Columbia River Project Water Use Plan

Mid-Columbia River Ecological Productivity Monitoring

Implementation Year 2018

Year 12

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MIDDLE COLUMBIA RIVER ECOLOGICAL PRODUCTIVITY MONITORING, 2007-2018

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ACRONYMS AND ABBREVIATIONS

AFDW	ash free dry weight
AICc	Akaike information criterion corrected for small sample sizes
ALR	Arrow Lakes Reservoir
BC Hydro	British Columbia Hydro and Power Authority
BRX	Brilliant Expansion
Caro Labs	Caro Environmental Laboratories (Kelowna, B.C.)
CFU	colony forming unit
chl-a	Chlorophyll-a
Didymo	*Didymosphenia geminata*
EPT	*Ephemeroptera* (mayflies), *Plecoptera* (stoneflies), *Trichoptera* (caddisflies)
FFI	Fish Food Index
HBI	Hilsenhoff Biotic Index
QA/QC	Quality assurance, quality control
km	kilometer
L	litre
LCR	Lower Columbia River
m	metre
m ASL	metres above sea level
max	maximum value
MCR	Middle Columbia River
min	minimum value
n	sample size
NMDS	Non metric multidimensional scaling
RVI	relative variable importance
SD	standard deviation
UTM	Universal Transverse Mercator

DEFINITIONS

The following terms are briefly defined as they are used in this report.

Term	Definition
Accrual rate	A function of cell settlement, actual growth and losses (grazing, sloughing)
Autotrophic	An organism capable of synthesizing its own food from inorganic substances, using light or chemical energy
Benthic	Organisms that dwell in or are associated with the sediments
Benthic production	Production originating from both periphyton and benthic invertebrates
Catastrophic flow	Flow events that have population level consequences of >50% mortality
Cyanobacteria	Bacteria-like algae having cyanochrome as the main photosynthetic pigment
Diatoms	Algae that have hard, silica-based "shells" frustules
Eutrophic	Nutrient-rich, biologically productive water body
Freshet	The flood of a river or stream from melted snow in the spring
Functional Feeding group	(FFG) Benthic invertebrates can be classified by their foraging mechanisms as functional feeding or foraging groups
Heterotrophic	An organism that cannot synthesize its own food and is dependent on complex organic substances for nutrition.
Lentic	Standing waters such as lakes and ponds (lacustrine), or swamps and marshes
Lotic	Running water (fluvial) habitats such as rivers and streams
Macroinvertebrate	An invertebrate that is large enough to be seen without a microscope
Mainstem	The primary downstream segment of a river, as contrasted to its tributaries
Microflora	The sum of algae, bacteria, fungi, *Actinomycetes,* etc., in water or biofilms
Morphology, river	The study of channel pattern and geometry at several points along a river
Picoplankton	Minute algae that are less than 2 microns in their largest dimension
Peak biomass	The highest density, biovolume or chl-a attained in a set time on a substrate
Periphyton	Microflora that are attached to aquatic plants or solid substrates
Phytoplankton	Algae that float, drift or swim in water columns of reservoirs and lakes
Ramping of flows	A progressive change of discharge into a stream or river channel
Reach 3 (R3)	The section of river extending from the Jordan River to the Illecillewaet River
Reach 4 (R4)	The section of river extending below Revelstoke Dam to the Jordan River
Riffle	A stretch of choppy water in a river caused by a shoal or sandbar
Riparian	The interface between land and a stream or lake
Substrates	The bottom material (boulder cobble sand silt clay) of a stream or lake.
Taxa Taxon	Taxonomic group(s) of any rank, including a species, family or class.
Thalweg	A line connecting the lowest points of a river, usually has the fastest flows
Varial Zone	The zone of periodically inundated substrate, spanning the upper edge of the permanently wetted zone to the lower edge of the floodplain

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CLBMON 15B Status of Objectives Management Questions and Hypotheses After Year 12			
Objectives	Management Questions	Management Hypotheses	Year 12 (2018) Status
A key environmental objective of the minimum flow release is to enhance the productivity and diversity of benthic communities. The benthic community of MCR is viewed as a key monitoring component in the Revelstoke Flow Management Program because the productivity and diversity of the benthic community may reflect ecosystem health, and the benthic community supports juvenile and adult life stages of fish populations. Therefore, the objectives of this monitoring program are to 1) provide long term data on the productivity of benthic communities and 2) assess how the recommended minimum flow releases influence benthic productivity as it relates to the availability of food for fishes in the MCR.	Q.1. What is the composition, distribution, abundance and biomass of periphyton and benthic invertebrates in the section of MCR subjected to the influence of minimum flows? Q.2. What is the effect of implementing minimum flows on the area of productive benthic habitat?	Ho_1: The implementation of the 142 m^3/s minimum flow release does not change the spatial area of productive benthic habitat for periphyton or benthic invertebrates in the MCR.	Ho_1: The hypothesis is rejected, but only under certain operating conditions. The spatial area of habitat supporting benthic communities increased with minimum flows, predominantly in Reach 4, but also in Reach 3 during periods when ALR reservoir did not create backwater conditions. More algal production was observed in areas that were regularly exposed before implementation of the minimum flow operating regime because submergence is the most important determinant of both accrual and total biomass. The spatial area of productive habitat is determined by the BC Hydro operating regime because it is directly responsible for the wetted history. The total productive area is determined by factors including the channel cross section, high daily average flows, backwatering from Arrow Lakes Reservoir, and weather conditions. The operating regime created three bands of growth that moved across the channel in response to mean low flows and duration of daily high flows. The reach-wide productivity model for chl-a was improved in 2018 by modifying the growth curves using time series data. Model results indicate that minimum flows increased productivity during periods of low ALR reservoir elevations, and the effects of minimum flow were more apparent for periphyton and invertebrates in Reach 4 than in Reach 3. The current model can be used to answer management questions with a focus on the area of productive habitat, but it does not account for other physical parameters. Velocity and light modelling were undertaken to determine both the feasibility and benefit of incorporation of these parameters into an integrated predictive model with increased accuracy. Velocity was not a highly important predictor for algal productivity (as measured by chl-a) in the range of observable velocities and flows (from 0 to just over 2 m/s from 0 to 2,124 m^3/s) in the MCR. However, velocity may improve model predictability for invertebrate biomass. Light was not determined to be a limiting factor from early spring to late fall, but may influence winter productivity which has not been sampled. Thus, incorporation of light into a predictive model will not dramatically improve predictability for algal or invertebrate production in the spring through fall periods at a minimum. Incorporation of velocity will also not dramatically improve predictability of the effects of minimum flow on algal production, but will help slightly improve predictability for invertebrates.
	Q3.What is the effect of implementing minimum flows on the accrual rate of periphyton biomass in the MCR? Is there a long term trend in accrual?	Ho_2: The implementation of the 142 m^3/s minimum flow release does not change the total biomass accrual rate of periphyton in the MCR.	Ho_2: This hypothesis is rejected but only under certain conditions. The implementation of minimum flows is most beneficial to the accrual rates of the area directly above or adjacent to the wetted edge at minimum flows. This is supported by peak production of periphyton occurring at the T2 and T3 samples from reduced mortality due to less exposure. However, the benefits of minimum flows on these areas are highly dependent on patterns in operating regimes, and seasonal and annual variations. The overall benefits of minimum flow are greatest during: • Periods of low ALR reservoir elevation, when backwatering does not cover substrates that would otherwise be exposed; • Periods of low daily flows (400 to 600 m^3/s) that exceed 12 hours with low humidity and >10-15°C or <0°C average daytime temperatures, particularly during extreme air temperatures. • During February-March, based on reach-wide model results.

CLBMON 15B Status of Objectives Management Questions and Hypotheses After Year 12			
Objectives	Management Questions	Management Hypotheses	Year 12 (2018) Status
		Ho_{2A}: There are no changes in accrual rates of periphyton at channel elevations that remain permanently wetted by minimum flow releases. Ho_{2B}: There are no changes in accrual rates of periphyton at channel elevations that are periodically dewatered during minimum flow releases.	Ho_{2A}: The hypothesis is accepted but only under certain physical conditions of the surrounding environment. Before the implementation of minimum flows, areas below the minimum flow line were usually dewatered at night for four to seven hours at a time. During periods that had moderate temperatures, rain, high humidity or ALR backwatering, the amount of periphyton loss in these periods was minimal, and accrual rates remain unchanged. However, dry weather in summer or winter caused higher death rates of periphyton that significantly reduced the periphyton accrual rate. Ho_{2B}: The hypothesis is rejected, but only under certain conditions. We conclude that minimum flows only benefit a small area of the varial zone that is located directly above the minimum flow line. Minimum flows result in higher daily average flows which cause the lower varial zone to undergo less substrate dewatering. Less substrate dewatering results in less periphyton mortality and lowers the accrual rate. During periods of ALR backwatering and higher rates of recovery such as fall, minimum flows are less beneficial to periphyton accrual rates in the area just above the minimum flow line.
	Q.4. What is the effect of implementing minimum flows on the total abundance, diversity and biomass of benthic organisms in the section of the MCR subjected to the influence of minimum flows? Is there a long term trend in benthic productivity?	Ho_{3A}: The implementation of the 142 m^3/s minimum flow release does not change the total abundance / biomass / diversity of benthic invertebrates in the MCR.	Ho_{3A}: The hypothesis is rejected, but only under certain operating conditions. Determining the benefits of minimum flows is challenging because there are many contributing but confounding physical factors, such as velocity, that are affected by flow regulation. Permanently submerged areas were the most productive and diverse, but frequently submerged varial zone areas also had comparable levels of productivity and diversity. Without any other operating constraints, minimum flows increased total abundance, biomass and diversity of benthic communities because they established a larger area of productive, permanently submerged habitat, that can donate taxa to the adjacent varial zone. Diversity among fish food components of the MCR benthic community was dominated by Dipterans with fewer Ephemeroptera, Trichoptera, Plecoptera (EPT), as is common below hydropeaking facilities. Community structure was generally similar pre and post implementation of minimum flows, with similar taxonomic representation that varied annually. Invertebrate diversity was slightly lower pre-implementation of minimum flows. Life history strategies of different benthic invertebrates or periphyton species may also act as limiting factors. The area of productive invertebrate habitat occurred from the permanently wetted mid channel areas to an upper edge that had high average daily submergence (i.e., greater than 9 to 10 hours of daytime submergence and only brief exposures periods during cool, moist air conditions). The wetted history was the most important determinant

