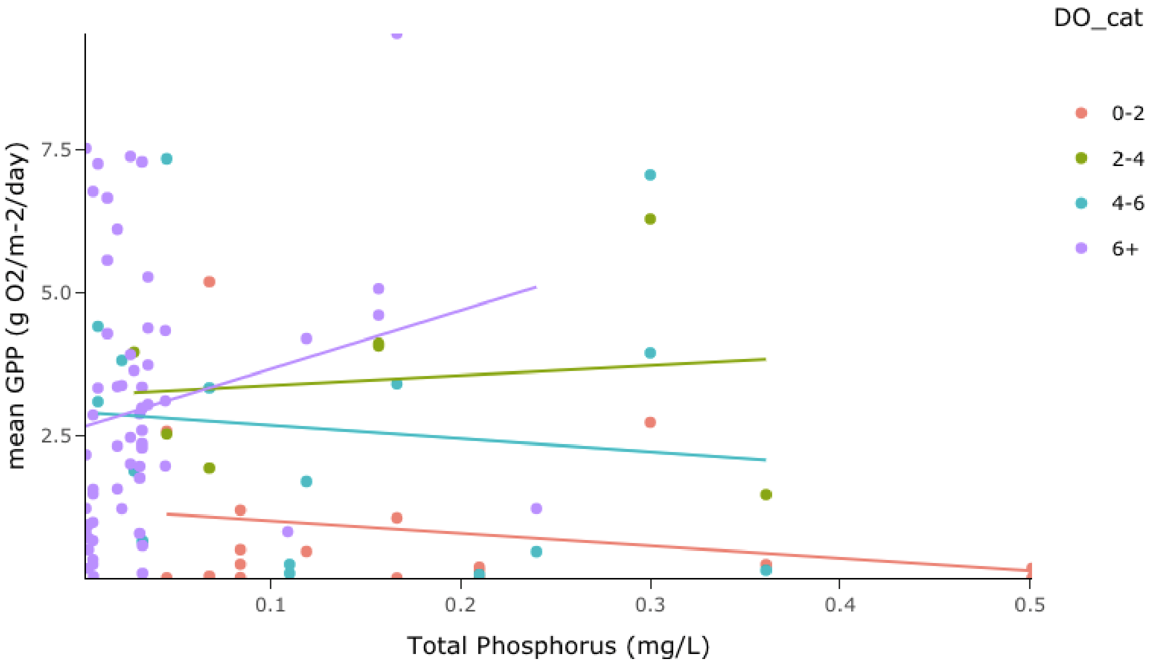


Figure 8 Relationship between total phosphorus and mean GPP for different categories of DO concentration (red= 0-2mg/L, green= 2-4mg/L, blue= 4-6mg/L, and purple is > 6mg/L), showing decreasing GPP at low (hypoxic) DO levels, and an insignificant trend towards negative effects of high P on GPP at low DO.

The apparently negative effect of total phosphorous on ER may be associated with very low dissolved oxygen at high phosphorous levels (Figure 9), with low dissolved oxygen presumably potentially suppressing heterotrophic (i.e., bacterial, fungal) metabolism under hypoxia. However, the pattern is weaker than for GPP, with a non-significant tendency for increased phosphorous to be associated with higher respiration at dissolved oxygen levels above 6 mg/l, and to be negatively associated with phosphorous at oxygen concentrations below 6 mg/l (non-significant interaction between oxygen class and total phosphorous: **$F_{1,95} = 2.1$, $P = 0.11$**).

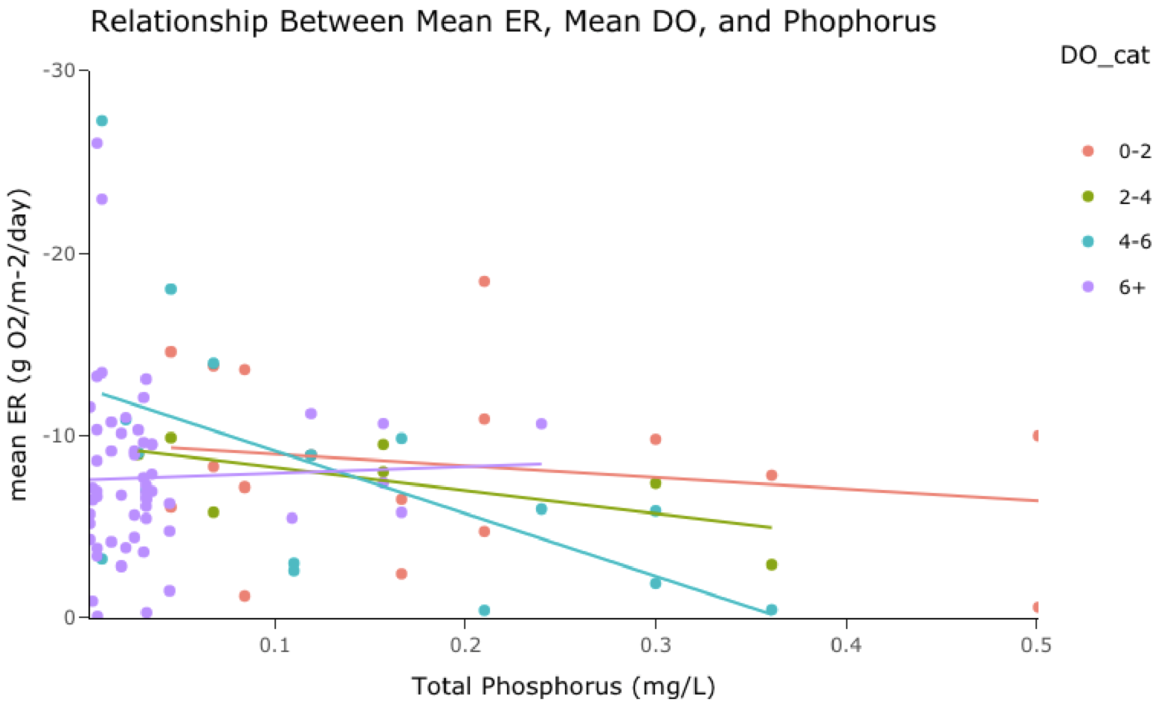


Figure 9 Difference in the relationship between total phosphorus and mean ER based on varying categories of DO concentration (red= 0-2mg/L, green= 2-4mg/L, blue= 4-6mg/L, and purple is > 6mg/L).

In general, the variables that were identified as significant drivers of both GPP and ER were consistent across each hierarchy of models tested, ranging from full models to reduced ones that included only easily measured variables, and parameter values for covariates were relatively stable across nested models. There were significant seasonal trends in primary production characterized by higher GPP in May and lowest primary production in Aug (Figure 7, Table 3).

Inclusion of month in the full models tended to allow the effects of water temperature to also be included (Table 3), suggesting an interaction between month and water temperature. In contrast, there was no significant effect of month on respiration (**$p=0.4$**), and inclusion of month in the full model for ER did not affect the significance of other variables (Table 3).

Contrary to expectation, there were no significant interactions among independent drivers for either GPP or ER. The proportion of total variation in GPP and ER explained by models was also relatively low, with R^2 values ranging from 0.18-0.39 for mean and maximum GPP, and 0.04-0.16 for mean and maximum ER. The comparatively low proportion of variance explained indicates significant unaccounted sources of variation in metabolism among sites.

2.4.2 Habitat and landuse effects on metabolism

Average gross primary production (g/m^2/day) was significantly higher in ponds than in stream habitats (roughly double; Figure 10, mean GPP: **$t_{58\text{ (ponds)}} = 7.4$, $t_{58\text{ (streams)}} = -2.6$, $P < 0.01$**; maximum GPP: **$t_{53\text{ (ponds)}} = 8.4$, $t_{53\text{ (streams)}} = -3.2$, $P < 0.01$**); in contrast, average respiration rates were similar between ponds and streams (mean ER: **$t_{73\text{ (ponds)}} = -8.9$, $t_{73\text{ (streams)}} = 0.6$, $P = 0.56$**; maximum ER: **$t_{69\text{ (ponds)}} = -9.5$, $t_{69\text{ (streams)}} = 0.95$, $P = 0.32$**). Primary production rate was also positively associated with total water column depth as a continuous variable (**$P < 0.01$**), consistent with higher GPP in ponds. This relationship appeared similar in both streams (**$t_{58\text{ (streams)}} = 1.8$, $P = 0.07$**) and ponds (**$t_{58\text{ (ponds)}} = 1.8$, $P = 0.08$**) in a simple regression analysis that did not include site as a random effect (Figure 11). However, the slope parameter relating GPP to depth was 3x steeper in ponds (**$t_{58\text{ (ponds)}} = 1.8$, $P = 0.07$**) than in streams (**$t_{58\text{ (streams)}} = 0.5$, $P = 0.60$**), when site was included as a random effect, although the relationship in streams remained insignificant.

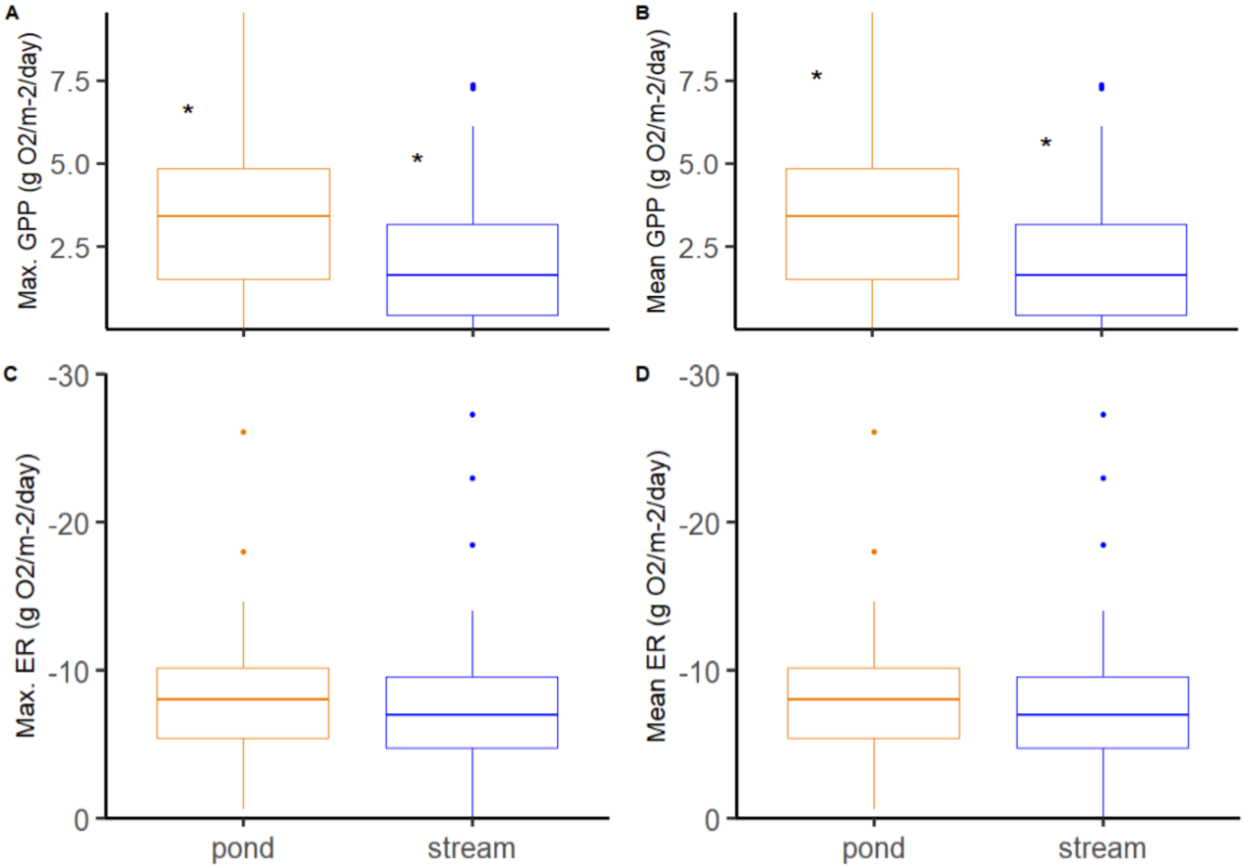


Figure 10 Differences in maximum and mean GPP and ER in ponds (n= 35) versus streams (n= 64) (orange= ponds, blue= streams). Mean and maximum GPP is significantly higher in ponds, but ER is similar in both habitats. Asterisk indicates significance at $p < 0.05$. Horizontal line in boxes represents the median, boxes represent the 2nd and 3rd quartiles, lines vertical lines represent the variability within each group, and dots represent data outliers.

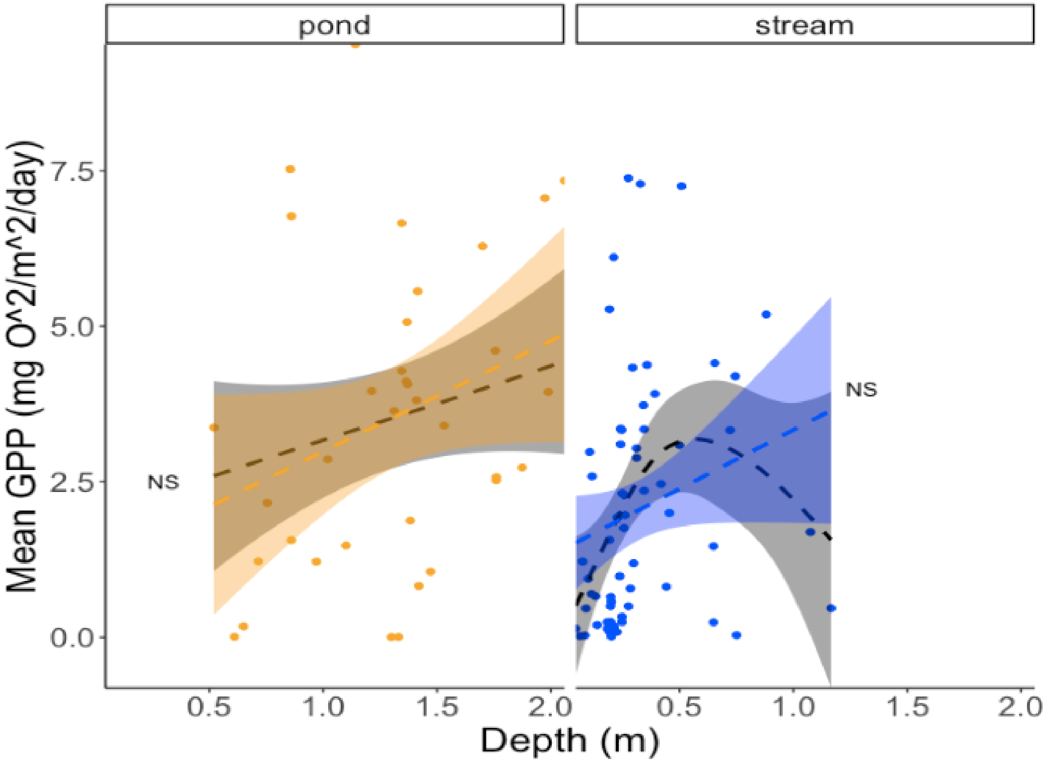


Figure 11 Differences in the relationship between depth and mean GPP in ponds (orange; n= 35) versus streams (blue; n= 64). Each point represents a single depth and GPP estimate per month. The coloured lines represent the linear relationship between the variables and the black lines represent the GAM relationship.

Both mean and maximum gross primary production rates were elevated at open canopy and partially shaded sites relative to reference sites (Figure 12; p=0.02); this pattern was not significantly affected by landuse (i.e., agricultural vs. reference site; p=0.72). Mean and maximum ER also appeared insensitive to landuse (p=0.67).