CLBMON 15B Status of Objectives Management Questions and Hypotheses After Year 12			
Objectives	Management Questions	Management Hypotheses	Year 12 (2018) Status
		$Ho_{3B:}$ There are no changes in abundance/biomass/diversity of benthic invertebrates at channel elevations that remain permanently wetted by minimum flow releases. $Ho_{3C:}$ There are no changes in abundance/biomass/diversity of benthic invertebrates at channel elevations that are periodically dewatered by minimum flow releases.	of this edge, and influenced the total abundance, biomass, and benthic diversity in areas exposed during operations. $Ho_{3B:}$ The hypothesis is accepted. We conclude that minimum flows have not affected abundance/biomass/diversity in permanently wetted areas. Benthic abundance and biomass did not appear to vary pre and post minimum flows in permanently wetted areas. However, our data indicate that other aspects of operation, such as high peak flows may be important determinants of invertebrate production in R4 through mechanisms driven by water velocity. All aspects of flow regulation are important and must be considered in conjunction with minimum flows to understand habitat structure and community diversity, total abundance and biomass in the MCR. $Ho_{3C:}$: The hypothesis is accepted, but only under certain operating conditions. We conclude that minimum flows do not affect invertebrate biomass, abundance or diversity in the periodically dewatered varial zone above the minimum flow elevation. However, there was likely increased benthic invertebrate abundance, diversity, and biomass in areas where minimum flows increased the wetted habitat available. Submergence was the most important determinant of abundance, biomass, and fish forage (EPT+D). Diversity of invertebrates appeared to be less dependent on minimum flows than abundance or biomass. Daytime submergence, velocity, seasonal patterns and historical operating cycles were also important determinants of benthic productivity and should be considered.
	Q5. If changes in the benthic community associated with minimum flow releases are detected, what effect can be inferred on juvenile or adult life stages of fishes?	Ho_4: The implementation of the 142 m^3/s minimum flow release does not change the availability of fish food organisms in the Middle Columbia.	Ho_4: This hypothesis is rejected, but only under certain operating conditions. Food for fish was assessed using a Fish Food Index (FFI) in 2013 and consisted of three parameters for each benthic taxon, 1) invertebrate abundance, 2) relative invertebrate biomass, and 3) fish food preference for a given benthic taxon. The total biomass of EPT and Dipteran taxa is the current metric being utilized to summarize fish forage availability, which is simplistic and does not account for key factors such as propensity to enter drift. These benthic invertebrates are commonly accepted as important fish forage. Reach-wide estimates indicate that fish forage is greatest in September. The overall benefits of minimum flow are greatest under the following conditions: • Periods of low daily flows that exceed 24 hours with freezing or high average daytime temperatures; • Dewatering periods greater than 12 hours. Substrates submerged for 450 to 500 hours (10 to 11 hours per day over approximately 45 days) during daytime hours had the greatest availability of preferred fish food items - the EPT and Diptera. EPT and Dipteran biomass was greatest in areas submerged for at least 750 to 1000 hours over at least 46 days. Both periphyton and invertebrates showed similar responses, suggesting that overall productivity and food for fish is directly affected by the operational cycles that create either submerged or exposed substrates, where increased periods of submergence result in an overall increase in benthic productivity. In addition to the area wetted by minimum flows

CLBMON 15B Status of Objectives Management Questions and Hypotheses After Year 12			
Objectives	Management Questions	Management Hypotheses	Year 12 (2018) Status
			acting as a species reservoir, tributaries including the Jordan River may be important donors of invertebrate species utilized by fish and these donations would assist with MCR recovery from exposure events.

EXECUTIVE SUMMARY

Aquatic habitats in the Middle Columbia River (MCR) are strongly influenced by operational releases from Revelstoke Reservoir. To lessen the effect of these variable flow releases, the Columbia River Water Use Plan supported implementation of a year-round minimum flow of 142 m^3/s from Revelstoke Dam (REV) to MCR. One objective of the minimum flow strategy is to enhance MCR benthic productivity and diversity to increase food for fish by expanding the permanently wetted river bed area by 32 -37 %.

CLBMON-15b Ecological Productivity Monitoring provides long-term data on MCR benthic productivity to assess the influences of a minimum flow operating regime. The pre-implementation study period considered fall 2007 to 2010 and the post implementation study period considers fall 2011 to 2014 and spring 2011 to 2018. Concurrent with the implementation of minimum flows, a fifth generating unit (REV 5) was added in December 2010, increasing the maximum flow discharge from 1699 to 2124 m^3/s. Separating the benefits of minimum flows from those of increased submergence from the recent operating regimes was difficult. This report summarizes the findings of all study sessions to date, with a focus on spring 2018 sampling. It also covers 2018 study developments including: determining if light is a limiting factor; greater consideration of velocity in MCR and on further development of a reach-wide productivity model to estimate the area and total production of the MCR.

Habitat conditions in the MCR were divided into three distinct zones of varying submergence - the permanently wetted zone, the lower varial zone and the upper varial zone. The **permanently wetted zone** is the thalweg area covered by minimum flows. It showed high periphyton and invertebrate productivity and rapid accrual rates despite periodic thinning by high water velocities. Immediately above the minimum flow elevation was the most productive zone**, the lower varial zone** that can extend to higher channel elevations during longer periods of flows exceeding 600 - 800 m^3/s. **The upper varial zone** was the least productive, located at elevations that were frequently dewatered. Over the 12 years of study, the boundaries between these three zones have shifted in response to growth conditions created by the operational flow releases over the preceding 30 to 70 days. Flows during the week preceding sample collection had the greatest effect on benthic productivity and species composition results.

Overall benthic community structure was stable at the family taxonomic level across all sites of variable submergence, with similar representation between years. However, some taxonomic differences occurred in the three zones. For example, filamentous green algae were more prevalent near the edge of permanently wetted areas (T2), and in the lower varial zone (T3/T4) where stable substrates and lower velocities were present. EPT (Ephemeroptera, Plecoptera and Trichoptera) taxa and chironomids were more abundant along the edge of minimum flow (T2) or in the lower varial zone (T3) (Schleppe et al. 2014). For both periphyton and invertebrates, productivity was greatest within the lower varial zone at mid-channel elevations extending from just below the elevation of minimum flow to slightly above it. Like all large rivers, diatoms dominated the periphyton, but diversity was lower than in unregulated rivers of similar size and latitude. Chironomidae were the prevalent fish food item, with fewer EPT taxa than in unregulated rivers, particularly in Reach 4 (closer to the dam). These data support the assertion that flow management exerts a powerful influence on the MCR periphyton and invertebrate community.

Daytime submergence and high average daily flows were key factors in determining overall MCR benthic productivity. Primary algal productivity in varial zone areas submerged for at least 9 to 12 daytime hours per day (400 to 500 hours over the deployment period) were usually as productive as areas constantly submerged by minimum flows. Results from previous years showed substrates

submerged for 10-11 daytime hours/day had the most preferred fish food items, which include EPT and Dipteran taxa. Similarly, the biomass of EPT+Dipterans was greatest in areas submerged for 750 - 1000 hours over the previous 46 days. Increased productivity was observed when submergence times in excess of 1000 hrs over the deployment period (1056 hours on average) were sampled. Peak production of either benthic invertebrates or periphyton in the MCR was not achieved within two months from the time of first wetting and may take longer than six months to fully develop if sites experience frequent dewatering. Benthic invertebrates were more sensitive to exposure than periphyton. Dewatering periods greater than 24 hours during warmer air temperatures caused substantial stresses and die-off in the invertebrate community. For periphyton, exposures exceeding 36-48 hours were usually required before similar losses were observed. Mortality from exposure of either invertebrates or periphyton was dependent upon weather patterns at the time of the event.

Minimum flows benefit productivity most during periods when average daytime flows over the preceding 30 to 70 days are lower (e.g., 400 to 600 m^3/s versus 1200 to 1600 m^3/s), and when periods of exposure were common. A small shift in water releases would increase the area of productive habitat and could occur under an operating regime that included brief excursions to <10 m^3/s flow, provided that flows of 400 to 600 m^3/s occurred every day for at least 9 to 12 daytime hours, and these periods of exposure occurred during cool, moist weather.

Benthic and algal productivity in the permanently submerged and lower varial zones were influenced by physical parameters such as velocity, water temperature, substrate conditions, reservoir/river donations, and by natural annual variability. MCR water temperatures were affected by the water temperature of Revelstoke Reservoir that strongly influenced periphyton production in spring. Warmer spring water temperatures resulted in more chl-a and more of the small low-profile algal taxa. The establishment of large high-profile algae was facilitated by cooler spring water temperatures and lower maximum flows.

Development of a reach-wide model of MCR productivity commenced in 2017. It uses a previously developed hydraulic model (Telemac-2D) to determine the wetted habitat area at a reach-wide scale. The reach-wide productivity (RWP) model assumed that periphyton and invertebrate productivity were a function of the wetted history only, since substrate submergence was consistently identified as the key parameter controlling invertebrate and periphyton production in the MCR. The modeled RWP estimates have large uncertainties and are only useful for comparison of flow scenarios such as minimum flow to answer management questions but are not suited for determining reach-wide productivity estimates with high degrees of accuracy.

Model validation and improvement of growth curves occurred in 2018, by incorporating refined periphyton growth curves. The spring and fall growth curves for chl-a were modified using weekly sampled Reach 4 time series data to determine MCR hourly reach-wide productivity over the study duration. The reach-wide model confirmed that the effects of minimum flow on MCR productivity are most apparent in Reaches 3 and 4 between February and March when ALR backwatering does not occur.

As expected, model validation of the RWP model using the spring 2018 data confirmed that its output does not accurately predict chl-a and invertebrate biomass data at individual transects. However, the modelled chl-a for the T6 samplers (shallow upper varial zone) was accurate, suggesting that while growth curves can be improved, the chl-a mortality curves were suitable for MCR. The invertebrate biomass model underestimated the productivity of 2018 samplers in the upper varial zone. This is because the invertebrate death curve was estimated from Trichoptera and Simuliidae taxa which were the only taxa that had death curves available and these taxa are more vulnerable to desiccation than the dominant taxa in MCR, resulting in a curve that was too steep for the broad array of invertebrate taxa observed in the MCR

Further investigation of the effects of velocity, light, and water temperature were undertaken in 2018 to determine if additional physical parameters could improve the accuracy of the reach-wide productivity model and improve our ability to answer the management questions. Sampler-specific velocity and flow relationships were derived from hourly data that were extracted from hydraulic models. The affect of maximum velocities was tested on periphtyon and invertebrate productivity metrics. Maximum velocities only reduced periphyton biovolumes in R4 areas near the thalweg but had no detectable effect on chl-a. Invertebrate abundance was lower at sites with higher maximum velocities. However, there was no detectable effect of maximum velocity on invertebrate biomass. Analyses indicated that the MCR is not light limited because there was enough light penetration for periphyton production during all flows. Warmer spring water temperatures were important in explaining the variability of chl-a in R3 and R4.

The inclusion of light and velocity will likely not improve the reach-wide productivity model, nor improve their ability to address questions around minimum flows. Although maximum velocity was an important predictor of invertebrate production and periphyton biovolume in the R4 samples, the velocities were not high enough to cause shearing of high profile periphyton taxa and to lower chl-a. Coupled with this, velocity added significant computational overhead. spring water temperatures would likely increase the accuracy of the reach-wide chl-a model. However, parametizing water temperature into the reach-wide productivity model would be complex and spring water temperatures are independent of minimum flows.

In summary, in the absence of other operating constraints, minimum flows benefit the benthic productivity in the MCR, but alternative operating regimes that have higher average daily flows without permanent minimum flows may also provide habitat conditions that could be equally productive. Substrate submergence was consistently identified as the single most important determinant of MCR benthic production. however, factors including ALR backwatering, operational flow patterns, velocities (e.g., during peak flows exceeding 1800 m^3/s), seasonal cycles, as well as species tolerances and life history are all important determinants of benthic productivity and should be considered when reviewing future operational flow regime guidelines.

TABLE OF CONTENTS

FIGURES

TABLES

APPENDICES

1.0 INTRODUCTION

Aquatic habitats in the Middle Columbia River (MCR) are heavily influenced by variable flow releases from the Revelstoke Dam (REV), and from backwatering of Arrow Lakes Reservoir (ALR) and to a lesser extent, tributary inflows. Introduction of the Columbia River Water Use Plan (WUP) in 2007 supported implementation of a year-round minimum flow from REV of 142 m^3/s to mitigate the effects of variable flow releases. In December 2010, BC Hydro (BCH) added a fifth generating unit (REV 5) that increased the maximum possible flow discharge of REV from 1699 to 2124 m^3/s.

One component of the WUP involved assessing how the productivity and diversity of benthic communities would change from the implementation of a minimum flow operating regime. It hypothesized that an increase in the area of permanently wetted channel downstream of the Revelstoke Dam would result in increased benthic production, thereby increasing food availability for fish and ultimately improving fish abundance (WUP, BC Hydro 2005).

CLBMON-15b Ecological Productivity Monitoring forms one component of a broader monitoring project under the Revelstoke Flow Management Program, designed to assess the effectiveness of minimum flows at improving habitat conditions for fish. The monitoring schedule consists of four years of monitoring before implementation of minimum flow / REV 5 operations (2007-2010), and up to ten years of subsequent monitoring under the new operating regime.

In the study years prior to the implementation of minimum flows, water releases from Revelstoke Dam varied from 8.5 m^3/s to 1700 m^3/s, depending on power demands, and could result in sudden water fluctuations between 3 to 5 vertical meters. With the initiation of REV 5 and the minimum flows operating regime (2011-present), flows have ranged from 142 m^3/s to 2124 m^3/s. These variable water releases and backwatering from the downstream ALR determine the extent of submergence of river substrates in the MCR.

The results from the Ecological Productivity Monitoring will be integrated with other BC Hydro monitoring programs, including Physical Habitat Monitoring (CLBMON15a), Fish Population Indexing Surveys (CLBMON16), Juvenile Habitat Use (CLBMON17) and Adult Habitat Use (CLBMON18). The findings from these monitoring programs will be used collectively to evaluate the benefits of minimum flows for fish, and if there is an advantage to establishing a long-term minimum operating release requirement for Revelstoke Dam. Data collected in CLBMON15b will serve to quantify long-term productivity trends for periphyton and benthic invertebrates and will provide valuable information on the ecological health of the riverine environment downstream of Revelstoke Dam.

This report summarizes Years 1 through 12 of the monitoring program and focuses on the spring 2018 (Year 12) sampling session. There is one year (2020) remaining in this program. The project is transitioning from understanding the effects of substrate submergence, including minimum flows, and important environmental factors (e.g., velocity, light, and depth), to understanding the spatial effects of the operating regime on productivity.

1.1 Objectives, Questions, and Hypotheses

The three main objectives of the Ecological Productivity Monitoring program are as follows (BC Hydro 2010):

- To design and implement a long-term program for tracking the productivity and diversity of key benthic community taxa (periphyton and invertebrates) within the MCR;
- To assess the response of the MCR benthic community taxa, both periphyton and invertebrates, to a minimum flow release from Revelstoke Dam and REV 5 operations; and
- To investigate and quantify the relationship between habitat attributes and benthic composition, abundance, and biomass within the section of the MCR most likely to be influenced by minimum flows and REV 5 operations.

The first objective was satisfied by the basic study design developed by Perrin et al. (2004). A conceptual model was developed (Figure 1-1) to address the second and third objectives, and to understand the potential interactions of the factors affected by changes in flow. With each study session, our understanding of the relative importance and role of each parameter increases. This conceptual model highlights the many variables and complex interactions that can influence benthic productivity and ultimately food for fish. Greyed boxes with bolded text in the conceptual model indicate the parameters under assessment in this study. At the forefront of the concept model are BC Hydro operations that determine quantity and duration of water release. Flows directly influence factors including velocity, turbulence, depth, submergence, scour, etc. and therefore have a direct effect on benthic productivity.

This conceptual model does not consider species-specific life histories. For example, hydropeaking systems with variable flows can influence species with a specific diurnal timing and habitat selection for egg laying (Kennedy et al. 2016). Species-specific responses increase the complexity of interactions, particularly with flow, and are beyond the bounds explored in this project.