Variance in gross primary production rates were almost significantly higher at open and partially shaded canopy sites (**$t_{25\ (open)}$ = -2, P = 0.08, $t_{25\ (partial)}$ = -2.5 , P = 0.07**) reflecting the limiting effect of light on photosynthesis, yet variance in GPP was not significantly higher at agricultural sites relative to reference ones (**t_{26} = -0.5, P = 0.66**).

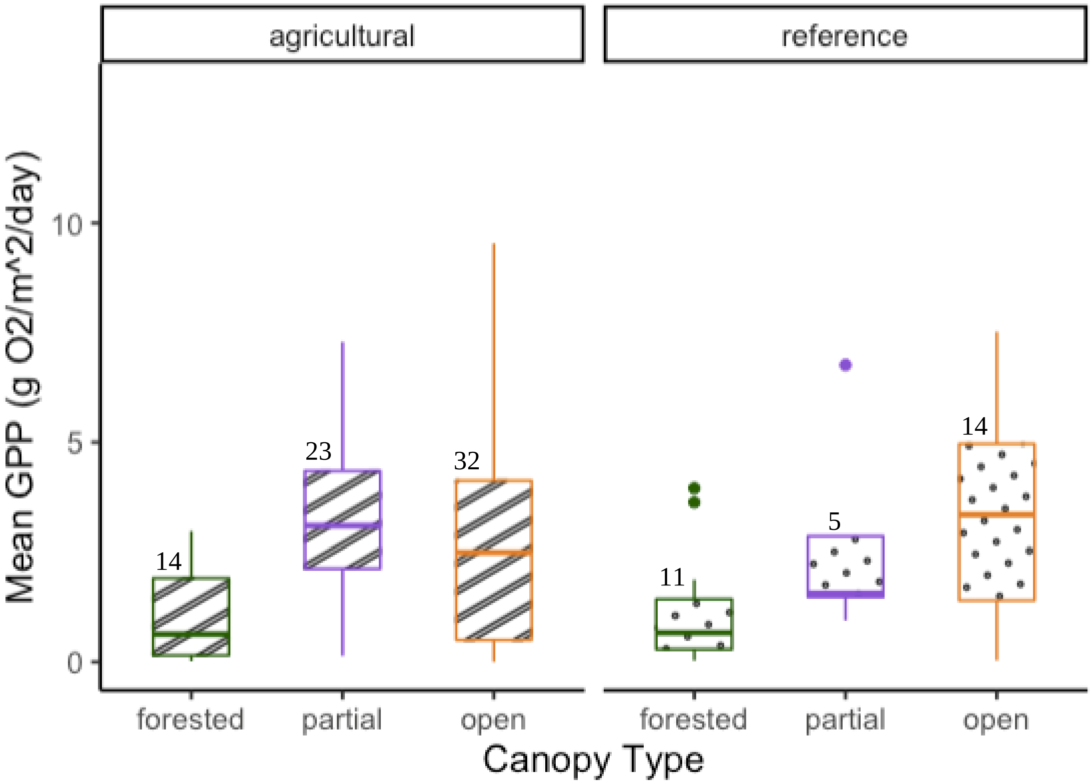


Figure 12 Differences in mean GPP across canopy types (green= forested, purple= partial, and orange= open) and landuse type (diagonal lines= agricultural, dots= reference). There is no significant difference between mean GPP in agricultural and reference land, regardless of canopy type. Numbers indicate treatment sample size.

The responses of mean and minimum DO to nitrogen and phosphorus concentration were similar (Figure 13) when analyzed as a GAM (including spatial effects) and a LMER (without spatial effects). At very low nitrogen and phosphorus concentrations (0-0.7 mg/L) increasing light availability has minimal influence on DO concentration (i.e., DO is high under both forested and open canopy; Figure 13), indicating nutrient limitation of photosynthesis irrespective of light levels. As nitrogen concentration increases, loss of canopy has a greater influence on DO. When nitrogen is in the eutrophic range (1.5 - 3.5 mg/L), sites with open canopy cover have significantly lower DO relative to forested sites (Figure 13; **$p < 0.05$**), with partial canopy cover sites intermediate between forested and eutrophic sites in the mesotrophic N range. A very similar pattern is evident with phosphorus concentration, although it is not statistically significant. This indicates that as nutrient input increases from agricultural and urban development, restoration of riparian vegetation should be a priority to mitigate hypoxic conditions.

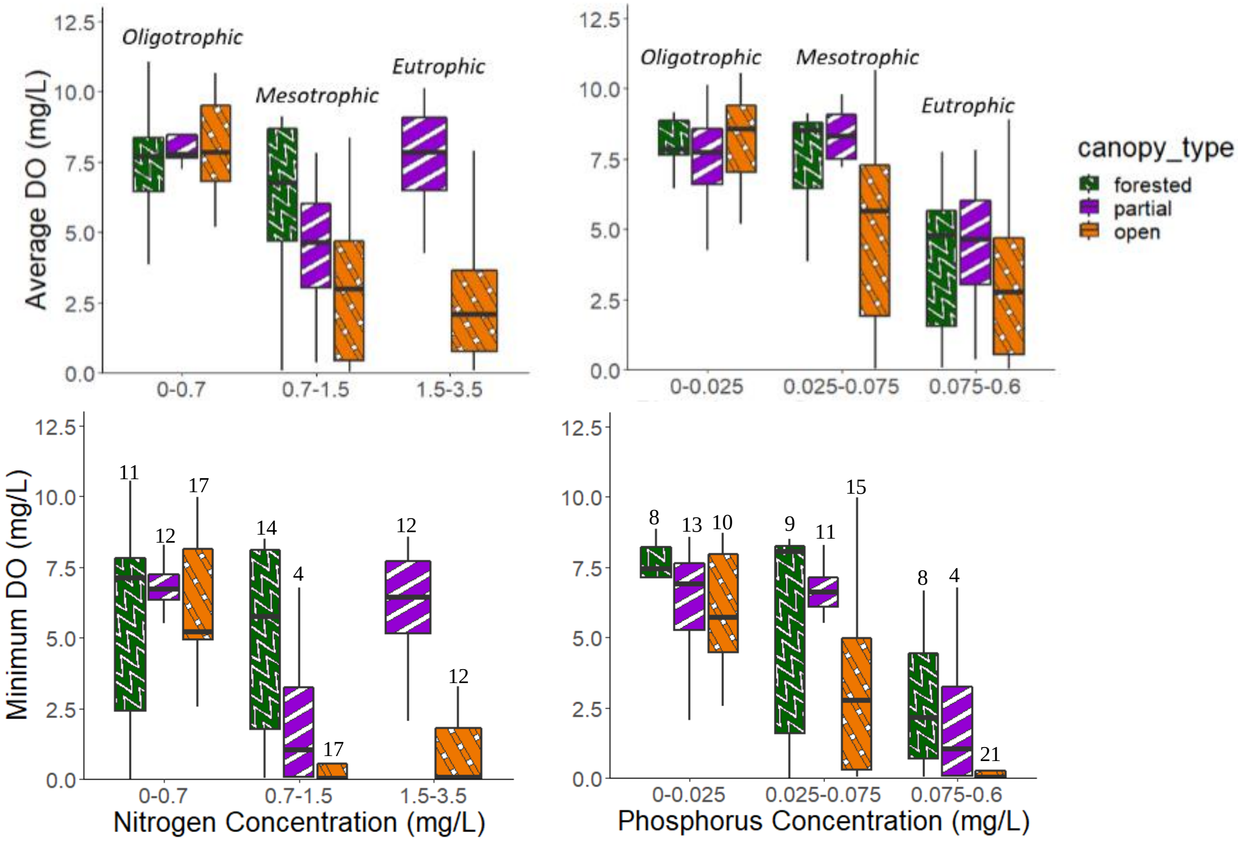
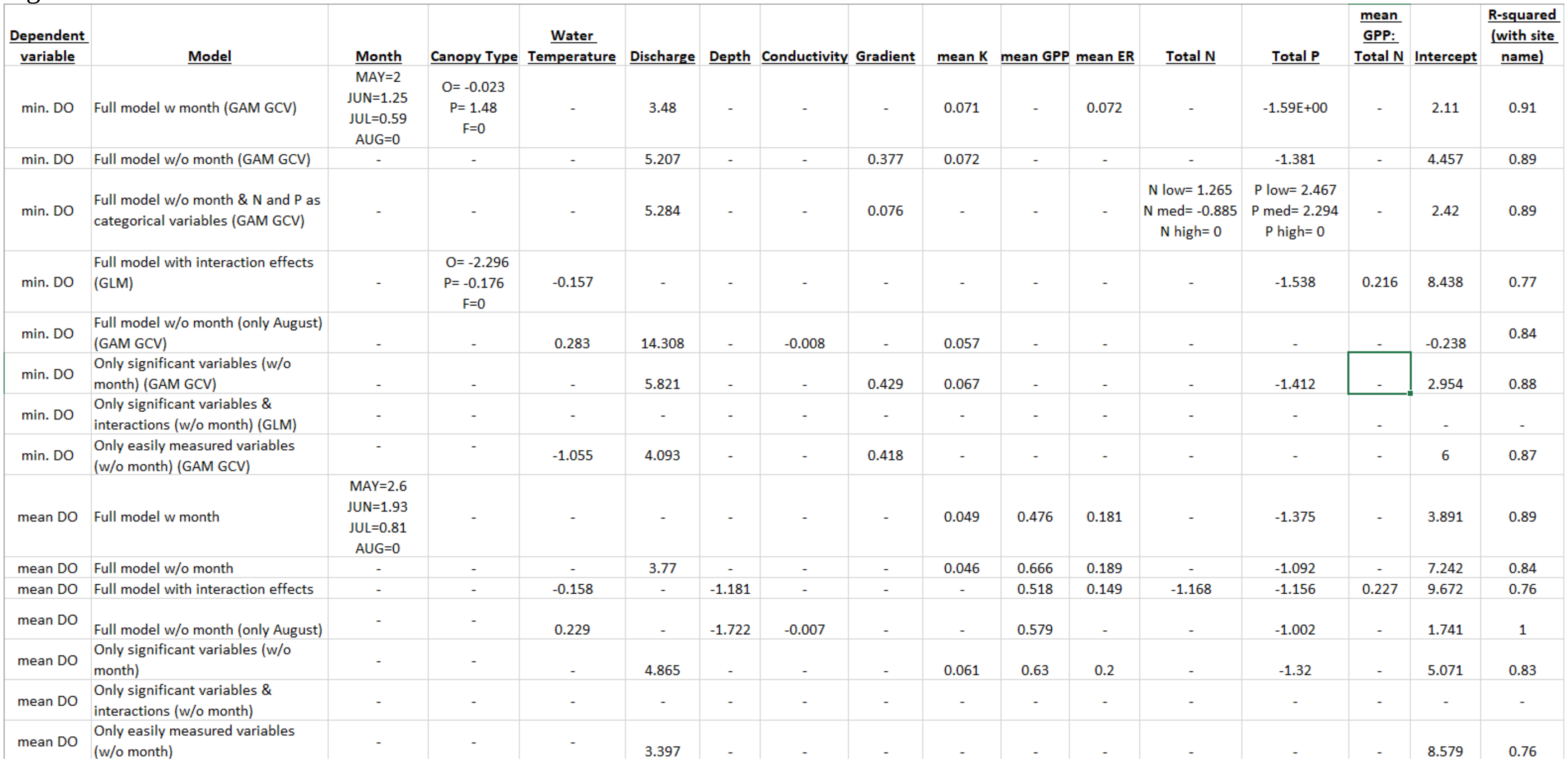


Figure 13 Difference in mean and minimum DO across canopy types (green= forested, purple= partial, and orange= open) in response to phosphorus concentrations. Each phosphorus bin is grouped based on average phosphorus concentrations for oligotrophic, mesotrophic, and eutrophic systems (after Dodds et al., 1998). Numbers indicate sample size.

Table 3 Summary of the GAM outputs for all dependent variables in this study along with the coefficient estimates for all predictor variables, adjusted r-squared values, the presence of x and y axis transformations, and the number of smoothing parameters (K) used in each model. Note, the positive relationship between DO and ER is actually negative, since more negative ER values correspond to higher rates of ER.



Dependent variable	Model	Month	Canopy Type	Water Temperature	Discharge	Depth	Conductivity	Gradient	mean K	mean GPP	mean ER	Total N	Total P	mean GPP: Total N	Intercept	R-squared (with site name)
min. DO	Full model w month (GAM GCV)	MAY=2 JUN=1.25 JUL=0.59 AUG=0	O= -0.023 P= 1.48 F=0	-	3.48	-	-	-	0.071	-	0.072	-	-1.59E+00	-	2.11	0.91
min. DO	Full model w/o month (GAM GCV)	-	-	-	5.207	-	-	0.377	0.072	-	-	-	-1.381	-	4.457	0.89
min. DO	Full model w/o month & N and P as categorical variables (GAM GCV)	-	-	-	5.284	-	-	0.076	-	-	-	N low= 1.265 N med= -0.885 N high= 0	P low= 2.467 P med= 2.294 P high= 0	-	2.42	0.89
min. DO	Full model with interaction effects (GLM)	-	O= -2.296 P= -0.176 F=0	-0.157	-	-	-	-	-	-	-	-	-1.538	0.216	8.438	0.77
min. DO	Full model w/o month (only August) (GAM GCV)	-	-	0.283	14.308	-	-0.008	-	0.057	-	-	-	-	-	-0.238	0.84
min. DO	Only significant variables (w/o month) (GAM GCV)	-	-	-	5.821	-	-	0.429	0.067	-	-	-	-1.412	-	2.954	0.88
min. DO	Only significant variables & interactions (w/o month) (GLM)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
min. DO	Only easily measured variables (w/o month) (GAM GCV)	-	-	-1.055	4.093	-	-	0.418	-	-	-	-	-	-	6	0.87
mean DO	Full model w month	MAY=2.6 JUN=1.93 JUL=0.81 AUG=0	-	-	-	-	-	-	0.049	0.476	0.181	-	-1.375	-	3.891	0.89
mean DO	Full model w/o month	-	-	-	3.77	-	-	-	0.046	0.666	0.189	-	-1.092	-	7.242	0.84
mean DO	Full model with interaction effects	-	-	-0.158	-	-1.181	-	-	-	0.518	0.149	-1.168	-1.156	0.227	9.672	0.76
mean DO	Full model w/o month (only August)	-	-	0.229	-	-1.722	-0.007	-	-	0.579	-	-	-1.002	-	1.741	1
mean DO	Only significant variables (w/o month)	-	-	-	4.865	-	-	-	0.061	0.63	0.2	-	-1.32	-	5.071	0.83
mean DO	Only significant variables & interactions (w/o month)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
mean DO	Only easily measured variables (w/o month)	-	-	-	3.397	-	-	-	-	-	-	-	-	-	8.579	0.76