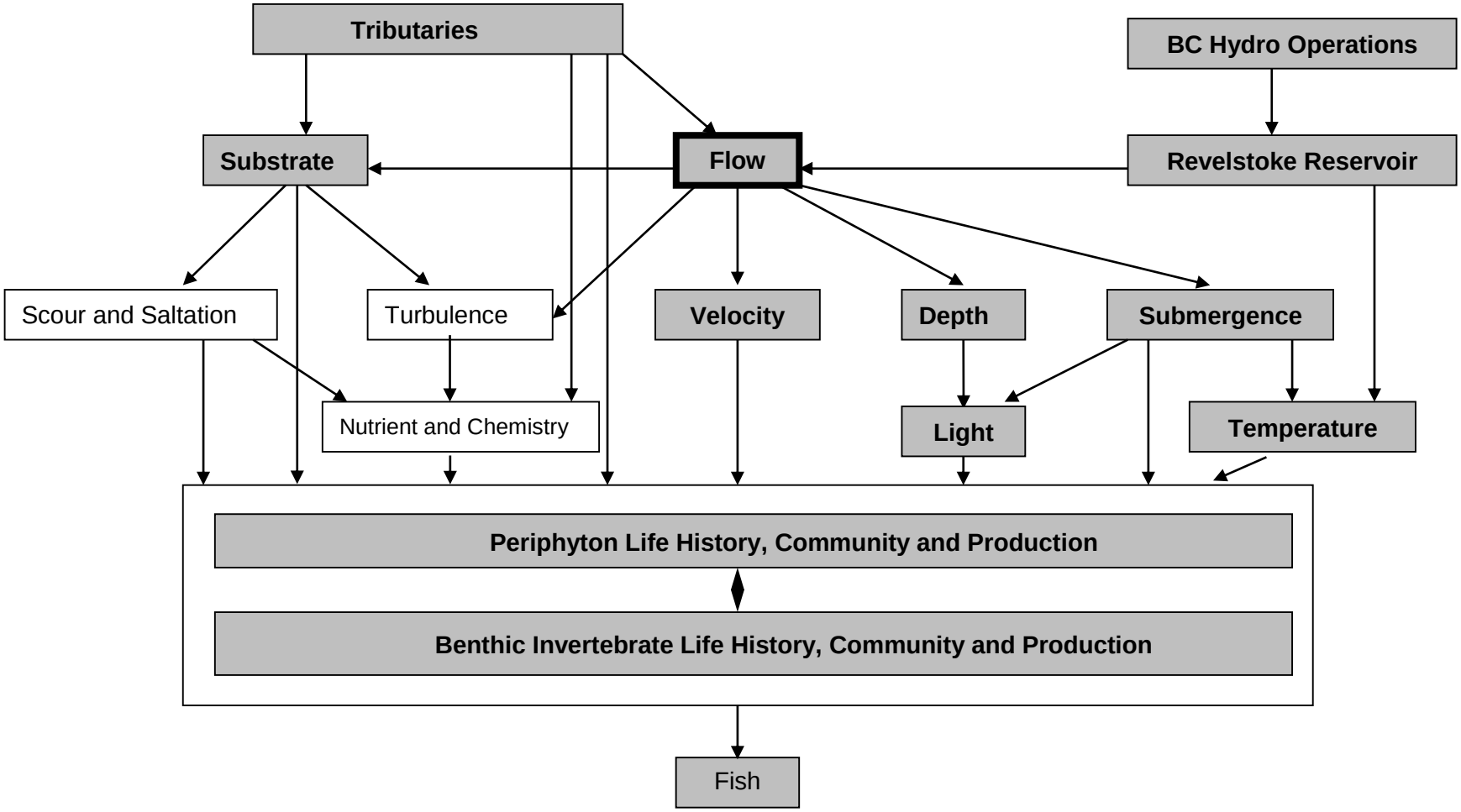


Figure 1-1: Conceptual interactions model of habitat variables and benthic production as they relate to food for fish in MCR. Parameters shaded in grey, with bolded text represent parameters under assessment in this study.

BC Hydro developed five management questions with related hypotheses to address the three main objectives (BC Hydro 2010). Table 1-1 lists each of the management questions/hypotheses and relevant components of this study that address them. Although several of the hypotheses/questions refer to the implementation of the minimum flow release, we understand as per the Request for Proposals, that the evaluation of minimum flow release is to include the operational changes associated with the commencement of REV 5 operations.

In this study, statistical models were used to understand the physical responses of periphyton and benthic productivity to flows. In a complex system like MCR, the effects of minimum flows and REV 5 flows could not be isolated from each other or the larger flow regime. In lieu of this approach, we identified relationships between benthic production and spatial features directly influenced by flows including area of wetted habitat, and frequency and duration of submergence. From this, we were able to infer the effects of the operating regime including minimum flows. This approach is advantageous because it allows consideration of alternative operating regimes that may be as, or more, beneficial than minimum flow from both a productivity and a financial perspective. The overaching project goal is to enable estimation of the spatial area of productive habitat in the MCR under a minimum flow or alternative operating regime. The ultimate goal is to identify and describe what habitat attributes are most influential and to identify how implementation of different operational regimes affect benthic productivity in the MCR including both a minimum flow and a REV 5 operating regime.

Table 1-1: Key Management Questions and Hypotheses, with Pertinent Components to Address Them

Key Management Questions	Management Hypotheses:	Study Components to Address Management Questions/Hypotheses
Q1. What is the composition, distribution, abundance and biomass of periphyton and benthic invertebrates in the section of MCR subjected to the influence of minimum flows? Q2. What is the effect of implementing minimum flows on the area of productive benthic habitat?	Ho_1. The implementation of the 142 m3/s minimum flow release does not change the composition, distribution, abundance, biomass, or spatial area of productive benthic habitat for periphyton or benthic invertebrates in MCR.	Artificial sampler arrays are deployed across the range of flows/elevations of the MCR. Data collection includes: • Abundance –periphyton & invertebrates • Diversity – taxonomy indices for periphyton and invertebrates • Production/Biomass – chlorophyll-a (chl-a), ash-free dry weight (AFDW)/dry weight (DW), biovolume, benthic invertebrate biomass • Natural substrate comparisons Productive habitat area is considered using the analogous measure submergence as a surrogate for minimum flow. Reach-wide productivity models were used to model periphyton chl-a and invertebrate biomass based on hourly submergence and exposure. The submergence and exposure were determined using a hydrological model. Daily productivity estimates from the models were compared before and after the implementation of minimum flows for Reach 3 and 4.
Q3. What is the effect of implementing minimum flows on the accrual rate of periphyton biomass in the MCR? Is there a long-term trend in accrual?	Ho_2. The implementation of the 142 m3/s minimum flow release does not change the total biomass accrual rate of periphyton in MCR. Ho_{2A}. There are no changes in accrual rates of periphyton at channel elevations that remain permanently wetted by minimum flow releases. Ho_{2B}. There are no changes in accrual rates of periphyton at channel elevations that are periodically dewatered by minimum flow releases.	Artificial samplers and time series samplers are deployed across the range of submerged habitat areas on the MCR. Data collection includes: • Abundance • Diversity – taxonomy indices for periphyton and invertebrates • Production/Biomass – chl-a, AFDW/DW, biovolume • Nano-flora heterotrophic plate counts (HTPC) Periphyton production (both accrual and peak biomass) are assessed using a variety of different measures of productivity. Periphyton productivity is considered using the analogous measure submergence as a surrogate for minimum flows because this data is easier to use in models. Periphyton models are developed to test the effects of submergence on periphyton peak biomass.
Q4. What is the effect of implementing minimum flows on the total abundance, diversity and biomass of benthic organisms in the section of MCR subjected to the influence of minimum flows? Is there a long-term trend in benthic productivity?	Ho_3. The implementation of the 142 m3/s minimum flow release does not change the total abundance/biomass/diversity of benthic invertebrates in MCR. Ho_{3A}. There are no changes in abundance/biomass/diversity of benthic invertebrates at channel elevations that remain permanently wetted by minimum flow releases. Ho_{3B}. There are no changes in abundance/biomass/diversity of benthic invertebrates at channel elevations that are periodically dewatered by minimum flow releases.	Artificial samplers are deployed across the range of submerged habitat areas on the MCR. Data collection includes: • Abundance • Diversity – taxonomy indices for periphyton and invertebrates • Production/Biomass – biomass Invertebrate production is assessed using a variety of different measures of productivity. Benthic productivity is considered using the analogous measure submergence as a surrogate for minimum flows because this data is easier to use in models. Invertebrate models are developed that test the effects of submergence on invertebrate biomass, abundance, and diversity.

Q5. If changes in the benthic community associated with minimum flow releases are detected, what effect can be inferred on juvenile or adult life stages of fishes?	Ho_4. The implementation of the 142 m3/s minimum flow release does not change the availability of fish food organisms in the Middle Columbia.	Potential effects of minimum flow on food for fish are considered using an index of fish food availability. The Fish Food Index (FFI) consists of three parameters, Relative Abundance, Relative Biomass, and Fish Food Preference for each different benthic taxon. Higher index values indicate a higher prevalence of preferred benthic species available as food for fish. This index is useful because it considers availability (abundance), biomass, and fish preference of benthic invertebrates as food. The fish food index is used in statistical models where a variety of measures of submergence (analogous to minimum flow) are used to test fish food availability.

2.0 METHODS

2.1 Study Area and Sampling Locations

The MCR is a section of the Upper Columbia River adjacent to the town of Revelstoke, British Columbia, encompassing approximately 38.5 km of river between the Revelstoke Dam and the Upper Arrow Lake Reservoir (ALR) near Shelter Bay. The MCR is sectioned into four Reaches, and this study focused on riverine Reaches 4 and 3, and did not consider lentic Reaches 2 and 1. Reach 4 extends approximately 5 km from the Revelstoke Dam to the confluence of the Jordan River. Reach 3 starts at the confluence of the Jordan River and extends approximately 3.5 km downstream to the confluence with the Illecillewaet River (Figure 2-1).

Reach 4 is characterized by a trapezoidal river channel with moderate to steep banks that confine the thalweg. The depth along the thalweg ranges from 1 to 5 m depending on flows. Reach 4 encompasses large areas of stable substrate consisting predominantly of larger gravels, cobble and boulder, and lesser amounts of sands, pebbles and smaller gravels that occur beneath and within the interstitial spaces of the cobble-armoured surface. The bankfull width in Reach 4 ranges from 147 – 223 m (Perrin and Chapman 2010a). Big Eddy occurs at the interface of Reaches 4 and 3, immediately downstream of the Jordan River. It consists of a large, 250 m wide, deep eddy bounded along the right bank by a vertical rock face. This habitat unit provides > 6 m deep water refuge during periods of lower flow and could be considered its own reach with the unique habitat it provides.

Upper Reach 3 starts immediately below Big Eddy, where the river turns 120° and the channel thalweg occurs on the left bank with a floodplain area on the right bank. The right riverbed is flat with gravel substrates and has a bankfull width of approximately 360 m. Further downstream, the 2 to 8 m deep thalweg occurs in the center of the channel and substrates become progressively finer and more mobile. The lower section of Reach 3 extends below the bridges, and the side-braided channels can become exposed when the water elevation in the ALR is <434 m and discharge from the Revelstoke Dam is minimal. The main channel bankfull width of Reach 3 is 489 m (Perrin and Chapman 2010a). Substrates in Reach 3 are finer than Reach 4 with sand, gravel and cobbles predominating throughout the reach.