max. GPP	Full model w month	MAY=2.89 JUN=1.21 JUL=1.33 AUG=0	O= 1.19 P= 1.7 F= 0	0.183	-	3.15	-	-	0.041	-	-	-	-0.88	-	-3.646	0.49
max. GPP	Full model w/o month	-	O= 0.39 P= 0.75 F= 0	-	-	0.947	-	-	0.014	-	-	-	-0.293	-	0.581	0.6
max. GPP	Full model with interaction effects	-	O= 0.43 P= 0.77 F= 0	-	-	0.96	-	-	0.015	-	-	-	-0.287	-	0.52	0.56
max. GPP	Full model w/o month (only August)	-	-	-	-	0.844	-	-	-	-	-	-	-0.463	-	0.759	0.34
max. GPP	Only significant variables (w/o month)	-	O= 0.417 P= 0.78 F= 0	-	-	0.941	-	-	0.015	-	-	-	-0.281	-	0.561	0.57
max. GPP	Only significant variables & interactions (w/o month)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
max. GPP	Only easily measured variables (w/o month)	-	O= 0.429 P= 0.693 F= 0	-	-	0.708	-	-	-	-	-	-	-	-	1.288	0.61
mean GPP	Full model w month	MAY=0.819 JUN=0.406 JUL=0.408 AUG=0	O= 0.522 P= 0.637 F= 0	0.049	-	0.571	-	-	-	-	-	-	-0.303	-	0.079	0.78
mean GPP	Full model w/o month	-	O= 0.464 P= 0.759 F= 0	-	-	0.705	-	-	-	-	-	-	-0.254	-	0.722	0.63
mean GPP	Full model with interaction effects	-	O= 1.083 P= 1.98 F= 0	-	-	2.043	-	-	0.031	-	-	-	-0.539	-	-0.309	0.35
mean GPP	Full model w/o month (only August)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
mean GPP	Only significant variables (w/o month)	-	O= 0.406 P= 0.656 F= 0	-	-	0.593	-	-	-	-	-	-	-0.259	-	0.973	0.6

mean GPP	Only easily measured variables (w/o month)	-	O= 0.458 P= 0.691 F= 0	-	-	0.511	-	-	-	-	-	-	-	-	1.138	0.63
max. ER	Full model w month	-	-	-	-	0.575	-	-	0.0166	-	-	-	-0.246	-	2.605	0.31
max. ER	Full model w/o month	-	-	-	-	0.576	-	-	0.011	-	-	-	-0.243	-	2.694	0.31
max. ER	Full model with interaction effects	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
max. ER	Full model w/o month (only August)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
max. ER	Full model w/o month (only August) (without canopy)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
max. ER	Only significant variables (w/o month)	-	-	-	-	0.617	-	-	0.016	-	-	-	-0.21	-	2.508	0.22
max. ER	Only significant variables & interactions (w/o month)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
max. ER	Only easily measured variables (w/o month)	-	-	-	-	0.376	-	-	-	-	-	-	-	-	3.038	0.08
mean ER	Full model w month	-	-	-	-	0.424	-	-	0.016	-	-	-	-0.225	-	2.504	0.3
mean ER	Full model w/o month	-	-	-	-	0.416	-	-0.104	0.015	-	-	-	-0.224	-	2.628	0.26
mean ER	Full model with interaction effects	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
mean ER	Full model w/o month (only August)	-	-	0.455	-	-	-	-	-	-	-	-	-	-	-14.479	0.43
mean ER	Only significant variables (w/o month)	-	-	-	-	-	-	-	0.014	-	-	-	-0.203	-	2.526	0.2
mean ER	Only significant variables & interactions (w/o month)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
mean ER	Only easily measured variables (w/o month)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

2.5 Discussion

Consistent with expectation, canopy cover and depth were key drivers of metabolism in Fraser Valley streams. Reduced GPP at sites with a forested canopy is consistent with light limitation of autotrophic metabolism, as widely observed elsewhere (Bernhardt et al., 2018; Mulholland et al., 2001; Griffiths et al., 2013). In contrast, ER was unrelated to canopy cover, which was surprising since respiration by autotrophs was expected to contribute substantially to overall ER. However, despite significant GPP rates at many sites, the dominance of heterotrophic metabolism across sites likely weakened any signal of algal respiration as mediated by canopy cover.

Higher GPP in ponds vs. streams and the significant positive effects of depth in model selection highlight the importance of water depth as a driver of metabolism across the aquatic landscape. However, high depth can diminish benthic production if it exceeds the depth of the euphotic zone; the generally positive relationship that I observed between depth and both GPP and ER suggests a depth-integrated contribution from water-column metabolism without a penalty to benthic production, likely because of the relatively limited depth range in these smaller streams.

In contrast with canopy cover and depth, the direction of nutrient effects on metabolism was unexpected. While absence of nutrient effects on metabolism could be attributed to power issues or simply an absence of nutrient limitation, the negative effects of increasing total P on both GPP and ER was not only inconsistent with expectation, but opposite from the positive slope expected between nutrient loading and ecosystem metabolism (e.g. Clapcott et al. 2016; Dos Reis Oliveira et al., 2019; Demars et al., 2011).

There are several possible causes of this apparent anomaly. First, although increased P loading is expected to stimulate both photosynthesis and heterotrophic metabolism in low productivity systems (Webster et al. 2016; Rosemond et al. 2015), high P loading that leads to eutrophication can trigger hypoxia, and create a negative feedback to metabolism if both autotrophic and heterotrophic metabolism becomes limited by a low oxygen supply (Breitberg 2001). Stratifying GPP by DO class tends to support this interpretation (Fig. 8), since P no longer has a negative association with GPP under normoxic conditions, whereas GPP appears greatly reduced under severe hypoxia (e.g., 0 - 2 $mg \cdot l^{-1}$ O_2) which appear more frequently at high P (Fig. 8). This pattern appears weaker for ER, suggesting that heterotrophic community metabolism may be more robust to hypoxia than autotrophic metabolism. However, in a global review of riverine hypoxia, Blaszczak et al. (2022) observed that very high values of ER were most common under well-aerated conditions and rare under hypoxia (their Fig. 6), indicating hypoxic limitation of respiratory metabolism. Alternatively, P is known to be mobilized from sediments under hypoxia (Molot et al. 2014), so that higher P under low DO may be in part a consequence of hypoxia rather than a cause of it. Similarly, reduced metabolic demand under low oxygen supply could also reduce demand and uptake of P, increasing the available supply. Blasczak et al. (2018) report a similar negative relationship between GPP and P in a set of urban streams which they also attribute to hypoxia. Although this process may represent an endogenous negative feedback loop whereby excessive production is ultimately self-limiting, it unfortunately entails transition to an undesirable hypoxic state, so has limited value as a management lever. Hypoxic limitation of metabolism is not well described, but may be more pervasive than expected (Blaszczak et al. 2022).

Although temperature and flow are both well-documented drivers of aquatic metabolism (e.g., Mejia et al. 2019; Griffiths et al. 2013), model selection failed to detect a meaningful signal of either on GPP or ER in my data set. It is unclear whether this reflects low statistical power due to low replication, a limited temperature range from May-August (Table 1), absorption of temperature effects by the random effect of stream identity, or a general insensitivity of autotrophic and heterotrophic community metabolism to temperature variation. However, Battin et al. (2023) highlight that temperature effects on river metabolism remain unclear, and poorly predicted by metabolic theory. Similarly, the absence of any significant interactions among drivers suggests a dominance of main effects, although the detection of interactions may again plausibly be limited by a relatively small sample size.

Nutrient guidelines for waterbodies depend on many factors including ecoregion, light availability, flow, and residence time (CCME, 2023). Streams entering lakes often have a lower recommended nutrient threshold due to concerns over nutrient accumulation in stagnant waters (CCME, 2023). In the Western Forested Mountains ecoregion the general total P threshold is identified as 0.01 mg/L and the total N threshold as 0.12 mg/L (CCME, 2023), both of which are exceeded at most of my sites, including reference ones. Research into N and P guidelines suggest that impairment thresholds are often site dependent and more work needs to be done to downscale guidelines to local conditions (Clune et al., 2020). However, the Dodds et al. (2000) N and P thresholds of transition from mesotrophy to eutrophy (0.7 and 0.025 $mg \cdot l^{-1}$, respectively) are consistent with observed changes in metabolism in this study. They are also roughly consistent with more recent N and P nutrient criteria (e.g., Ostermiller et al. 2019a,b: 0.4 - 0.8 $mg \cdot l^{-1}$ for N, 0.035 - 0.08 $mg \cdot l^{-1}$ for P).

Stream metabolic rates can follow different temporal trajectories linked to changes in light, temperature, or hydrology (Mejia et al. 2019; Bernhardt et al. 2022), and a variety of seasonal metabolic regimes have been identified including Spring Peak and Summer Peak GPP regimes (Savoy et al. 2019). In aggregate, lower Fraser Valley streams appear to best fit the profile of a Spring Peak River as identified by Savoy et al. (2019), characterized by maximum spring GPP associated with higher light and nutrient inputs from the spring freshet, and a summer decline in GPP associated with canopy closure and/or declining flows. Spring peak rivers tend to be smaller (< 8-9m channel width, < 1 $m^{-3} \cdot s^{-1}$ mean discharge; Savoy et al. 2019, Koenig et al. 2019) and to demonstrate a weak relationship between GPP and temperature, which also broadly characterizes lower Fraser Valley streams. However, despite an overall tendency towards a spring peak in GPP, aggregate trends across sites remain variable (Fig. 7), likely reflecting site-level asynchrony in timing of discharge, temperature, and light (e.g., Mejia et al. 2019).

The inclusion of pond habitats in this study highlights the role of ponds, wetlands, and deep off-channel habitat as comparative metabolic hot-spots for producing energy and storing nutrients in low gradient aquatic landscapes (Bellmore et al. 2014; Schmadel et al. 2019). However, it also highlights their relative vulnerability to hypoxia because of greater depth, low turnover rates, and low gas exchange rates associated with standing water (Zinn et al. 2021; Blascczack et al. 2022); a recent meta-analysis also found lentic habitats to me more vulnerable to stressor impacts associated with nutrient inputs than streams and rivers (Birk et al., 2020). The relative sensitivity of ponds to water quality impairment is of particular concern because ponds represent preferred critical habitat for endangered species like Salish sucker (Rosenfeld et al. 2021; Pearson and Healey, 2003) and are also disproportionately productive for juvenile salmonids like coho salmon and cutthroat trout (Roni et al. 2006; Colvin et al. 2019). Their vulnerability to invasion by hypoxia-tolerant exotics (Mandic et al., 2008; Rahel and Olden, 2008) further emphasizes the need to manage oxygen supply and demand in these habitats to avoid impaired water quality, which will be challenging in a climate of reduced flows and expanding anthropogenic impacts (Chapra et al. 2021; Datry et al. 2023).

Regulation of hypoxia is usually based on benchmark thresholds of dissolved oxygen (Jankowski et al. 2019; Rosenfeld and Lee 2022). Continuous dissolved oxygen data is much more reliable at detecting the frequency and occurrence of water quality violations that spot measurements (Pardo and Garcia, 2016; Rosenfeld et al. 2021), which until recently have been the standard monitoring approach. Estimating GPP and ER rates has also become much easier with free software like streamMetabolizer; these rates can provide additional insight into processes that drive state variables like DO, and help refine management decisions (Jankowski et al. 2021; Munn et al. 2020). For example, if a site experiencing hypoxia is characterized by high GPP, management to decrease light or nutrient availability may be useful strategies (i.e., through increased shading, or reduced P or N loads). In contrast, if hypoxia is associated with high ER rather than GPP, light reduction through riparian shading would be less effective at reducing hypoxia. Metabolic rate estimates may also directly inform whether system production is outside of a reference condition, or inform whether hypoxia is driven by metabolism vs. physical factors like low discharge or a low gas exchange coefficient. GPP has also been shown to predict reach-scale juvenile salmonid densities (Saunders et al. 2018), confirming the bottom-up effect of stream metabolism on fish production.

Modelling metabolism requires a considerable investment in post-processing of DO data, even with the advent of user-friendly software like streamMetabolizer. However, even without metabolism estimates the continuous measurement of DO has great value for management decisions, and estimation of metabolic rates is rarely essential for routine management. For instance, if primary production is excessively high and driving hypoxia, this will often be visually evident in high algal biomass, oxygen supersaturation, or a large diurnal range in DO (Heiskary and Markus, 2001; Heiskary et al. 2013), without the necessity of estimating metabolic rates. Metabolic rate may not always correlate well with indices of biotic impairment (Batt et al. 2013; Munn et al. 2020), while accurate measurement of diel changes in DO remains an unambiguous direct metric of water quality. Similarly, moderately high aquatic metabolic rates are not always problematic unless a system experiences hypoxia, meaning that DO remains the best short-term direct indicator of impairment; however, metabolic rate may be the better indicator of the potential for future water quality problems in a changing climate.

It is understood that the ratio of predictor variables to the number of sites may pose a potential risk of model over-fitting and result in unreliable predictions and substantial error. The risk of this was lessened by re-running models with fewer predictor variables based on the significance of each predictor variable within the full model (Table 3). After re-running the model with only significant variables, 0-2 variables were removed in the process. It is important to note that after initially running the full model, on average 42% of predictor variables were insignificant. In some cases the relationship between predictor and dependent variables could be masked by other variables, for example the effect of water temperature could be masked by month, yet models were run both with and without month to account for this.

Although a powerful technique for estimating metabolic rates with limited data, the diurnal oxygen method is not without it’s limitations, which include trade-offs between predictive accuracy and investment in input parameters. For example, limited resources in this study precluded deployment of light sensors to collect photosynthetically active radiation at each site, which might have considerably improved model fit and statistical power. Inverse modelling also relies on a strong diurnal signal in dissolved oxygen, and reliable estimation of metabolic rate is impossible when GPP or ER are so low that DO flatlines with no discrete temporal trend (Blaszczak et al. 2018; Appling et al. 2018). This is a common problem in low productivity streams or stream with a very high diffusion co-efficient (Blaszczak et al., 2019), and occurred in 22 of 126 site-month combinations in my study, resulting in the loss of 20% of all observations. While my study retained sufficient power to detect significant trends and drivers of metabolism, the proportion of total variance in GPP and ER explained was comparatively low; many of the lost sites were low productivity sites or hypoxic ones with stable DO, which may have reduced power to detect landscape-scale trends. Insensitivity to low GPP or ER is an intrinsic limitation of the diurnal oxygen change method; one possible solution is to cross-validate estimates with more sensitive direct metabolic chamber measurements (i.e., the benthic equivalent of light-bark bottles; Rosenfeld and Roff 1991; Biggs et a. 1999; Grace and Imberger 2006).

The range of GPP and ER in lower Fraser Valley streams is comparable to that observed in other agriculturally developed landscapes across Europe (Baattrup-Pedersen et al., 2022; Izagirre et al., 2008), North American (Griffiths et al. 2013; Appling et al. 2018b), and New Zealand (Clapcott et al. 2016). Despite elevated levels of GPP, lower Fraser Valley streams remain predominantly heterotrophic (ER > GPP), likely indicated both elevated direct inputs of organic matter and differential stimulation of heterotroph metabolism by nutrient enrichment (e.g., Warren et al. 2017; Rosemond et al. 2015). The impacts of agricultural and urban development on valley bottom streams - a syndrome of reduced flow from irrigation, loss of riparian forest, stream channelization, increased fine sediment, and eutrophication - leads to a trajectory of habitat degradation often culminating in range collapse for sensitive species like salmonids. Developed valley-bottom landscapes vary in their location on this trajectory; some are well-advanced, and have lost most of their historic cold-water species. For instance, southern Ontario and the NE United States have seen major range contractions and extirpations of native brook charr associated with agricultural and urban development (Stranko et al. 2008; Hudy et al. 2005; Smith et al. 2023). Broadly speaking, the lower Fraser Valley is at an earlier stage on this impact trajectory; range contractions have primarily been limited to direct conversion of streams to storm sewers in urban areas. Broader impacts have been buffered in part by a cool maritime climate that partially moderates summer temperatures, and significant groundwater inputs associated with alluvial deposits on the valley bottom and snowmelt from adjacent mountain slopes. However, ongoing development and water quality impacts under climate change will likely elevate nutrient inputs and temperatures while reducing flows (Rosenfeld et al. 2021; Putt et al. 2019), and associated changes in stream metabolism will play a significant role in how water quality shapes the future distribution of hypoxia and fish habitat at a landscape scale.

The streams in the lower Fraser Valley have some unique characteristics compared to those of southern Ontario that may help mitigate the negative impacts of climate change and human development. This includes snowmelt from the North Shore and Cascade Mountains, and significant groundwater inputs that help keep summer water temperatures cool, and the oceanic climate which moderates air temperature and increases rainfall. These mitigative characteristics have likely been a lifeline for salmonid persistence in a highly developed landscape. However, summers in the Lower Fraser Valley are becoming hotter and longer, while droughts are becoming more frequent. With this lifeline slowly diminishing, fisheries management efforts must prioritize stream ecosystem health by better protecting habitat, in particular groundwater recharge areas that contribute to baseflow (EPA 2015), implementing mitigative measures like riparian restoration, and more effectively regulating development impacts.

Chapter 3: Drivers of Hypoxia

3.1 Summary

Hypoxia occurs when dissolved oxygen falls below saturation levels, with potential negative effects on fish and other aquatic life. Hypoxia is typically caused by elevated oxygen consumption (respiration) by microorganisms and fungi decomposing organic matter exceeding the oxygen supply available at the air-water interface. Hypoxia has many negative effects on fish including reduced immunity to disease (Colby et al., 1972; Magnoni et al., 2019) and decreased growth (Abdel-Tawwab et al., 2019; Del Rio et al., 2019; Rosenfeld and Lee 2022). There are many different factors that contribute to hypoxia, including nutrient and light availability, reduced flow, and high water temperatures. These factors are elevated by agricultural and urban development along with the effects of climate change and global warming. When environmental conditions favour excess algal production, subsequent decomposition of dead algal biomass often triggers hypoxic conditions (Diaz, 2001).

By measuring how oxygen concentrations vary between streams in reference and developed landscapes, and more specifically how dissolved oxygen responds to different stream attributes, we can start to predict the underlying drivers and likelihood of a waterbody going hypoxic. This chapter is based on field work focusing on determining the influence of GPP, ER, light availability, water temperature, nutrients, conductivity, stream gradient, and flow on dissolved oxygen and hypoxia. This research aims to provide guidance for conservation managers to help inform which waterbodies are likely to become hypoxic based on specific stream characteristics, and the most appropriate management levers for avoiding hypoxia.

As described in Chapter 2, I used the R-based modelling software streamMetabolizer to estimate GPP and ER so that metabolic rate could be included as predictors of hypoxia.

Minimum DO did not differ between agricultural and reference sites under forested or partial canopy cover, but did differ at open canopy sites; average minimum DO was also significantly lower at open canopy sites relative to forested and partial canopy cover, suggesting that riparian canopy restoration could partially mitigate the negative effects that agricultural landscapes have on hypoxia. Surprisingly, there was no interaction effect between water temperature and canopy type. Open canopy types were simply more likely to have lower DO concentrations. The best predictors of hypoxia were canopy type, phosphorus concentration, discharge, mean K, depth, and nitrogen, with depth and nitrogen being the least significant.

3.2 Introduction

Hypoxia occurs when dissolved oxygen falls below saturation levels, with potential negative effects on fish and other aquatic life. Hypoxia is typically caused by elevated oxygen consumption (respiration) from microorganisms and fungi decomposing organic matter, which exceeds the oxygen supply available at the air-water interface. Hypoxia has pervasive effects on aquatic organisms (Vaquer-Sunyer and Duarte 2008), and is known to increase O_2 consumption during exercise (Magnoni et al., 2018), damage gill structure (Araujo-Luna et al., 2018), reduce fish immunity to disease (Colby et al., 1972; Magnoni et al., 2019), reduce fish appetite (Jobling, 1995), limit fish growth (Abdel-Tawwab et al., 2019; Del Rio et al., 2019), induce fish migration (Breitburg et al., 2018), and inhibit natural reproduction (Colby et al., 1972). Hypoxia tolerance varies widely among taxa (Vaquer-Sunyer and Duarte 2008), but most normoxic fish species experience individual effects on growth or behaviour at thresholds of ~ 5-6 $mg \cdot l^{-1}$ DO (Rosenfeld and Lee 2022; Mandic et al., 2009), which corresponds to British Columbia's Water Quality Guidelines for aquatic life threshold of 5 mg/L of DO in salmon-bearing streams (BC

Ministry of Environment and Climate Change Strategy, 2021; British Columbia Ministry of Environment, 2023). Although water quality guidelines for DO in marine environments are scarce, reference to hypoxia in the marine environment usually refers to DO < 2 (Diaz 2001), which represents a threshold for ecosystem collapse rather than a decrease in individual fitness (Rosenfeld and Lee 2022).

The balance of autotrophic and heterotrophic metabolism, can have far-reaching effects on the prevalence of hypoxia. Excess nutrients and light that stimulate high algal production (eutrophication) can lead to elevate biological oxygen demand (BOD), initially associated with high autotroph biomass, and later with microbial decomposition of senescent algae; if BOD is sufficiently high (e.g., from pulsed algal senescence) it can reduce oxygen concentration towards zero (Diaz, 2001). DO also often exhibits a daily cycle with peak DO in daylight hours when aquatic plants and algae are photosynthesizing, and lows at night when metabolism shifts to respiration. DO concentration and the potential for system hypoxia is therefore directly influenced by rates of primary production and respiration.

DO is also directly influenced by physical controls that mediate oxygen flux from the atmosphere, which include discharge, stream gradient, depth, and water temperature. Low flows reduce DO by decreasing the surface turbulence that aids gas exchange (Bernhardt et al., 2018), and DO is particularly flow sensitive in low gradient streams with low gas exchange coefficients (Blaszczak et al. 2019). The solubility of DO also decreases with temperature, so that high water temperatures are associated with low DO independent of biological demand (Rajwa-Kuligiewicz et al., 2015; Blaszczak et al. 2022; Carter et al., 2021).

Waterbodies are constantly exchanging O_2 with the atmosphere at the water surface, and this flux needs to exceed metabolic demand to prevent hypoxia. However, gas diffusion at the water surface is largely limited to the top few centimetres of air-water interface in still-water habitats. Reaeration is therefor strongly influenced by local hydraulic and geomorphologic factors that increase turbulence, in particular surface roughness and hydraulic jumps in riffles and rapids (Beaulieu et al., 2013). Deeper, stratified water bodies are therefore more likely to go hypoxic since organic decomposition and respiration is most intense close to the stream bed, and furthest from the re-aeration source at the air-water interface (Coloso et al., 2008). Streams with lower gradients typically have lower velocities, less turbulence, and often deeper water, reducing the air-water gas flux and increasing the risk of hypoxic events (Blaszczak et al., 2019; Churchill et al., 1964). Hypoxia is a well-known threat to at-risk species, and a key concern in many cumulative effect assessments (Boyd et al., 2022).

This study aims to identify the dominant controls on hypoxia, as well as the current incidence and future risk of hypoxia in a high biodiversity aquatic landscape dominated by existing and expanding urban and agricultural land. The Lower Fraser valley in British Columbia, Canada, is a typical valley bottom landscape with a high density of small, productive fish-bearing streams embedded in a dense urban and agricultural matrix. However, most streams are low gradient and receive high nutrient inputs which makes them highly vulnerable to hypoxia, which is a well documented management concern (Scott et al. 2016; Putt et al. 2019; Rosenfeld et al. 2021). The fish community is dominated by abundant juvenile coho salmon (*Oncorhynchus kisutch*) and cutthroat and rainbow trout (steelhead), as well as federally threatened Salish sucker (*Catostomus sp. cf. catostomus*) and Nooksack dace (*Rhinichthys cataracte*). Given the complex cumulative drivers of hypoxia, the goal of this research was to generate a better understanding of causative mechanisms underlying hypoxia, both to improve model prediction and prioritize management strategies to avoid it.

To this end, I measured daily changes in DO for one week a month between May and August at 37 representative sites in waterbodies throughout the lower Fraser Valley, and extracted the mean and minimum DO concentrations for all sites. I concurrently measured a suite of potential hypoxia drivers at each site, including water temperature, depth, discharge, conductivity, gradient, total phosphorus (P), total nitrogen (N), and light availability (canopy cover). I then used a series of Generalized Additive Models (GAM) to determine which variables best predicted mean and minimum DO across sites. More specifically, I wanted to assess **1)** the respective roles of water temperature and stream metabolism (estimated in Chapter 2) in driving hypoxia; **2)** the linkages between the extent and severity of hypoxia and landuse /canopy cover; and **3)** whether interactions were present that could exacerbate hypoxia.

3.3 Methods

3.3.1 Study sites

I used stratified sampling to select 37 stream sites across a broad range of environmental attributes (landuse, gradient, flow, light, water temperature & nutrients) representative of the range of conditions present in small streams in the lower Fraser Valley, ranging from open-canopied eutrophic agricultural sites to oligotrophic forested sites. Daily changes in DO were recorded every month from early May to late August using MinDot data loggers deployed for 5-7 day continuous intervals. Sites with different combinations of potential environmental drivers were selected to increase the likelihood of detecting the most consequential interactions. The study design aimed to include approximately 30% low nutrient reference sites, 40% high nutrient impacted sites, and 30% moderately impacted sites, with all canopy types represented within each trophic class. Final trophic classifications based on water chemistry sampling were 37%

oligotrophic, 26% mesotrophic, and 37% eutrophic based on nutrient thresholds identified by Dodds et al. (1998; oligo/meso/eutrophic thresholds for nitrogen: 0.7<, 0.7-1.5, > 1.5, respectively; for phosphorous: 0.025<; 0.025-0.075; > 0.075). Stream habitat characteristics measured at each site included canopy type (open, partial, forested), water temperature, discharge, conductivity, gradient, total nitrogen, total phosphorus, average depth, algal cover, landuse (reference or agricultural), and sediment type. On average, agricultural sites had 5-10X higher concentrations of nitrogen and phosphorus, respectively, in comparison to reference sites (Figure 14).

3.3.2 Stream Metabolism Estimates

I used the single station method to measure stream metabolism, which assumes homogeneity of gradient, channel structure, and canopy type in the upstream reach above the DO logger. Assessment of homogeneity of canopy cover, stream geomorphology, and land use was conducted using a visual assessment of Google Earth Satellite Imagery and a field site visit.

3.3.3 DO Logger placement

Loggers were installed in a location at each site that was broadly representative of the reach, with sufficient velocity to ensure that the water column was well mixed (i.e., avoiding areas with stagnant water). The DO data logger was attached to a metal rod at 50% of total water column depth with the sensor was oriented downstream to prevent debris interfering with DO measurements.

Two DO loggers were deployed at the majority of pond sites (n= 10) to account for vertical stratification in DO, with one logger installed 10-15 cm below the surface and a second 10-15 cm above the substrate. Two pond sites lacked temperature stratification and therefore received a single DO logger placed at 50% depth. Loggers recorded DO, time, and water temperature at 10 minute intervals. A limited number of available DO loggers precluded simultaneous measurement at all 37 sites; logger deployments were therefore rotated among sites to obtain a minimum of 5 days of continuous data each month between May and August, which exceeds the recommended 3-day duration for an integrated metabolism measurement (Staehr et al., 2010).

3.3.4 Stream & Pond Habitat Assessment

At every site I visually estimated percent tree canopy cover in the 100 m reach upstream of the logger; threshold for the three canopy classes - open, partial, and forested - were 0-25%, 25-75%, 75-100%. I also measured average channel depth, gradient, conductivity, DO concentration at the time of logger placement and retrieval (measured using a handheld YSI meter), water velocity at the logger location, percent algae and macrophytes, and discharge using standard velocity depth transects. All sampling took place in 2021 with the exception of water quality samples to classify sites by nutrient status (Dodds et al., 2000), which were collected in mid-August 2022 and analyzed for total nitrogen and phosphorus. The mean value and range of each continuous stream variable collected in this study can be found in Table 1 from Chapter 2.

3.3.5 Data Analysis

Mean monthly DO at each sites was calculated by averaging all 10 minute interval DO measurements within each monthly time series of continuous daily data. The monthly minimum observed DO was also extracted as a metric of the worst conditions at each site. The three-parameter inverse modelling software streamMetabolizer was used in R version 4.2.2 to estimate the best fit between modelled and observed changes in DO (Appling et al., 2018). StreamMetabolizer generates an estimate of observed DO using six input variables; observed DO, saturation DO (i.e., DO concentration in equilibrium with air), depth, water temperature, light, and solar time. Detailed criteria for an acceptable model fit are provided in Table 2, Chapter 2, and include an R^2 greater than 0.5. A total of 35 out of 134 metabolic estimates were poor fits and excluded from analysis based on these criteria.

Mean and minimum DO were modelled using GAM regressions in R version 4.2.2 using the ‘gam’ function from the ‘mgcv’ package, and the ‘dredge’ function from the ‘MuMln’ package was used to rank models using AIC selection. To minimize multi-collinearity, paired correlations among independent variables was assessed, and only one variable of a pair was included in regression when a correlation exceeded 0.7 ($R^2 > 0.49$). Since most response variables did not have a clear best model (i.e., multiple models were within 2ΔAIC of the top model), model averaging was used to derive average model coefficients (Dormann et al., 2018).

Ranked models were removed from the model averaging process when **1)** models were below the cumulative Akaike weight threshold of 0.95 (Symonds and Moussalli, 2011), **2)** ΔAIC exceeded 7 (Burnham et al., 2011; Symonds and Moussalli, 2011), and **3)** novel variables were introduced between ΔAIC 5 and 7 with low coefficients that contribute minimally to predictions, and the cumulative weight of models including the new variables is less than 0.05 (Symonds and Moussalli, 2011).

Model averaging was done on the full model for each response variable, including interactions as well as month (May, June, July, August) as a class variable. Because many of the environmental drivers were strongly correlated with month (i.e., discharge, temperature), a reduced model was also included with month dropped as an explanatory variable. Reduced models were also included that retained only statistically significant variables, and a model with only easily measured explanatory variables was also included (i.e., excluding ER and GPP as predictors).

As a coarse correction for potential non-linear spatial autocorrelation among sites, latitude and longitude were included in all GAM models as non-linear covariates. All other drivers were modelled as linear because i) variability in the data reduced sensitivity to detect non-linear effects, ii) there was no clear expectation for non-linear relationships among most responses and drivers, and iii) to simplify the analysis.

Assumptions of normality were evaluated by testing the normality of residuals using the Shapiro-Wilk statistic from the 'stats' package. If residuals were not normally distributed the response variable was transformed to improve normality (typically log or square root transformation). Homogeneity of variance was assessed by regressing residuals against predicted values. Model assumptions were tested using the full model, which was assumed to be a worst case scenario for violating assumptions.

Transformations varied based on the severity and direction of skew in the distribution of residuals, ranging from a square root transformation for moderately positively skewed data, to log base 10 transformation, and inverse transformation for severely positively skewed data. Response variables with negatively skewed residuals were first reflected then transformed as described above (Anatomise Biostats, 2017).

In addition to the GAM regressions, simple linear analysis of covariance and 2-way ANOVAs were also used for a posteriori tests and to test ancillary patterns in the data. I then ran various univariate logistic regressions to explore the likelihood of hypoxia as a function of phosphorus, nitrogen, discharge, depth, and mean K, using the 'glmer' function from the 'lme4' package. I also created contingency tables for the likelihood of hypoxia as a function of discharge and phosphorus. Classification thresholds for determining frequency of hypoxia in contingency tables were determined using the ‘cutpointr’ function from the ‘cutpointr’ package in R, which uses bootstrapping to determine the optimal cutpoint. A cutoff point of 5 mg/L was chosen because it is the British Columbia provincial government guidelines for minimum DO required for fish, 4 mg/L is the minimum requirement for specific Species At Risk in the area such as Salish Sucker and Nooksack Dace, and 2 mg/L was chosen because this indicates extreme cases of hypoxia.