The main tributaries that influence the MCR are the Jordan and Illecillewaet rivers (Figure 2-1). The Illecillewaet River is the largest tributary in the study area of MCR. The lower Illecillewaet receives secondary treated sewage effluent from the City of Revelstoke.

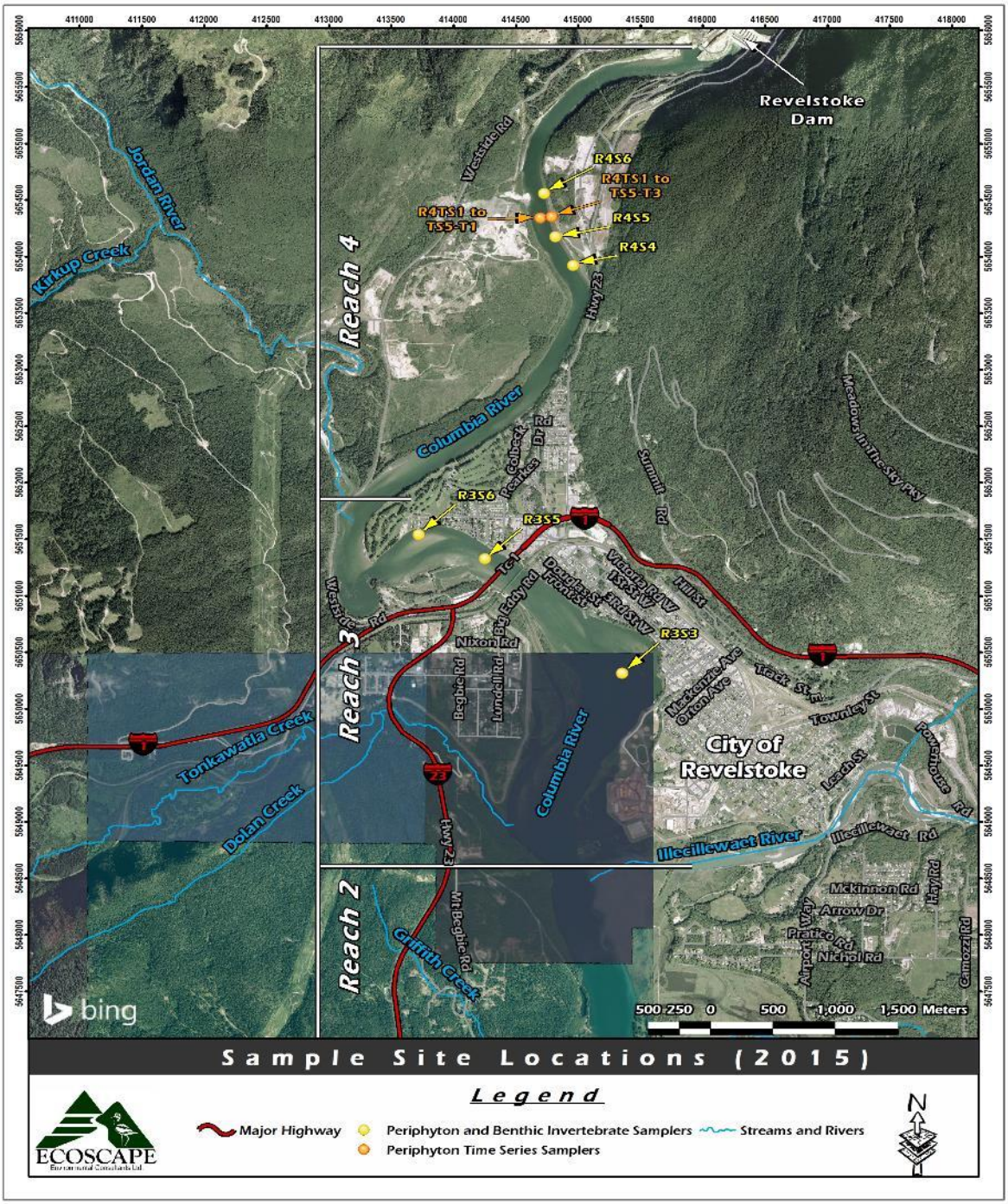


Figure 2-1: Map of the study area and sampling locations. Site labels are defined in Table 2-2. R = reach, S = site, T= transect, TSS=Time Series Sampler.

2.2 Periphyton and Invertebrate Community Sampling Using Artificial Samplers

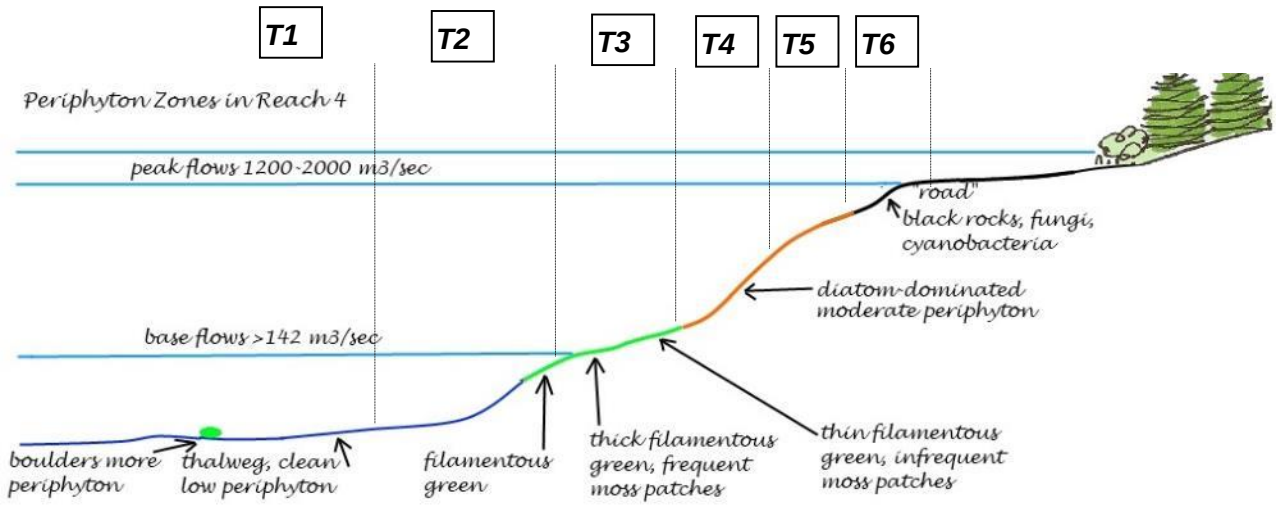
2.2.1 Artificial Sampler Design and Deployment

Year 12 of the CLBMON 15-b study involved a spring 2018 sampling session, where artificial samplers were placed in the river and left for a minimum of 43 days (Table 2-1). Data for earlier years are available in previous CLBMON15b reports. The sample sites used in 2018 were consistent with previous years, and the same naming system was used to reference sampling sites. Site references include Reach, Site, and Transect. Samplers were deployed in Reach 3 (R3) at S3, S5, and S6. Reach 4 (R4) samplers were deployed at sites S4, S5, and S6.

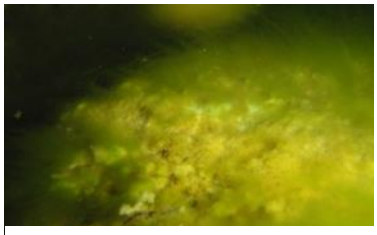
Sampling sites at transect depths T1 through T6 were deployed in R3 and R4 as shown in Figures 2-2 and 2-3. Transect position refers to the position of the sampler within the river cross-section, as explained in Table 2-1. During the fall 2010 sampling session, a T7 position in the infrequently wetted floodplain was also used. This sampler elevation was subsequently deleted, and new sampling sites in R4 at the bedrock (BR) location were studied instead. However, in spring 2018 Big Eddy (BE), bedrock (BR), and backwater areas (BW) sites were not sampled.

Table 2-1: Description of transect depths sampled in Reach 3 and 4.