3.4 Results

Model selection indicated that the mean and minimum DO were sensitive to almost all of the tested drivers (Table 3, Chapter 2). Month, canopy type, water temperature, discharge, depth, conductivity, site gradient, the gas exchange coefficient (k), GPP, ER, and total N and P all had significant influence on DO. However, the most consistently influential drivers of both mean and minimum DO appeared to be discharge and total P (See Table GAM).

Regression coefficients for turbulence-related physical factors like discharge, gradient, and mean k all indicated positive effects on DO as expected. The subset of models that included month as an independent predictor of DO indicated a significant monthly decline in DO that was most pronounced at open-canopied sites (Fig. 16). Although temperature was identified as having a significant negative effect on DO in model selection, it was not a dominant driver, and was positively related to DO in the August-only regression.

Total P, and to a lesser extent total N, was consistently identified as a significant driver of DO both as class or continuous variables, supporting the expected negative effect of eutrophication on DO (i.e., association of hypoxia with nutrient loading). Univariate plots of DO as a function of total N and P (Figure 14) suggest both non-linearity as well as hypoxia thresholds that roughly coincide with the oligotrophic N and P trophic categories identified by Dodds et al. (1998; nitrogen: 0.71<; phosphorous: 0.025<).

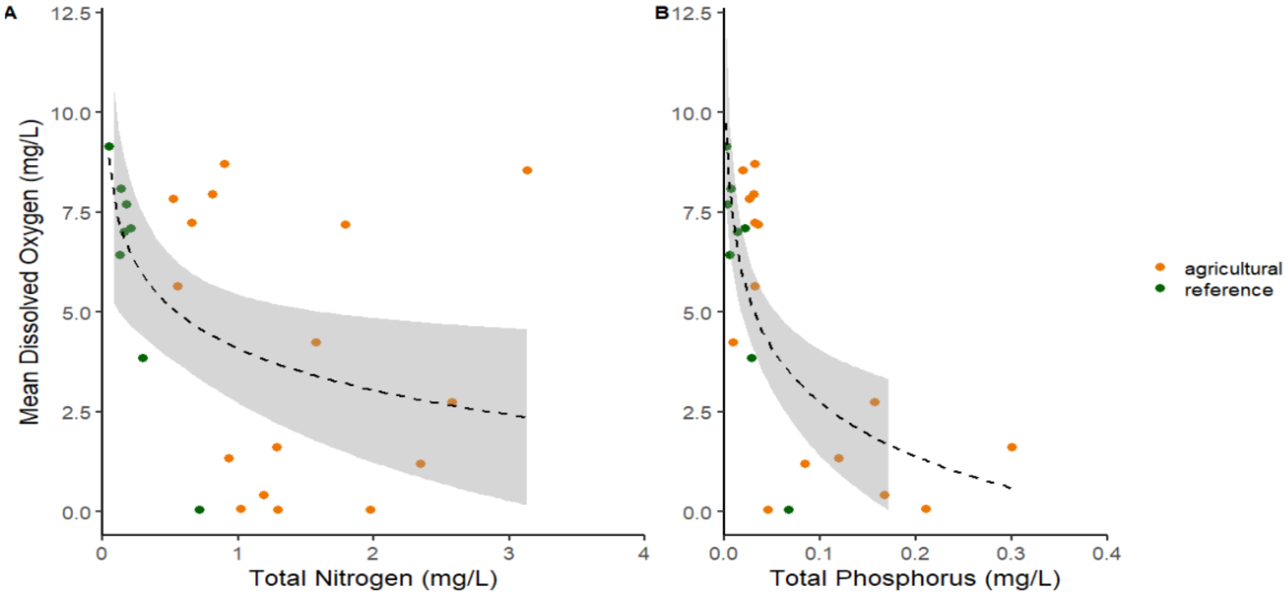


Figure 14 Relationship between mean dissolved oxygen and total nitrogen and phosphorus concentration. Each point represents the average of a 3-5 day time series of DO for the month of August when N and P were collected. Orange points represent agricultural sites and green points represent reference sites (Nitrogen p= 0.01, r^2= 0.26 ; Phosphorus p < 0.0001 , r^2= 0.60).

Stream metabolism estimates (GPP and ER, derived and discussed in Chapter 2) were identified as strong predictors of mean but not minimum DO in model selection (see Table 3), with elevated GPP and reduced respiration both increasing site-level DO, confirming the contribution of biological production to the net oxygen balance. As expected, open canopy sites had both lower mean and minimum DO in simple t-tests comparing open-canopied sites with partial and forested canopy sites (Figure 15; mean DO: **t_{38} = -1.9, P = 0.07**; Figure 15; minimum DO**: t_{41} = -2.2, P = 0.05**). A paired t-test showed that average minimum DO was significantly lower at sites with agricultural land use relative to reference sites (**p= 0.04, t_{97} = 0.04**). However, among canopy types the difference in minimum DO between agricultural and reference sites was only significant at open canopy sites (**t_{20}= -2.5, p= 0.01**, Figure 15).

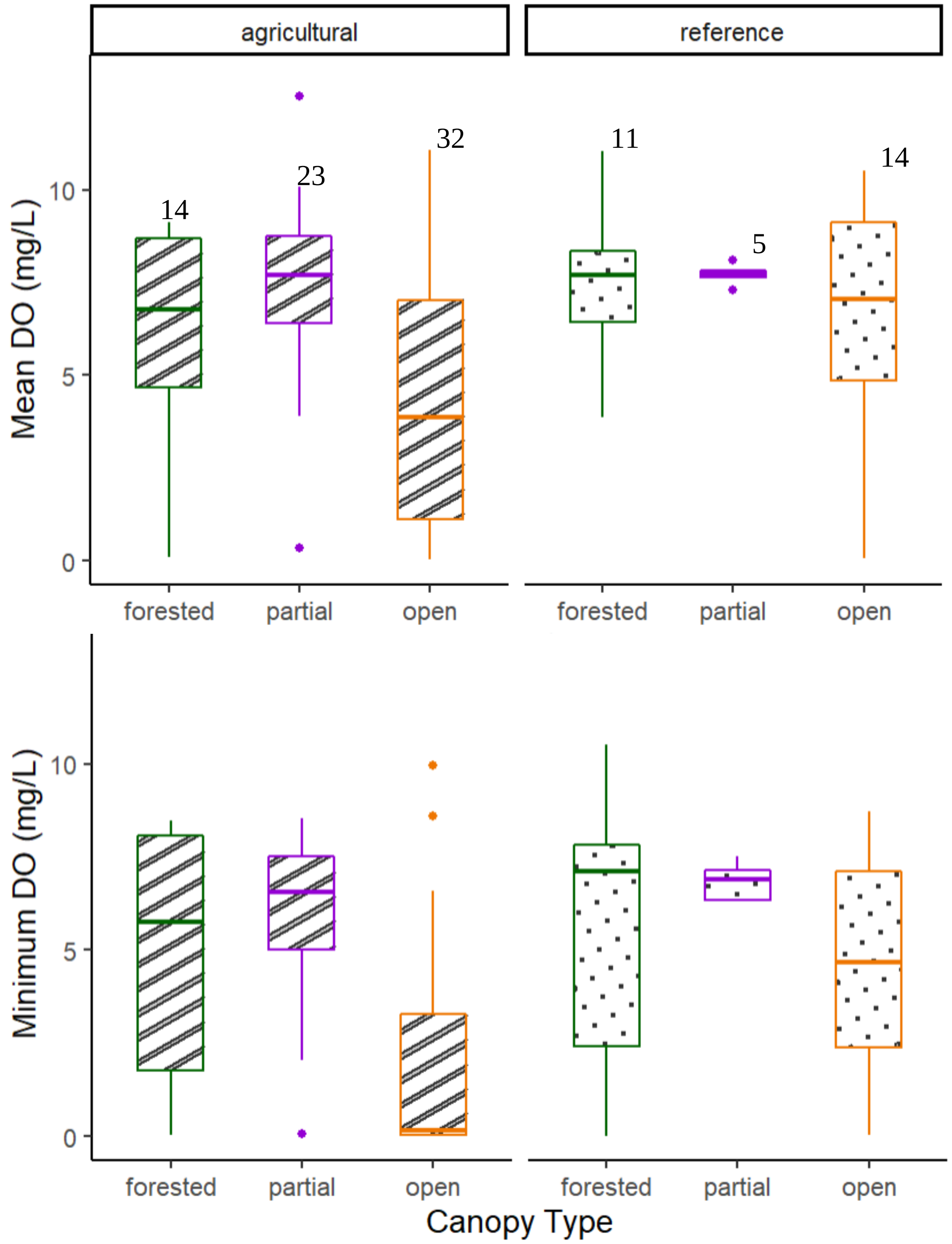


Figure 15 Differences in minimum DO between landuse types (agricultural= diagonals stripes, references= dots) and canopy cover (forested= green, partial= purple, open= orange). There is no significant effects of landuse on minimum in forested and partial canopy types, but minimum DO is significantly lower at open canopy sites on agricultural land (orange). Numbers indicate sample size.

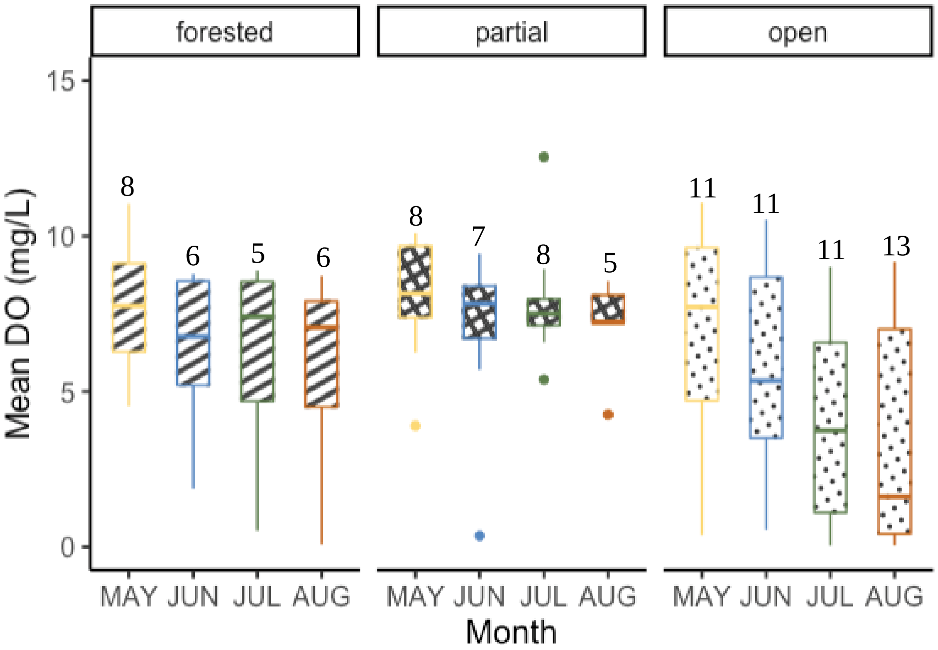


Figure 16 Seasonal trends in mean DO by month (May= yellow, June= blue, July= green, and August= orange) and canopy type (forested (75-100%)= diagonal stripes, partial (25-75%)= cross-hatch, and open (0-25%)= dots) showing greater seasonal decline and higher variance at open canopy sites. Numbers indicate sample size.

Although temperature was not identified as a consistent driver of DO in GAM model selection, a simple analysis of covariance (DO = temperature + canopy cover) indicates a significant reduction in minimum DO with increasing temperature (**$p<0.01$, $F_{1,95} = 7.7$**, Figure 19) as well as a significant reduction in minimum DO at open canopy sites (**$F_{2,95} = 10.8$, $p < 0.01$** ; Figure 19). Although agricultural sites tended to be ~1.5°C warmer, the effect of landuse on water temperature was insignificant (**$t_{97} = -0.7$, $p=0.5$**, Figure 18). Model selection also identified relatively few interactions among drivers, indicating a dominance of main effects. The only significant interaction was a positive effect of total N and GPP on mean and minimum DO, suggesting that the negative effects of high N loading could potentially be reduced by high GPP, particularly at sites where high N stimulates primary production more than microbial respiration.

However, this effect could be transient and lead to hypoxia when excess algal biomass decomposes in the fall (Rosenfeld et 2021).

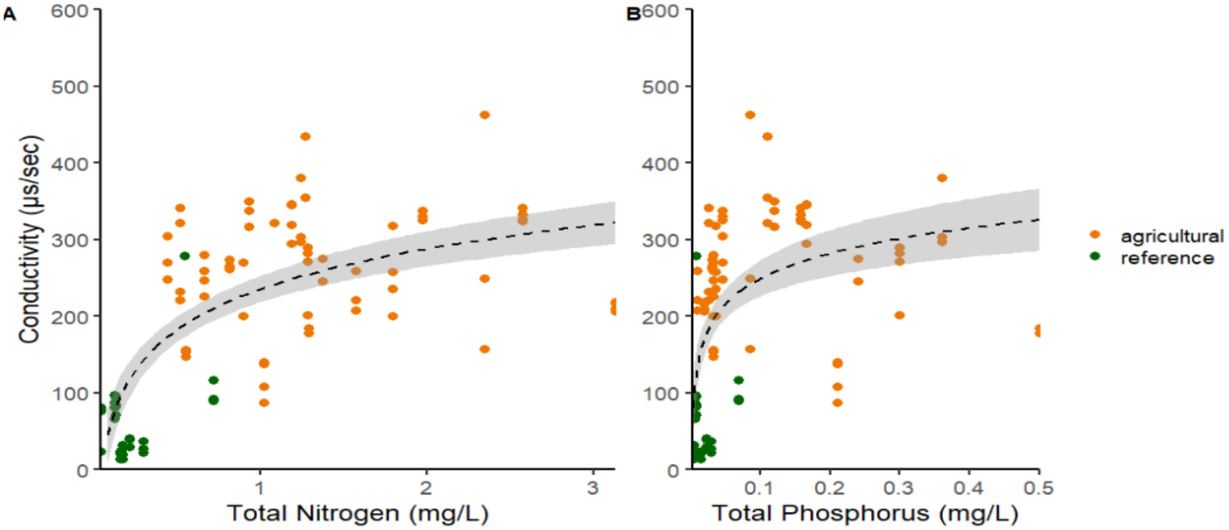


Figure 17 Relationship between conductivity and total nitrogen and phosphorus concentration to show the potential for conductivity as a surrogate of nutrient loading. Each point represents a single conductivity reading at a specific site across multiple months. Orange points represent agricultural sites and green points represent reference sites (Nitrogen $p < 0.0001$, $r^2 = 0.50$; Phosphorus $p < 0.0001$, $r^2 = 0.30$).

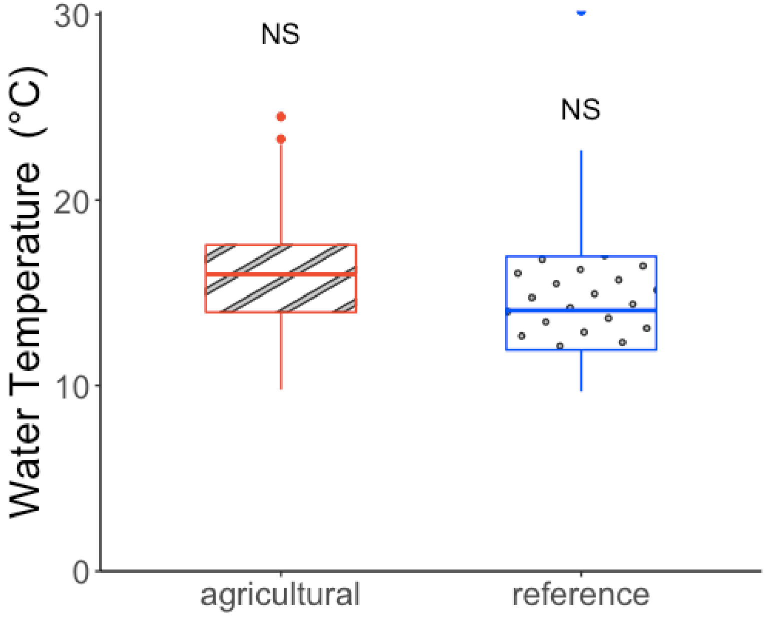


Figure 18 Water temperatures were slightly higher at agricultural (red diagonal stripes; n= 69) relative to reference sites (blue dots; n= 30), but the landuse effects was not significant.

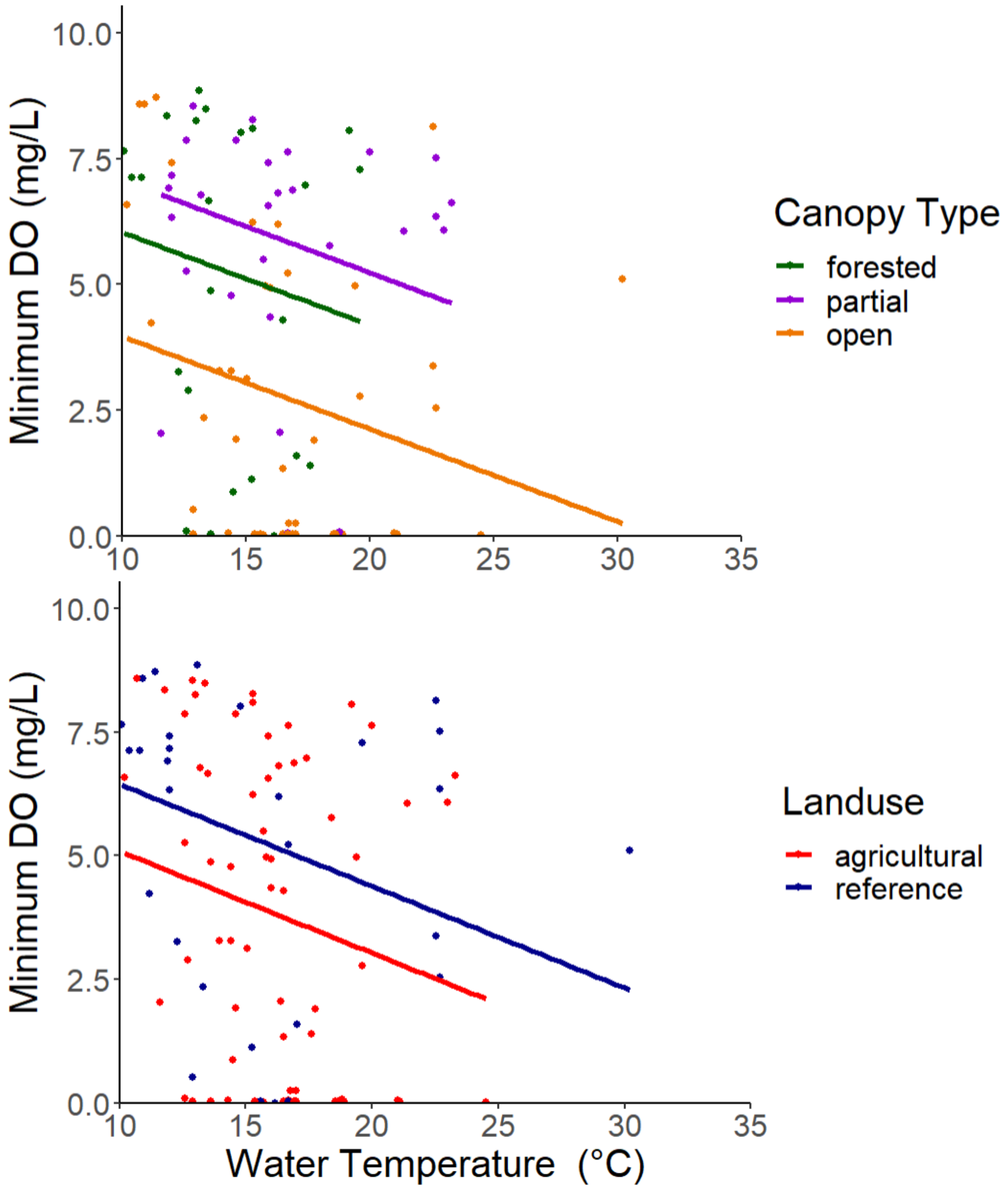


Figure 19 Significant relationship between water temperature and minimum DO (black solid line) categorized by canopy type (forested= green, partial= purple, and open= orange). Asterisk denotes significance and NS denotes insignificance (open p = 0.03; partial p = 0.94; forested p = 0.25).

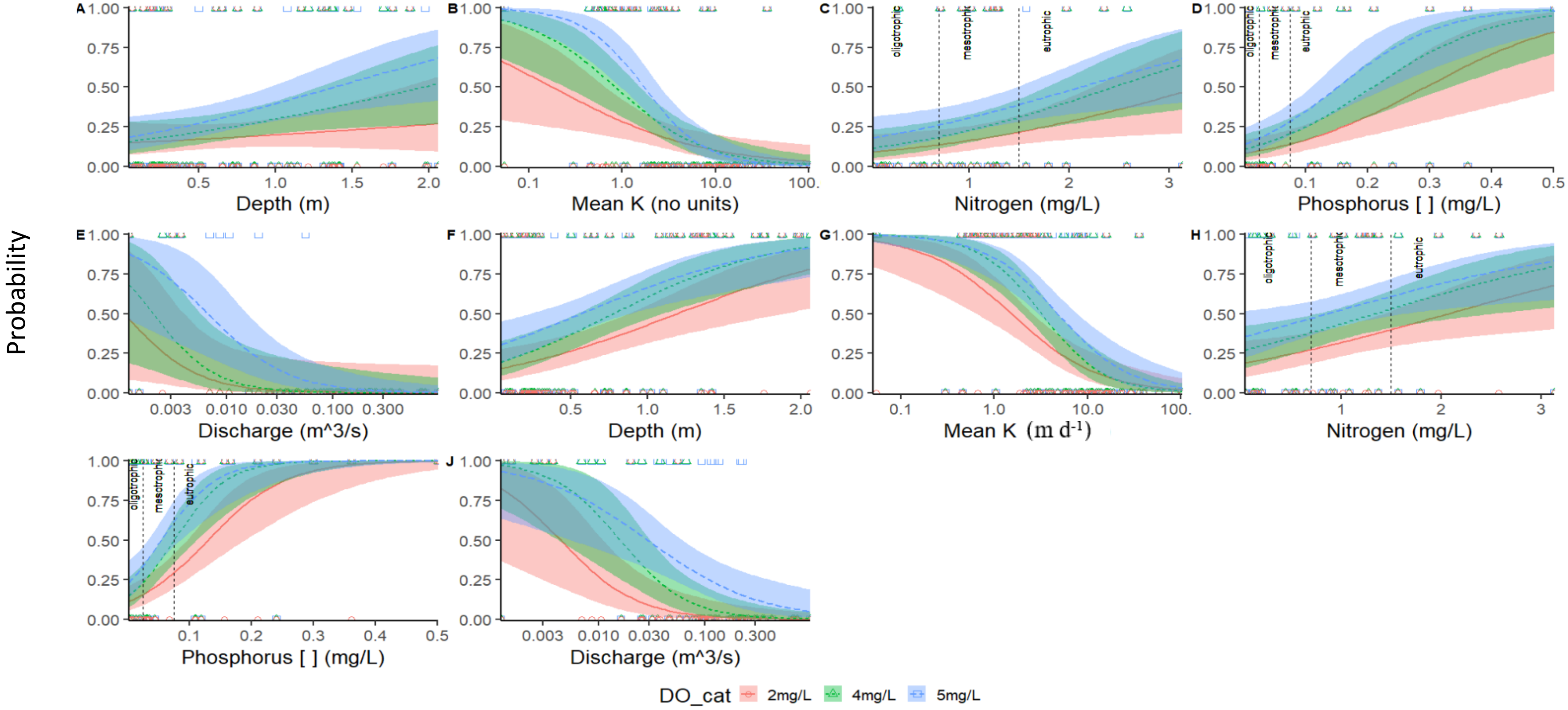


Figure 20 Univariate logistic regressions between the likelihood of a hypoxic event (i.e., where DO at a site falls below a designated threshold; 1 = hypoxic event, 0 = no hypoxic event) and key environmental drivers. There are three logistic curves in each plot: the blue long-dashed line sets the threshold for a hypoxic event as less than 5 mg/L of DO, the green short-dashed line sets the hypoxic threshold at 4 mg/L, and the red solid line sets the hypoxic threshold at 2 mg/L. Plots A-E are for minimum DO and plots F-J are for mean DO dataset.

In order to generate predictive models of the likelihood of sites going hypoxic, I modelled the probability of minimum or mean DO at a site going below each of 3 different DO thresholds (5, 4, and 2 mg·l^{-1} DO) using univariate logistic regression for total P, N, discharge, depth, and the diffusion coefficient (mean k). All ten regressions generated significant relationships (Figure 20, Table 4). In general, transitions to a hypoxic state showed steep non-linearities (i.e., thresholds) for discharge, total P, and mean k, but more graded transitions for depth and nitrogen. State transitions to hypoxia occurred at lower stressor levels for 5 mg·l^{-1} DO (the BC water quality threshold for protection of aquatic life) than for the less conservative threshold of hypoxia (2 mg·l^{-1}) commonly used in marine systems. For example, a 50% probability of minimum DO falling below 5 mg·l^{-1} occurs at 0.04 mg·l^{-1} P, whereas a 50% probability of falling below a 2 mg·l^{-1} threshold requires an average total P of 0.135 mg·l^{-1} P (Fig. 20D). Stressor magnitudes required for mean DO to exceed thresholds were generally much higher than magnitudes for transition in minimum DO state. Probability of transitions to minimum DO hypoxic states under nutrient (N and P) loading broadly matched the thresholds for oligo, meso, and eutrophic states identified by Dodds et al. (1998) reasonably well (vertical black lines in Fig. 20 C, D, H, I).

Table 4 Logistic regression coefficients for estimating the likelihood of hypoxia at different thresholds (5, 4, or 2 $mg \cdot l^{-1}$) as univariate functions of nitrogen, phosphorus, discharge, depth, and mean K. Likelihood of hypoxia uses either mean or minimum DO, where minimum DO regressions has a higher sensitivity thresholds and is the worst case scenario. *** denotes $p < 0.01$, * $p < 0.05$ and ** $p < 0.1$.

Dependent Variable	Hypoxic Class	Predictor Variable	Bo	B1 (rate)	B2 (rate)
mean DO	> or < 5mg/L	Phosphorus	-3.788*	19.765*	-
	> or < 4mg/L	Phosphorus	-3.657*	16.15*	-
	> or < 2mg/L	Phosphorus	-4.605*	16.046*	-
min. DO	> or < 5mg/L	Phosphorus	-1.9152*	29.0454*	-
	> or < 4mg/L	Phosphorus	-3.221*	34.277*	-
	> or < 2mg/L	Phosphorus	-4.56*	27.029*	-
mean DO	> or < 5mg/L	Discharge	0.4406	-76.1145*	-
	> or < 4mg/L	Discharge	0.3649	-509.8634**	-
	> or < 2mg/L	Discharge	-0.6487	-678.4509	-
min. DO	> or < 5mg/L	Discharge	2.184*	-28.198***	-
	> or < 4mg/L	Discharge	3.104	-108.833**	-
	> or < 2mg/L	Discharge	0.7158	-103.7273*	-
mean DO	> or < 5mg/L	Discharge + P	-0.763	-62.4927*	9.3950**
	> or < 4mg/L	Discharge + P	-0.7711	-466.6735	7.8952
	> or < 2mg/L	Discharge + P	-2.153	-661.57	9.926
min. DO	> or < 5mg/L	Discharge + P	-1.041	-17.560*	31.070*
	> or < 4mg/L	Discharge + P	-0.4719	-62.4159*	24.9685*
	> or < 2mg/L	Discharge + P	-1.498	-91.867*	16.271*
mean DO	> or < 5mg/L	Depth	-3.555***	1.82*	-
	> or < 4mg/L	Depth	-3.887***	1.693*	-
	> or < 2mg/L	Depth	-4.528***	1.375	-
min. DO	> or < 5mg/L	Depth	-2.333***	3.555***	-
	> or < 4mg/L	Depth	-4.184***	4.996***	-
	> or < 2mg/L	Depth	-5.193***	1.382	-
mean DO	> or < 5mg/L	Mean K	-3.065	-0.565	-
	> or < 4mg/L	Mean K	-2.485***	-0.075	-
	> or < 2mg/L	Mean K	-3.396***	-0.038	-
min. DO	> or < 5mg/L	Mean K	0.669	-0.165***	-
	> or < 4mg/L	Mean K	0.072	-0.470***	-
	> or < 2mg/L	Mean K	-4.678*	-0.088	-
mean DO	> or < 5mg/L	Nitrogen	-5.161***	2.560***	-
	> or < 4mg/L	Nitrogen	-5.081***	2.175***	-
	> or < 2mg/L	Nitrogen	-5.745***	2.053*	-
min. DO	> or < 5mg/L	Nitrogen	-2.616***	2.498***	-
	> or < 4mg/L	Nitrogen	-4.919*	3.525	-
	> or < 2mg/L	Nitrogen	-7.663***	3.503*	-

3.5 Discussion

The overall goals of this study were to identify the key drivers of variation in dissolved oxygen, the potential contribution of habitat and landuse to hypoxia occurrence, and to identify the subset of drivers with the potential to be exploited as management levers to reduce the likelihood of future hypoxia. Generalized linear mixed models confirmed that DO was controlled both by physical habitat features that govern gas exchange at the air-water interface, and biological processes that generate or consume oxygen. Site gradient and discharge were identified by model selection as the dominant physical drivers associated with high dissolved oxygen, reflecting their positive influence on surface turbulence. Identification of GPP, ER, and total P and N as the key biological drivers of DO was consistent with expectation and many earlier studies (Wurtbaugh et al. 2019), and reflects the role of community photosynthesis and respiration as metabolic sources and sinks of oxygen. Total P was also the most consistent predictor of both mean and minimum DO in model selection, unlike GPP and ER which were primarily relevant only to the prediction of mean DO. The consistent negative association of DO with total P, and to a lesser extent total N, suggests a footprint of eutrophication, i.e., nutrient-driven bottom-up effects on biological oxygen demand that lead to oxygen deficit.

The identification of total P as a more consistent predictor of hypoxia than GPP or ER (Table GAM) suggests that nutrient levels may do a better job of predicting trophic state and long term oxygen demand than field estimates of metabolism. While estimates of GPP and ER clearly have value for inferring mechanisms underlying hypoxia, their apparently lower predictive value may reflect poorer temporal representation of metabolic demand (GPP and ER were only measured 5 contiguous days at a site each month). The negative association of nutrients with DO could also in part reflect increased nutrient cycling from sediment under hypoxia, because both P and N are known to be mobilized under hypoxia (Jantti and Hietanen 2012; Mollot et al. 2014). However, low concentrations of total P under hypoxia at reference sites, as well as an abundance of earlier studies linking eutrophication and hypoxia (Breitburg et al. 2009; LeMoal et al. 2019) suggests a general causative relationship between elevated nutrients and hypoxia, rather than the reverse. The strength of the relationship, however, could also reflect transient positive feedback dynamics where nutrient release under hypoxia stimulates additional microbial respiration that further depletes oxygen, ultimately limiting ecosystem metabolism (Birk et al. 2020).