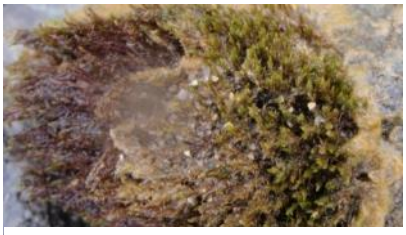
Reach	Sampler	Relative depth/zone	Submergence	Years Sampled
3 and 4	T1	Mid channel / thalweg	Permanently submerged by minimum flows	2010-2018
	T2			2010-2018
	T3	Mid channel / lower varial zone	Submerged by flows from 200 to 800 cm/s	2010-2018
	T4			2010-2018
	T5	Upper varial zone	Submerged by flows > 1000 cm/s	2010-2018
	T6			2010-2018
	T7	Infrequently wetted floodplain		2010



thalweg
(low periphyton



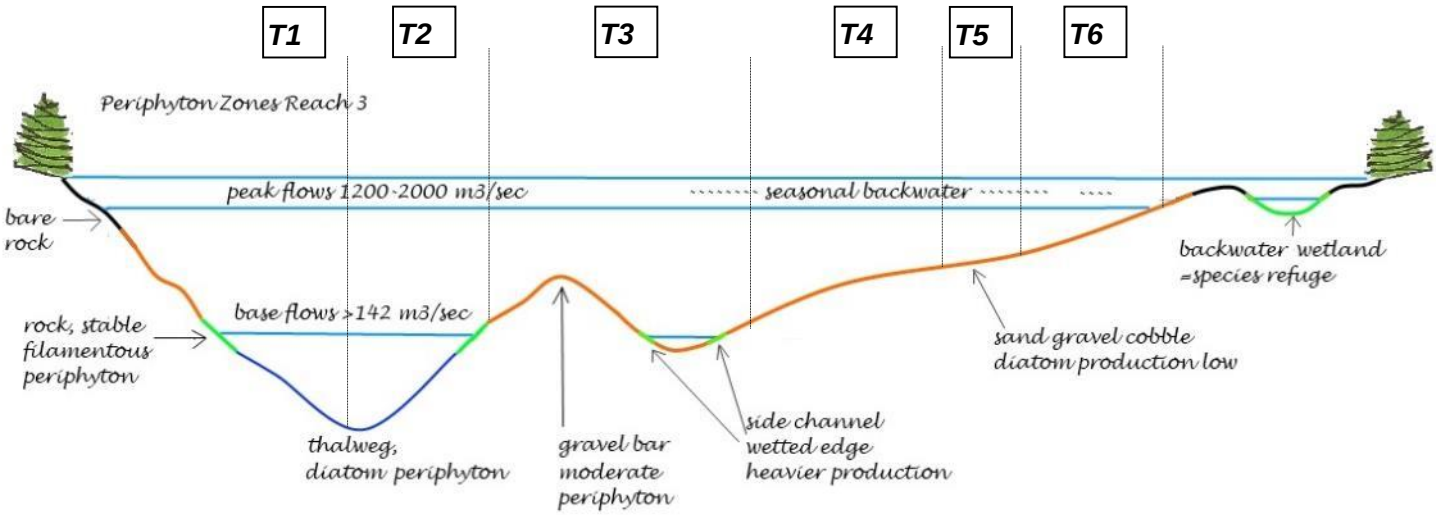
filamentous green zone



filamentous green + moss zone

diatom dominated zone

Figure 2-2: Conceptual drawing of transect positions and periphyton establishment in MCR using data collected from fall 2010 and 2012 in R4.



filamentous green+, sand

thalweg, diatom periphyton

wetted edge heavy diatom zone

low diatom, bacteria zone

Figure 2-3: Conceptual drawing of periphyton establishment in MCR using data collected from fall 2010 and 2011 samples in R3.

Samplers and associated rigging were assembled and deployed April 10-11, 2018 (Table 2-2). One day was spent preparing gear, followed by deployments in both R4 and R3 when flows were minimal to moderate. Figure 2-4 illustrates our standard artificial sampler design that was identical to previous years. Time series samplers were modified with a concrete weight 10 m from the sampler and float attached to the rear of the plate using rope rather than the sampler anchor. At the time of deployment, the elevation and location of each artificial sampler was recorded using a Trimble R8 RTK survey system, using Survey Controller software for data collection to obtain the geodetic elevation of each sampler.

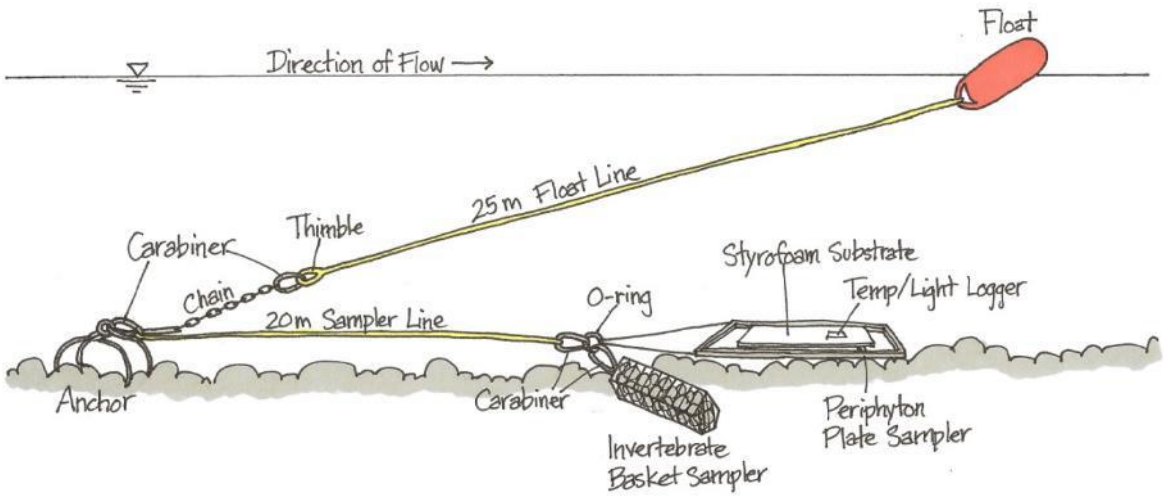


Figure 2-4: Schematic drawing of the artificial substrate sampler used in MCR.

Table 2.2: Summary of artificial sampler deployment, retrieval and sampling in 2018

Season	Reach	Site	Periphyton Samplers		Invertebrate Basket Samplers	
Spring (Apr 10 – May 25 2018)	Reach 4 (R4)	Site 6 (S6)	6	6 (100)[1]	6	5 (83)
		Site 5 (S5)	6	6 (100)	6	6 (100)
		Site 4 (S4)	5	6 (100)	5	4 (67)
	Reach 3 (R3)	Site 6 (S6)	6	6 (100)	6	6 (100)
		Site 5 (S5)	4	4 (67)	4	4 (67)
		Site 3 (S3)	6	6 (100)	6	6 (100)
2018 Totals			**60**	**34 (94.5)**	**60**	**31 (86)**

Notes: [1]The success of weekly retrieval of time series samplers was dependent on flow conditions. Some weekly Styrofoam punches were not taken due to high flows, or the inability to pull plates. The number retrieved reflects the samplers pulled on the final time series trip.

2.2.2 Artificial Sampler Retrieval

Artificial samplers remained in the river for a total of 43-44 consecutive days in spring 2018. This deployment period matches earlier MCR deployments and is within the incubation period required for attainment of peak biomass defined by Perrin et al. (2004). Spring samplers were retrieved either by boat, wading or by foot on May 23-24, 2018.

Four Styrofoam punches were randomly collected from each sampler to assess the following metrics:

1) Chlorophyll-a to give an estimate of live autotrophic biomass;
2) Ash-Free Dry Weight (volatile solids) / total dry weight to give an estimate of the carbon component (Stockner and Armstrong, 1971);
3) Taxa and biovolume to give an accurate estimate of live and dead standing crop (Wetzel and Likens, 1991); and
4) A second sample was frozen as back-up, in case a sample was damaged.

At the time of collection, Styrofoam punches were placed in pre-labeled containers and stored on ice in the dark until further processing.

Benthic invertebrate baskets were retrieved similar to previous years following guidelines developed by Perrin et al. (2004). A 250 µm mesh net was placed beneath baskets while still in the water column to collect any invertebrates that could have been lost as baskets were lifted from the water. The net was inverted and contents were rinsed into a labeled bucket with pre-filtered river water. The retrieved baskets were placed immediately in the labeled buckets until further field processing. Use of the net was conditional on safety of the crew and was not used when water velocity was high and the ability to safely retrieve the sampler was difficult.

Upon completion of sampler retrievals from each site, individual rocks from each basket were scrubbed with a soft brush to release clinging invertebrates. Washed rocks were then rinsed in the sample water before being placed back in the basket and stored for re-use in future years. The contents from each bucket were then captured on a 100 µm sieve, rinsed into pre-labeled containers and preserved in alcohol for analysis.

2.2.3 Time Series Samplers

The purpose of time series collections is to understand the rates of periphyton accrual and to detect differences that may exist between permanently submerged areas and periodically dewatered areas within the varial zone. Time series samplers were retrieved once per week following deployment, as opposed to sampling once at retrieval. Artificial substrate time series samplers were deployed across the river at transect positions from T1 through T7 in 2010. In these positions, observed accrual rates were very complex in response to rapid flow changes, weather during dewatered periods, and varying degrees of exposure. Subsequent effort was focussed in two key areas to develop better statistical models: the deep area permanently wetted by minimum flows (T1) and the lower varial zone (T3/T4), located above the permanently wetted edge. In spring 2018, five time-series samplers were deployed in R4 in both T1 and T3/T4 transect positions. T3 and T4 time series samplers represent the conditions of the varial zone because samplers cannot be accurately placed, retrieved and re-deployed at the same location/depth during sample collection in MCR's

swift water. These time series samples are therefore considered representative of accrual in the varial zone rather than accrual at a discrete sampling location.

During each weekly sample, the light/temp loggers were wiped clean with a paper towel so light measurements were accurate during time series sampling. Every week, two periphyton punches were randomly collected from the Styrofoam and were immediately packed on ice and placed in the dark until they could be delivered to Caro Labs Kelowna for chlorophyll-a analysis. Taxonomy of time series samples has not been conducted since 2013.