Despite our expectation of abundant interactions among metabolic drivers as suggested in recent meta-analyses of aquatic stressor dynamics (e.g., Jackson et al. 2016; Birk et al. 2020), model selection identified only one significant interaction: the positive effect of GPP on mean and minimum DO was enhanced under high total N. While this suggests a net positive effect of N enrichment on dissolved oxygen through elevated photosynthesis, it's generality needs to be interpreted with caution. First, differential stimulation of GPP over respiration is very sensitive to temporal dynamics; while it can lead to net carbon storage as algal biomass accumulates, particularly in the spring and summer, rapid algal senescence in late summer and fall can cause an excess of respiration as stored algal carbon decomposes, reversing the balance of oxygen supply and demand. These transient dynamics appear to peak in September in Fraser Valley streams (Rosenfeld et al. 2021), and may not have been captured by our May - August sampling. Second, sensitivity of the balance between GPP:ER to nutrient enrichment is temperature dependent; Cross et al. (2022) demonstrated that respiration responds more strongly than GPP to both N and P enrichment at high temperatures, and Song et al. (2018) similarly projected a net increase in heterotrophy of streams under global warming. The general absence of detectible interactions in this study may be due in part to low power associated with limited replication. Nevertheless, power was sufficient to detect abundant main effects, which simplifies management priorities to improve water quality.

Some logistical limitations of this study may include the incorporation of a continuous measurement for light availability and discharge to catch small-scale changes, and may also want to explore 1-hour interval DO readings to minimize noise associated with extremely hypoxic sites. Future research could incorporate the inclusion of fall and winter months to consider how hypoxic conditions may change spatially and temporally throughout the overwintering season. To better my own research I could have included more urban sites and had three different landuse groups to investigate whether there were differences between agricultural and urban landuse impacts. Lastly, future research should consider using 10-minute interval DO readings to investigate how long sites remained in hypoxic conditions for, as many fish species are known to experience adverse growth impacts and/or death when DO remains below 1-2 mg/L.

DO variation across sites was also strongly influenced by temporal and landuse effects. Average monthly DO declined from May to August, indicating an accumulating oxygen deficit at most sites as the summer progressed (Fig. 16). This deficit was likely driven by low and stable flows that allowed the accumulation of algal and heterotroph biomass over the summer without significant spates to scour algae and export organic detritus (Biggs et al. 1998; Biggs and Close 1999; Alberts et al. 2017), highlighting the role of flow regime in shaping stream metabolism (Palmer and Ruhi 2019; Battin et al. 2023). Algal senescence with declining daylight hours in August and subsequent stimulation of heterotrophic metabolism likely also contributed to seasonal declines in DO, which were noticeably more pronounced at open-canopied sites (Fig. 14). Previous studies have observed a higher frequency of oxygen supersaturation in the spring in lower Fraser Valley streams (Rosenfeld et al. 2021), suggesting a temporal mismatch between peak primary production in the spring when algal biomass accrues, and community respiration which peaks in the late summer and fall when lower light levels trigger algal senescence. This interpretation is supported by a larger oxygen deficit at open-canopied sites at the end of summer, independent of canopy effects on temperature (Fig. 17).

The pronounced effect of canopy cover on mean and minimum DO indicates that light is generally limiting overall stream metabolism, and that canopy cover is a good integrated measure of site-potential metabolic oxygen demand. The lack of a significant difference in DO between forested and partial canopy sites suggest that even a partial reduction in incident light can reduce the likelihood of hypoxia. Although minimum DO tended to be lower at both reference and agricultural sites with open canopies, the trend towards a larger canopy effect at agricultural sites suggests that agricultural land use is a composite stressor integrating multiple impacts (e.g., nutrients, flow, habitat effects) as observed elsewhere (Brauns et al. 2022).

The impacts of agricultural and urban development on valley bottom streams - a syndrome of reduced flow from irrigation, loss of riparian forest, stream channelization, increased fine sediment, and eutrophication - leads to a trajectory of habitat degradation often culminating in range collapse for species like salmonids that are sensitive to low dissolved oxygen and elevated temperatures (Wenger et al. 2011; Rosenfeld and Lee 2022). Developed valley-bottom landscapes vary in their location on a degradation trajectory; some are well-advanced, and have lost most of their historic cold-water species. For instance, southern Ontario and the NE United States have seen major range contractions and extirpations of native brook charr associated with landuse change (Stranko et al. 2008; Hudy et al. 2005; Smith et al. 2023). Broadly speaking, the lower Fraser Valley is at an earlier stage on this impact trajectory, with range contractions primarily limited to direct conversion of streams to storm sewers in urban areas or barriers like dikes that isolate upstream reaches (Scott et al. 2016). Broader impacts have been buffered in part by a cool maritime climate that partially moderates summer temperatures, and significant groundwater inputs associated with alluvial deposits and snowmelt from adjacent mountain slopes. However, ongoing development and water quality impacts under climate change will likely accelerate nutrient inputs and temperatures while reducing flows (Shupe 2013; Rosenfeld et al. 2021; Putt et al. 2019), and associated changes in stream metabolism will play a significant role in how water quality shapes the future distribution of hypoxia and fish habitat at a landscape scale.

Recent research has identified freshwater hypoxia as a major global concern, with 12.6% of locations exhibiting at least one hypoxic measurement below 2 mg/L and 35% below 5 mg/L (Blaszczak et al., 2022). In comparison, 40% of my sites experienced hypoxia below 2 mg/L and 63% experienced hypoxia below 5 mg/L, indicating worse water quality in the developed lower Fraser Valley than expected relative to a global database. This comparison must be tempered by the fact that my study streams were predominantly small and low gradient, key attributes which increase vulnerability to hypoxia (Blaczack et al. 2022); nevertheless, incidence of hypoxia in my study sites exceeded that in the landuse category (wetlands) with the highest frequency of hypoxia (18.5% < 2mg/l) in a global database (Blackzack et al. 2022).

The widespread noncompliance with provincial and federal DO guidelines (5 and 6 mg/l, respectively; BCMOE 2021; CCME 1999) is more extensive than earlier estimates based on day-time spot measurements of DO (Rosenfeld et al. 2021), likely reflecting the superior detection of nocturnal hypoxia with continuous DO loggers (Pardo and Garcia 2016). Although the current state of water quality in the lower Fraser Valley is dire, it is likely broadly representative of conditions in many lowland valley bottom landscapes with intense agriculture (e.g., Oliviera et al. 2019). A coherent management program to mitigate ongoing hypoxia is badly needed to avoid further loss of ecosystem function or local extirpation of endangered species like Salish sucker (Pearson 2015; Rosenfeld et al. 2021), and reflects a broader need for co-ordinated recovery action to bend the curve on global biodiversity loss (Tickner et al. 2020; Zipper et al. 2020). An essential component of any recovery plan would include routine monitoring of dissolved oxygen at representative index sites (e.g., Appling et al. 2018b), which is currently lacking in Canada. Application of logistic regression to predict occurrence of hypoxia provides a simple approach for linking stressor levels to the likelihood of regulatory non-compliance. Logistic regression can also be used to inform stressor management targets and to predict future landscape-scale hypoxia under alternate land management or climate warming scenarios. Although we only modelled mean or minimum DO at a site, the duration of hypoxic events is also highly consequential for individual and population-level impacts. The logistic regression approach can easily be extended to modelling the frequency and duration of hypoxic events of different severity (Blasczack et al. 2022).

Recent studies have called for more research to identify drivers of complex interactions among multiple stressors (e.g., Pelletier et al. 2020; Spears et al. 2021), and advocate for the development of thresholds related to process-based metrics of ecological function (e.g., Brauns et al. 2022). However, my analysis suggests that addressing stressor main effects with reference to existing water quality guidelines can be effective at mitigating impaired water quality. Rather than develop new benchmarks, metrics, and thresholds of impairment, current DO guidelines are well-established and clearly linked to ecological impacts (Vaquer-Sunyer and Duarte 2008; Saari et al. 2018; Rosenfeld and Lee 2022), and existing trophic thresholds such as Dodds et al. (2000) and Ostermiller et al. (2019a) show reasonably strong relationships with DO.

The science basis for regulating and mitigating landuse stressors is now generally well established, as are best management practices, although their effectiveness in many cases is hampered by legacy effects and needs to be refined through adaptive management cycles (Lintern et al. 2020; Basu et al. 2022). My results highlight three key regulatory needs to reduce the incidence of hypoxia: establishment of riparian buffers on private agricultural land, which is broadly exempt from current riparian protection legislation (Rosenfeld et al. 2021), regulation of nutrient loading to streams, and ongoing monitoring to ensure management efforts result in the reduction of hypoxia. It will be essential for governments to also provide incentives for private agricultural land owners to use best management practices and to conserve and restore riparian habitats (Wollstein and Davis 2017). Regardless of the combination of regulatory and stewardship approaches used to mitigate hypoxia, the primary bottleneck to improving water quality now relates to direct management and regulation of landuse activities that elevate stressor levels, and enforcement of existing guidelines which are currently discretionary (Boesch 2019; Giling 2013). This is a challenging issue because of the diffuse nature of cumulative effects in watershed and the multiplicity of stakeholders involved, but integrated watershed-scale stressor management is essential for natural resource management agencies to succeed in protecting aquatic ecosystems (Tickner et al. 2020).

Canada's 2020 Emissions Reduction Plan aims to reduce emissions by 40-45% below 2005 levels by 2030 (ECCC, 2022). This plan includes a $470 million investment in the Agricultural Climate Solutions: On-Farm Climate Action Fund to help farmers adopt sustainable practices such as improved fertilizer management (ECCC, 2022). This initiative will likely have the side effect of significantly reducing nutrient inputs to streams through improved fertilizer management, and should be used as the cornerstone for a broader initiative to reduce freshwater eutrophication and associated hypoxia in vulnerable watersheds.

Chapter 4 - Conclusion

Chapter 2 highlighted that nutrient enrichment and reduced canopy cover were major contributors to high rates of algal production and respiration, especially in stagnant ponds. Results showed that high nutrient inputs creating hypoxic conditions may eventually limit the photosynthetic ability of aquatic plants and algae to produce oxygen for fish. To the best of my knowledge this finding is novel as no previous research was found on hypoxia limiting photosynthesis in streams. Forested canopy cover was shown to effectively mitigate high rates of GPP in agricultural landscapes, yet the effect of partially forested canopy was insufficient. Chapter 3 sheds light on some optimistic mitigation measures including the strong influence of forested or partially forested canopy cover on reducing hypoxia, and the strong potential for riffle restoration to increase reaeration (K) and DO concentrations in streams.

Chapter 2 and 3 shows how important it is to conserve and restore riparian vegetation on agricultural land to mitigate excessive algal production and reduce the risk of hypoxia. Prioritizing riparian conservation and restoration addresses multiple stressors to streams including limiting light availability which simultaneously reduces excess algal production and respiration and cools water temperatures allowing greater solubility of DO. Riparian buffers greater than 11 meters wide also act as a sufficient filter for nutrient runoff from surrounding landscapes (Lind et al., 2019).

There is limited understanding of the relative importance of landscape characteristics on water quality. Some previous studies have attempted to identify the most influential landscape characteristics affecting spatial variability in water quality using multiple regressions. Many studies have only included a subset of the many potential factors driving water quality or are limited by the number of sites used. Previous studies have noted that future research must aim to understand the interaction effects between drivers, how one characteristic changes based on other characteristics and the interannual and inter-seasonal variability in the relationships between landscape characteristics and water quality responses. This study highlighted that nutrient enrichment and reduced canopy cover were both major contributors to high rates of algal production and respiration, especially in stagnant ponds. My research produced the novel finding that high nutrient input may create hypoxic conditions that eventually limit the photosynthetic ability of aquatic plants and algae to produce oxygen for fish, highlighting the severity of high nutrient input. A valuable finding for future management strategies was that greater canopy cover may effectively mitigate hypoxic conditions in agricultural landscapes. More specifically, both partial and fully forested canopy cover was shown to mitigate the impacts that high nitrogen and phosphorus concentrations have on producing hypoxic conditions. Another interesting finding is the influence that the re-aeration coefficient has on predicting hypoxic conditions making riffle restoration a promising management strategy to increase DO in streams. These findings will help improve our ability to set realistic target and cost-effective management strategies and better equip future researchers when building tools and models to predict water quality (Lintern et al., 2018).

Previous research has shown that environmental policy geared towards the problem of nutrient enrichment has had variable success over the long term (1982-2012), with decreasing nutrient concentrations at urban sites and little to no change at agricultural sites (Edward et al., 2020). With water treatment plants dispersed throughout urbanized areas, the increase in the human population in urban areas is less likely to have detrimental impacts on water quality in comparison to agricultural areas where increasing food demand, directly increases the amount of land required to meet these requirements. As demand increases, agricultural producers are also less likely to let their land rest to help restore nutrients to the soil, which results in soil quality declining and farmers increasing fertilizer inputs to compensate for this nutrient loss (Ramirez et al., 2020). There are many drainage ditches throughout agricultural land in the Lower Fraser Valley, and this practice, along with the high proportion of groundwater is highly problematic for water quality because it reduces the retention and filtering time of water in the soil and offers a fast transport route for dissolved nutrients into streams and rivers (Lintern et al., 2018).

Recent studies have explored the impacts of stream flow and watershed management on water quality in US rivers (Murphy and Sprague, 2019). Results showed that water quality trends, specifically nutrient concentration, was more strongly affected by changes in watershed management versus trends in streamflow (Murphy and Sprague, 2019). On the other hand, trends in major ions, salinity, and sediment concentrations were more strongly affected by changes in streamflow (Murphy and Sprague, 2019). Chapter 2 and 3 shows how important conserving and restoring riparian vegetation is on agricultural land to mitigate excessive algal production and reduce the risk of hypoxia. Riparian buffers zones help reduce the velocity of overland runoff and provides time for the water to percolate into the soil. They also have higher microbial community diversity which is important for the decomposition of organic agro-chemicals such as nitrogen and phosphorus (Unger et al., 2013). With the loss of profits from reduced planting area and increased shading to crops, conserving riparian vegetation is not a priority or financially feasible option for some agricultural land owners. Therefore, it should be the responsibility of governments to provide subsidies or incentives for conserving or restoring riparian vegetation. With greater rewards to farmers based on riparian buffer width, plant diversity, and presence of understory and overstory layers as this relates to the total benefits provided to the stream (Lind et al., 2019). Countries like Germany and Switzerland have implemented a national regulation requiring a minimum 5 m riparian buffer on all land. Since 1977, the state of Minnesota has mandated a minimum 16.5 foot riparian buffer of perennial vegetation on agricultural and rural land (Minnesota Board of Water & Soil Resources, 2014). A 2006 study determined that 72% of the watercourses required to have buffer strips were in compliance at that time (Minnesota Board of Water & Soil Resources, 2014). Prioritizing riparian conservation and restoration addresses multiple stressors to streams including limiting light availability which simultaneously reduces excess algal production and respiration and cools water temperatures allowing greater solubility of DO. Previous research found that to sustain fish populations as well as provide sufficient habitat for insects, a minimum ~25 m buffer width must be implemented, to adequately filter (75-100% removal efficiency) N and P a minimum 11 m buffer zone, and to provide shading to mitigate water temperatures a 21 m buffer width. (Lind et al., 2019). It was also found that drainage size should influence how wide a riparian buffer should be, with larger drainage areas corresponding to higher nutrient and sediment concentrations, a wider riparian zone is required to sufficiently filter the runoff. Management must note that in agricultural areas with extensive tile drainage systems the riparian will not function as a filter to the same extent because water bypasses the riparian zone through pipes (Gökkaya et al., 2017).

As this thesis has shown, along with previous studies, what influences stream metabolism and hypoxia is very complex and cumulative. Like many ecological modelling studies, especially those incorporating so many predictor variables, this study is limited by sample size. With only 30 sites with accurate stream metabolism estimates, this was not a sufficient sample size given 10 different predictor variables, not including interaction effects. Both Chapter 2 and 3 were limited by the lack of continuous measurements for light availability and discharge, along with insufficient high N concentrations. To obtain a more informative and accurate understanding of what drives hypoxia and stream metabolism, future studies should aim for a higher sample size when addressing such a complex and intertwined model to ensure that diverse interactions between stream and landscape characteristics are included. Studies should also strive for continuous variable measurements to catch small-scale changes in light availability and discharge. In doing so, management organizations will have more robust models for detecting the likelihood of hypoxia in waterbodies to help conserve fish and fish habitat.

The Mainland of British Columbia became a crown colony in 1858 and has therefore seen just over 150 years of development. When we compare the effects of development to the region of southern Ontario, which has about an additional 200 years of development, we see what the future has in store for streams in the Lower Fraser Valley. As early as the 1870s, Ontario’s state fish culturist Samuel Wilmot noted that brook trout had become “exceedingly scarce” especially in the “older settled sections” and in 1877 began a hatchery (Knight, 2007). In southern Ontario brook trout populations declined by 23% between 1970-1980 and 17% from 2000-2010 (Smith et al., 2022). With the lower Fraser Valley being Canada’s now number one agricultural economy and population growth as high as 7% per year, sensitive species inhabiting these lowland streams are likely to experience greater likelihoods of hypoxia resulting from increased nutrient input. With no federal or provincial regulations set in place on private agricultural land, it will be difficult to minimize the nutrient loading that the future has in store for these streams. It will be essential for governments to provide incentives for private agricultural land owners to use best management practices and to conserve and restore riparian habitats. Additionally, this study has shown the importance of incorporating water quality guidelines within the management and recovery strategies for fish and fish habitat legislated under the *Fisheries Act* and the *Species at Risk Act*. Federal and provincial monitoring programs should prioritize the deployment of DO loggers in reaches where agricultural land and sensitive fish habitat is most prominent to ensure that fish most susceptible to hypoxic conditions are actively monitored.

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Appendix

Table 5 Proportion of sites per each categorical variable. Oligotrophic (O)/mesotrophic (M)/eutrophic (E) thresholds for nitrogen: 0.7<; 0.7-1.5; > 1.5 and for phosphorous: 0.025<; 0.025-0.075; > 0.075.

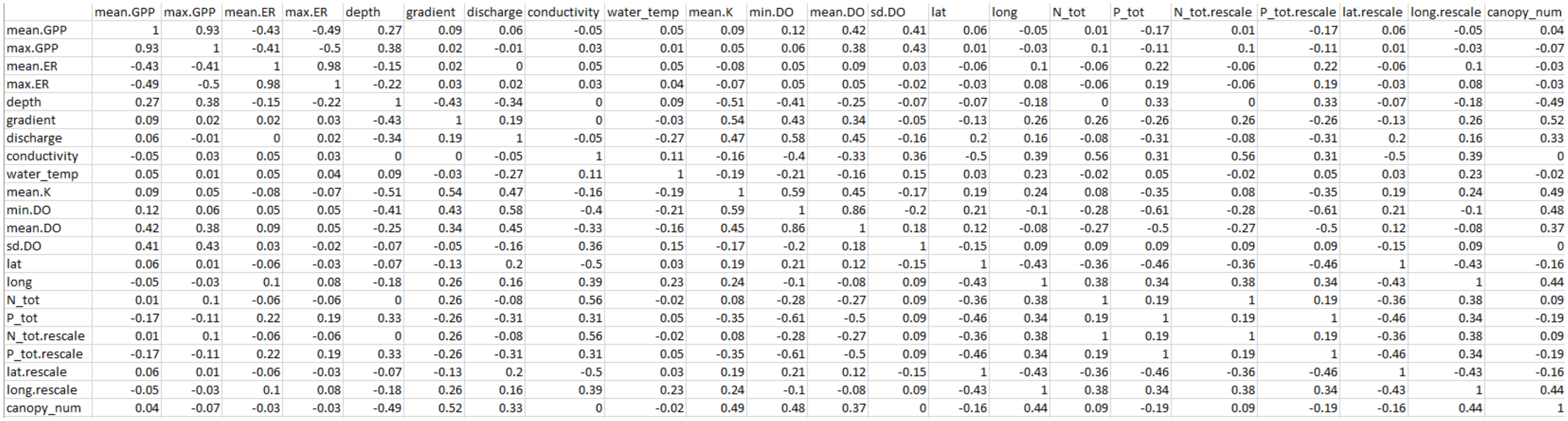
Agricultural									**References**								
Open			**Partial**			**Forested**			**Open**			**Partial**			**Forested**		
O	**M**	**E**	**O**	**M**	**E**	**O**	**M**	**E**	**O**	**M**	**E**	**O**	**M**	**E**	**O**	**M**	**E**
2	0	6	2	3	5	0	0	4	3	3	0	1	1	0	4	3	0

Table 6 Summary of different treatments.

Number	**SITE**	**LANDUSE**	**HABITAT**	**CANOPY**	**N TROPHIC LEVEL**	**P TROPHIC LEVEL**
1	Chawathil Pond	REFERENCE	POND	OPEN	OLIGOTROPHIC	OLIGOTROPHIC
2	Chawathil Stream	REFERENCE	STREAM	FORESTED	MESOTROPHIC	MESOTROPHIC
3	Blaney Creek	REFERENCE	STREAM	FORESTED	MESOTROPHIC	MESOTROPHIC
4	Spring Creek	REFERENCE	STREAM	PARTIAL	MESOTROPHIC	MESOTROPHIC
5	Jacobs Creek	REFERENCE	STREAM	FORESTED	OLIGOTROPHIC	OLIGOTROPHIC
6	Elk Creek Upstream	REFERENCE	STREAM	FORESTED	MESOTROPHIC	MESOTROPHIC
7	Elk Creek Downstream	IMPACTED	STREAM	OPEN	MESOTROPHIC	MESOTROPHIC
8	Atchelitz Creek	IMPACTED	STREAM	OPEN	OLIGOTROPHIC	MESOTROPHIC
9	Agassiz Slough	IMPACTED	POND	OPEN	EUTROPHIC	MESOTROPHIC
10	Brunette River	IMPACTED	STREAM	PARTIAL	OLIGOTROPHIC	MESOTROPHIC
11	Stoney Creek	IMPACTED	STREAM	FORESTED	MESOTROPHIC	MESOTROPHIC
12	Pepin Creek (Aldergrove Park)	IMPACTED	STREAM	FORESTED	MESOTROPHIC	MESOTROPHIC
13	Pepin Creek (At diversion)	IMPACTED	STREAM	PARTIAL	MESOTROPHIC	MESOTROPHIC
14	Pepin Creek (downstream of bridge)	IMPACTED	STREAM	OPEN	MESOTROPHIC	EUTROPHIC
15	Pepin Deep Pond	IMPACTED	POND	OPEN	EUTROPHIC	EUTROPHIC
16	Pepin Shallow Pond	IMPACTED	POND	OPEN	MESOTROPHIC	EUTROPHIC
17	Bertrand Creek (At 0 Avenue)	IMPACTED	STREAM	PARTIAL	EUTROPHIC	MESOTROPHIC

18	Cave Creek Pond (upstream)	IMPACTED	POND	OPEN	MESOTROPHIC	EUTROPHIC
19	Cave Creek	IMPACTED	STREAM	FORESTED	MESOTROPHIC	MESOTROPHIC
20	Bertrand Creek (Otter Park)	IMPACTED	STREAM	PARTIAL	MESOTROPHIC	MESOTROPHIC
21	Salmon River (Downes Road)	IMPACTED	STREAM	OPEN	EUTROPHIC	EUTROPHIC
22	Salmon River (at 232nd)	IMPACTED	STREAM	PARTIAL	EUTROPHIC	OLIGOTROPHIC
23	Mountain Creek	REFERENCE	STREAM	OPEN	MESOTROPHIC	MESOTROPHIC
24	McCallum Creek	IMPACTED	STREAM	OPEN	MESOTROPHIC	MESOTROPHIC
25	Mountain Slough	IMPACTED	POND	PARTIAL	MESOTROPHIC	MESOTROPHIC
26	Miami River	IMPACTED	STREAM	FORESTED	MESOTROPHIC	EUTROPHIC
27	Fishtrap Creek	IMPACTED	STREAM	PARTIAL	EUTROPHIC	OLIGOTROPHIC
28	Hopedale Slough Stream	REFERENCE	STREAM	FORESTED	OLIGOTROPHIC	OLIGOTROPHIC
29	Hopedale Slough Pond	REFERENCE	POND	PARTIAL	OLIGOTROPHIC	OLIGOTROPHIC
30	Little Campbell River (A Rocha)	IMPACTED	STREAM	FORESTED	MESOTROPHIC	MESOTROPHIC
31	Little Campbell River (Langley Municipal Park)	IMPACTED	POND	OPEN	MESOTROPHIC	EUTROPHIC
32	Little Campbell River (At the nursery)	IMPACTED	STREAM	PARTIAL	MESOTROPHIC	MESOTROPHIC
33	Howes Creek	IMPACTED	POND	PARTIAL	MESOTROPHIC	MESOTROPHIC
34	South Alouette River Pond	REFERENCE	POND	OPEN	OLIGOTROPHIC	OLIGOTROPHIC
35	Chilliwack River Valley Pond	REFERENCE	POND	OPEN	OLIGOTROPHIC	OLIGOTROPHIC
36	Borden Creek	REFERENCE	STREAM	FORESTED	MESOTROPHIC	MESOTROPHIC
37	Malcom Knapp Research Forest Fire Pond	REFERENCE	POND	FORESTED	OLIGOTROPHIC	MESOTROPHIC

Table 7 Correlation matrix between all variables used in the models.



	mean.GPP	max.GPP	mean.ER	max.ER	depth	gradient	discharge	conductivity	water_temp	mean.K	min.DO	mean.DO	sd.DO	lat	long	N_tot	P_tot	N_tot.rescale	P_tot.rescale	lat.rescale	long.rescale	canopy_num
mean.GPP	1	0.93	-0.43	-0.49	0.27	0.09	0.06	-0.05	0.05	0.09	0.12	0.42	0.41	0.06	-0.05	0.01	-0.17	0.01	-0.17	0.06	-0.05	0.04
max.GPP	0.93	1	-0.41	-0.5	0.38	0.02	-0.01	0.03	0.01	0.05	0.06	0.38	0.43	0.01	-0.03	0.1	-0.11	0.1	-0.11	0.01	-0.03	-0.07
mean.ER	-0.43	-0.41	1	0.98	-0.15	0.02	0	0.05	0.05	-0.08	0.05	0.09	0.03	-0.06	0.1	-0.06	0.22	-0.06	0.22	-0.06	0.1	-0.03
max.ER	-0.49	-0.5	0.98	1	-0.22	0.03	0.02	0.03	0.04	-0.07	0.05	0.05	-0.02	-0.03	0.08	-0.06	0.19	-0.06	0.19	-0.03	0.08	-0.03
depth	0.27	0.38	-0.15	-0.22	1	-0.43	-0.34	0	0.09	-0.51	-0.41	-0.25	-0.07	-0.07	-0.18	0	0.33	0	0.33	-0.07	-0.18	-0.49
gradient	0.09	0.02	0.02	0.03	-0.43	1	0.19	0	-0.03	0.54	0.43	0.34	-0.05	-0.13	0.26	0.26	-0.26	0.26	-0.26	-0.13	0.26	0.52
discharge	0.06	-0.01	0	0.02	-0.34	0.19	1	-0.05	-0.27	0.47	0.58	0.45	-0.16	0.2	0.16	-0.08	-0.31	-0.08	-0.31	0.2	0.16	0.33
conductivity	-0.05	0.03	0.05	0.03	0	0	-0.05	1	0.11	-0.16	-0.4	-0.33	0.36	-0.5	0.39	0.56	0.31	0.56	0.31	-0.5	0.39	0
water_temp	0.05	0.01	0.05	0.04	0.09	-0.03	-0.27	0.11	1	-0.19	-0.21	-0.16	0.15	0.03	0.23	-0.02	0.05	-0.02	0.05	0.03	0.23	-0.02
mean.K	0.09	0.05	-0.08	-0.07	-0.51	0.54	0.47	-0.16	-0.19	1	0.59	0.45	-0.17	0.19	0.24	0.08	-0.35	0.08	-0.35	0.19	0.24	0.49
min.DO	0.12	0.06	0.05	0.05	-0.41	0.43	0.58	-0.4	-0.21	0.59	1	0.86	-0.2	0.21	-0.1	-0.28	-0.61	-0.28	-0.61	0.21	-0.1	0.48
mean.DO	0.42	0.38	0.09	0.05	-0.25	0.34	0.45	-0.33	-0.16	0.45	0.86	1	0.18	0.12	-0.08	-0.27	-0.5	-0.27	-0.5	0.12	-0.08	0.37
sd.DO	0.41	0.43	0.03	-0.02	-0.07	-0.05	-0.16	0.36	0.15	-0.17	-0.2	0.18	1	-0.15	0.09	0.09	0.09	0.09	0.09	-0.15	0.09	0
lat	0.06	0.01	-0.06	-0.03	-0.07	-0.13	0.2	-0.5	0.03	0.19	0.21	0.12	-0.15	1	-0.43	-0.36	-0.46	-0.36	-0.46	1	-0.43	-0.16
long	-0.05	-0.03	0.1	0.08	-0.18	0.26	0.16	0.39	0.23	0.24	-0.1	-0.08	0.09	-0.43	1	0.38	0.34	0.38	0.34	-0.43	1	0.44
N_tot	0.01	0.1	-0.06	-0.06	0	0.26	-0.08	0.56	-0.02	0.08	-0.28	-0.27	0.09	-0.36	0.38	1	0.19	1	0.19	-0.36	0.38	0.09
P_tot	-0.17	-0.11	0.22	0.19	0.33	-0.26	-0.31	0.31	0.05	-0.35	-0.61	-0.5	0.09	-0.46	0.34	0.19	1	0.19	1	-0.46	0.34	-0.19
N_tot.rescale	0.01	0.1	-0.06	-0.06	0	0.26	-0.08	0.56	-0.02	0.08	-0.28	-0.27	0.09	-0.36	0.38	1	0.19	1	0.19	-0.36	0.38	0.09
P_tot.rescale	-0.17	-0.11	0.22	0.19	0.33	-0.26	-0.31	0.31	0.05	-0.35	-0.61	-0.5	0.09	-0.46	0.34	0.19	1	0.19	1	-0.46	0.34	-0.19
lat.rescale	0.06	0.01	-0.06	-0.03	-0.07	-0.13	0.2	-0.5	0.03	0.19	0.21	0.12	-0.15	1	-0.43	-0.36	-0.46	-0.36	-0.46	1	-0.43	-0.16
long.rescale	-0.05	-0.03	0.1	0.08	-0.18	0.26	0.16	0.39	0.23	0.24	-0.1	-0.08	0.09	-0.43	1	0.38	0.34	0.38	0.34	-0.43	1	0.44
canopy_num	0.04	-0.07	-0.03	-0.03	-0.49	0.52	0.33	0	-0.02	0.49	0.48	0.37	0	-0.16	0.44	0.09	-0.19	0.09	-0.19	-0.16	0.44	1