2.2.4 Post Processing of Periphyton Samples

Four Styrofoam punches were obtained from each artificial substrate. One 6.6 cm^2 punch was frozen and delivered to Caro Analytical Labs in Kelowna, BC, for the processing of low-detection limit fluorometric chl-a analysis. A larger 56.7 cm^2 punch was chilled and transferred to Caro Labs in Kelowna, BC for analysis of dry weight and ash free dry weight. The remaining 6.6 cm^2 punches were used for taxonomic identification that was completed by H. Larratt, with initial QA/QC and taxonomic verifications provided by Dr. J. Stockner. Fresh, chilled samples were examined within 48-hrs for protozoa and other microflora that are difficult to identify from preserved samples. The final punch was preserved using Lugol's solution and was stored until taxonomic identification and biovolume measurements could be taken. Species cell density and total biovolume were recorded for each sample. A photograph archive was compiled from MCR samples. Detailed protocols on periphyton laboratory processing are available from Larratt Aquatic.

2.2.5 Post Processing of Invertebrate Samples

Following retrieval, fixed benthic invertebrate samples were transported to Cordillera Consulting in Summerland, BC. Samples were sorted and identified to the genus-species level where possible. Benthic invertebrate identification and biomass calculations followed standard procedures. Briefly, field samples had organic portions removed and rough estimates of invertebrate density were calculated to determine if sub-sampling was required. After samples were sorted, all macro invertebrates were identified to species and all micro portions were identified following The Standard Taxonomic Effort lists compiled by the Xerces Society for Invertebrate Conservation for the Pacific Northwest (Richards and Rogers 2011). A reference sample was kept for each unique taxon found. A sampling efficiency of 90% was used for benthic invertebrate identification and was determined through independent sampling. Numerous identification keys were referenced in the identification of benthic invertebrate taxa and a partial list of references is provided in Schleppe et al. (2012). Species abundance and biomass were determined for each sample. Biomass estimates were completed using standard regression from Benke et al. (1999) for invertebrates and Smock (1980) for Oligochaetes. If samples were large, subsamples were processed following similar methods. Detailed protocols on invertebrate laboratory processing are available from Cordillera Consulting.

2.3 Variable Descriptions and Analytical Methods

2.3.1 Determination of Submergence

For 2018 spring data, modelled water depths from the hydraulic river model, and water and air temperature data obtained from the HOBO light/temperature loggers were used to determine how long an artificial sampler was submerged. Two HOBO light/temperature loggers were placed in the upland areas above the high water level within R4 and R3 to measure air temperature. Similar to Schleppe et al. (2011), a script that considered a temperature difference of ± 0.5ºC was used to compare samplers from permanently submerged locations with samplers across a transect. A sampler was considered exposed to air when the logger temperature differed from the permanently submerged logger by more than ±0.5ºC. In addition, samplers that had a modelled water depth less than 0.1 m were considered exposed to air.

To ensure that the determination of submergence was accurate, the entire database was reviewed for each session and professional judgment and field experience were used to assess whether a plate was submerged or exposed. During this review, the following criteria were used: average air temperature from HOBO loggers, average water temperature, transect location, average air temperature from Environment Canada data, light intensities of exposed versus submerged samplers, and time of day. Temperature data from exposed sites had distinct peaks, and we expect that localized effects such as metal frame heating may help separate similar temperature points between exposed and submerged samplers on sunny days. Data corrections were frequently greatest on sites exposed to the air for longer periods.

2.3.2 Variables and Statistical Analyses

The focus of the 2018 analysis was to validate the reach-wide productivity model for periphyton chl-a and benthic invertebrate biomass and to explore the importance of other physical factors that affect invertebrate and periphyton productivity. A primary focus of this year's analysis was to determine if velocity should be integrated into the invertebrate and periphyton reach-wide productivity models. Determining if light is a limiting factor on chl-a production was another primary focus of this year's analysis.

During the 2019 spring deployment period, PAR profiles (ambient and through the water column) were measured to determine the continuous light attenuation coefficient based on in-situ turbidity. The ambient light measurements were obtained on April 9, 2019 and the PAR profiles were obtained on April 29, 2019. These measurements represent typical MCR spring conditions prior to freshet.

To better understand the effect of light attenuation in the MCR, light intensity, turbidity and depth were modelled using data from S3 and S6 sites in both reaches. An additional light metric was calculated which determines the total hours over 10 photons/m^2/sec. This 10 photon metric was calculated from the light tidbit data for each periphyton sampler and was graphed by transect and reach. The 10 photons/m^2/sec light threshold was chosen because it is based on the known light tolerances of periphytic algae (Sigee 2005). Periphyton productivity metrics are expected to increase with the total hours over 10 photons/m^2/sec. This is roughly 2% of full sunlight striking the water surface (<1% is usually accepted as the photosynthetic limit) (Jassby and Platt 1976; Hill and Fanta 2008). Hourly light intensity from 10:00-15:00 from 2018 HOBO loggers at T1 samplers were compared to hourly discharge

from Revelstoke Dam. The purpose of this analysis was to determine if the T1 samplers are light limited at high flows.

To model light availability, model parameters were estimated using Bayesian estimates that were produced using STAN (Carpenter et al. 2017). Refer to McElreath (2016) for additional information on Bayesian estimation. Unless indicated otherwise, the Bayesian analyses used normal and uniform prior distributions that were vague in the sense that they did not constrain the posteriors (Kery and Schaub 2011, 36). The posterior distributions were estimated from 1500 Markov Chain Monte Carlo (MCMC) samples thinned from the second halves of 3 chains (Kery and Schaub 2011, 38–40). Model convergence was confirmed by ensuring that the potential scale reduction factor $\widehat{R} \leq 1.05$ (Kery and Schaub 2011, 40) and the effective sample size (Brooks et al. 2011) $\mathrm{ESS} \geq 150$ for each of the monitored parameters (Kery and Schaub 2011, 61).

The parameters are summarized in terms of the point estimate, standard deviation (sd), the z-score, lower and upper 95% confidence/credible limits (CLs) and the p-value (Kery and Schaub 2011, 37, 42). The estimate is the median (50th percentile) of the MCMC samples, the z-score is $\mathrm{mean}/\mathrm{sd}$ and the 95% CLs are the 2.5th and 97.5th percentiles. A p-value of 0.05 indicates that the lower or upper 95% CL is 0.

Model adequacy was confirmed by examination of residual plots for the full model(s).

The results were plotted with the modeled relationships between variables and the response(s) with the remaining variables held constant. In general, continuous and discrete fixed variables were held constant at their mean and first level values, respectively, while random variables were held constant at their typical values (expected values of the underlying hyperdistributions) (Kery and Schaub 2011, 77–82). When informative, the influence of variables was expressed in terms of the effect size (i.e., percent change in the response variable) with 95% confidence/credible intervals (CIs, Bradford, Korman, and Higgins 2005).

The analyses were implemented using R version 3.5.1 (R Core Team 2018) and the mbr family of packages.

The attenuation of light with water depth has been well-studied (Julian et al. 2008). The following equation captures the relationship between the irradiance at the surface (E_s) and the irradiance at depth (E_d)

$$E_d = E_0 \cdot \exp(-K_d \cdot y)$$

where E_0 is the initial irradiance, E_d is the irradiance at distance y and K_d is the diffuse attenuation coefficient (Julian, Doyle, and Stanley 2008).

The light attenuation model was used to calculate the euphotic zone depth ($z_{1\%}$) which is defined as the depth at which photosynthetic available radiation (PAR) is 1% of its surface value.

It is given by the equation

$$y = \frac{\log(100) - \log(1)}{K_d}$$

which simplifies to

$$y = \frac{4.6}{K_d}$$

All statistical tests were conducted using R (R Development Core Team 2017) and model averaging was completed using the R package “MuMIn” (Barton 2016).

The seasonal differences of benthic invertebrate and periphyton productivity metrics were compared. A paired t-test was performed with sample pairs from fall and spring 2011-2013 for the invertebrate metrics of abundance, biomass fish food metric, and the periphyton metrics of chl-a, abundance, and biovolume. Benthic invertebrate abundance, invertebrate biomass and fish food metric were log10 transformed to meet t-test assumptions.

Trait-based periphyton ecological guild analyses were undertaken this year to help explain differences in periphyton community composition. The method developed by Passy (2007a), and the planktic guild (PG) developed by Rimet & Bouchez (2011, 2012) were employed. We applied the diatom guild descriptions to non-diatom algae. The guild assignment of each taxa is recorded in the periphyton taxonomy table. Based on the literature, we expected: Low profile guild to dominate areas of turbulence, scour, and hydrologic disturbance; High Profile guild to do best in regions with stable flows; Motile guild to do best in silty areas and areas regularly exposed to variable water discharge, and finally, Planktic guild was expected to do best immediately downstream of reservoir discharges. Use of the guild approach highlights large-scale changes and drivers as opposed to the more nuanced and complex approach of considering each taxa’s distribution individually.

In previous years, the mean velocity measured during deployment and retrieval was used. This velocity does not necessarily represent the velocity conditions the sampler experienced throughout the duration of the deployment period. To consider the full range of velocity conditions over the deployment period, the hydraulic model (TELEMAC-2D) was used to determine hourly velocities throughout the 2018 spring deployment period.

The spatial location of spring 2018 MCR samplers were recorded using a Trimble Geo7X GPS. A spatial join in ArcGIS was conducted to determine which river polygon each sampler intersects. The hourly velocities from the TELEMAC-2D model were extracted for the spring 2018 MCR samplers. The hourly velocities when the samplers were submerged were predicted from the hourly flows at REV 5 for each sampler. Three types of models (linear, log linear, and quadratic) were compared and the one with the lowest AIC was selected to predict velocities for each sampler. The sampler-specific velocity models were used to predict hourly velocity for all spring sampling sessions and are presented in Appendix D. Only the velocities for spring were predicted because the extensive backwatering during fall sampling sessions is expected to reduce the accuracy of fall velocity predictions. The maximum and median velocity for each sampler was calculated from the hourly velocities when samplers were submerged. The maximum velocities were graphically compared by transect and reach.

The effects of water temperature, maximum velocity, median velocity and hours over 10 photons/m^2/sec on invertebrate and periphyton production metrics were explored using linear mixed effects models and multi-model averaging. Separate spring linear mixed effects models were run for each reach that included sites that were regularly sampled in all years (i.e. S3-S7) and sites that were submerged >95% of the deployment period. All periphyton R4 models and the R3 periphyton abundance and biovolume models used the combination

of site and year as the random effect. The R3 chl-a model was a multiple linear regression because it did not include a random effect. The R4 invertebrate production models used year as a random effect, whereas the R3 invertebrate production models used the combination of year and site as a random effect. The periphyton production metrics of chl-a, total abundance and total biovolume and the invertebrate production metrics of abundance, biomass and fish food were natural log transformed. Linear mixed effects models for percent high and low profile guilds were also used to better understand the effects of velocity and flow on periphyton community composition in R4. The random effect for the R4 percent high profile and low profile models was the combination of site and year.

The relative support for the effects of the explanatory variables was evaluated using an all model combinations approach. Model uncertainty was assessed using AICc and multi-model averaging (Burnham and Anderson 2002; Anderson 2008). We used the MuMIn package in R (Barton 2016) to compete models based on Δ AICc values and AICc weights (wi), and to calculate multi-model averaged parameter estimates from 95% confidence sets for each response variable (Burnham and Anderson 2002; Grueber et al. 2011). The relative variable importance (RVI) is the sum of AICc weights from all models containing the variable of interest, with variables having RVI values above 0.6 considered to be of high importance in subsequent interpretations. We also calculated pseudo R^2 for high ranking models, derived from regressions of the observed data versus fitted values (see Cox and Snell 1989; Magee 1990; Nagelkerke 1991; Piñeiro et al. 2008 for details) which gives an indication of the proportion of the variance in response variables explained by an individual model. These analyses were conducted after standardizing continuous explanatory variables by subtracting global means from each value (centering) and dividing by two times the SD (scaling), to compare among all parameters and interpret the main effects in conjunction with interaction terms (Gelman 2008; Schielzeth 2010).

Model results are presented in Appendix E and Appendix F.

Consecutive hours below minimum flow were calculated for 2007-2010 to determine the approximate duration of exposure in areas that were dewatered before the implementation of minimum flows. The percent loss of chl-a using three different death curves was calculated using the hours below minimum flow that were experienced from 2007-2010. The three different death curves used (conservative death curve, summer/winter death curve, spring/fall death curve) were from Schleppe et al. 2015. The conservative death curve was used in the MCR reach-wide model, whereas the summer/winter and spring/fall death curves were used for periphyton abundance and biovolume in the LCR.

2.3.3 Artificial Sampler and Time Series Sampler Assumptions

Community losses along the edges of the artificial substrate were assumed to be negligible. Our visual observations of periphyton growth on the samplers support this assumption but we do not have empirical data to otherwise confirm it. In any case, we did not draw samples from the plate perimeters if possible, however, Styrofoam damage over the deployment occasionally necessitated collecting a sample near the edge.

The effects of foraging invertebrates were assumed to be randomly distributed over the artificial substrate within and between all sites. It is acknowledged that invertebrates may spend more time foraging along the edges of substrata and therefore disproportionately affect productivity along the perimeter of artificial samplers. Therefore, we avoided collecting samples from substrate edges unless no other viable alternative was available. Foraging

intensity on MCR samples is still considered to be a small effect, reducing any potential data-skewing. Further, invertebrate distributions around plates were often clumped, reducing the potential for effects across multiple replicates. Finally, the populations of invertebrates in the MCR were low relative to other large rivers, and we did not do a power analysis to determine if the sample size is adequate.

Our analysis assumed that artificial substrates did not bias results toward a given algal taxa nor did they bias towards those taxa actively immigrating at the time and location of the sampler submergence. Although we made this assumption, data collected suggests that artificial substrate types and natural substrates do respond differently within the MCR. Future investigations may be required to accurately relate artificial samplers to natural substrates and determine if artificial substrates reflect actual riverine conditions.

Sampler assessments were not intended to address immigration, sloughing, or any other aspects of the periphyton or invertebrate community. Thus, artificial substrate samples that were obviously biased from sloughing from rock flipping, etc. were excluded from collection. For invertebrate analyses, this means we did not consider emigration or immigration from within or between sites and that operations did not unduly affect any community or result in changing densities of invertebrates through mortality over the duration of deployment. In cases where periphyton artificial substrates were damaged, but sufficient material was available for a sample, it was collected and not treated differently than any other sample except in cases when the sample was biased by slough or the substrate sampler was inverted by flows. For invertebrates, damaged samplers were not analyzed as they were considered biased. These field decisions were easy to make because large boulders rolling over artificial substrates, or those dragged upside down, left distinct trails of compressed Styrofoam or because sampling baskets were broken open. This field decision reduced the potential area available to sample, but likely did not bias the results. It is acknowledged that substrate mobility and periphyton sloughing/drift are important components of periphyton production in the MCR.

2.4 Reach-wide Productivity Model

The Reach-wide productivity model was implemented to calculate daily productivity for chl-a from 2007 to 2018. These model results were used to test the effect of minimum flows on benthic productivity. The first component of the model is a hydrologic river elevation model that determines water depth on an hourly basis and defines the wetted perimeter of the river. The second component of the model used wetted history to determine riverine production using growth/ death curves for chl-a. The chl-a growth curves were refined this year for spring and fall.

2.4.1 River Model

Ecoscape completed the hydrologic modelling using a calibrated Telemac-2D model developed by Northwest Hydraulic Consultants (NHC, 2016). Initially Northwest Hydraulic Consultants completed two models referred to as the Full MCR Model and the Upper MCR Model. As indicated in the NHC report the model coverages are as follows:

1. "The Full MCR Model extends from the Revelstoke Dam to Shelter Bay. The model has in the order of 320,000 nodes and 631,500 elements. The mean mesh element length is 15 metres.
2. The Upper MCR Model extends from the Revelstoke Dam to Greenslide Creek (from the Revelstoke Dam to 25km downstream). The model has in the order of 533,000 nodes and 1, 051,000 elements. The mesh element length ranges from 5 metres in the regions where wetting and drying processes are expected to occur to 15 metres in the main channel." (NHC, 2016)

Ecoscape compared the Full MCR Model and the Upper MCR Model for use in the study area. The study area covers R3 and R4 that cover approximately 10 kilometers below the Revelstoke Dam. After running simulations of the two models, Ecoscape determined that the Upper MCR Model best represented the physical and hydraulic characteristic of the study area compared to the Full MCR Model. Increased complexity and magnitude of the Upper MCR Model caused much longer runtimes, but these were needed to achieve maximum resolution.

The Upper MCR Model was run for R3 and R4 using hourly discharge data from BC Hydro covering January 1, 2007 to December 31, 2018. The 12 years of data were divided up into monthly runs and programmed into the Telemac-2D simulations. The last simulated data from a given month was extracted and used as a seed file for the next monthly computation to ensure seamless transitions and accurate flow results between time blocks. This was done to manage both database size and runtime.

The Telemac-2D simulations output selafin files (.slf) containing all the programmed attributes for any given hour within the programmed date-time range. Each monthly selafin output was read into the program Blue Kenue. Blue Kenue was developed by the National Research Council Canada and is used as an analysis, data preparation, and visualization tool for hydraulic models. Blue Kenue was used to extract the hourly water depths for each point in the study area. The resulting data from the intersection was exported to a CSV file for use in the productivity analysis within R.

A full resolution intersection is currently not feasible within R due to the large sizes of the databases. To accommodate this limitation, Ecoscape created a polygon mesh covering the maximum potential water level within R3 and R4. This was done by drawing a polyline from the thalweg of the river and offsetting it to both sides by 1 meter. This process was repeated until the full breadth of the maximum inundation potential of the river was covered. The linear polygons were then cut in 20 meter lengths perpendicular to the thalweg polyline essentially dividing the river into 1 meter by 20 meter polygons oriented with the flow of the river. A point file was generated from the centroids of each polygon and the area of each polygon was added as an attribute to the database.

All hourly depth data was imported into a PostgreSQL database using RPostgreSQL package version 0.6-2 (Conway et al. 2017). A separate database was generated for R3 and R4. Each point had a polygon associated with it. The areal productivity of each polygon was calculated hourly using growth or death curves that were developed based upon the time spent either exposed or submerged. The growth and death functions were derived as part of the BRX productivity work (Schleppe et al. 2015), then coded in C++ by Sean

Anderson and subsequently modified slightly by Ecoscape to address transitions between different seasons and the specific growth or death function that was used for each metric.

2.4.2 Productivity Model Notation

The following reach-wide productivity model notation was employed:

- $C(t)$ – total overall response as a function of time
- $c_i(t)$ – response for an individual river polygon of area s_i
- $\mu_i(t)$ – response per unit area for an individual river polygon of area s_i

Since the output of all functions are density- dependent responses (units/m^2), the derivation of formulae is identical between responses with only the coefficient values differing among them. For periphyton, we considered chl-a and for benthic invertebrates we considered benthic biomass, each with their respective units.

The total response at any time is given by the sum of the responses of each individual polygon:

(1) $$C(t) = \sum_i c_i(t) = \sum_i \mu_i(t) \cdot s_i$$

2.4.2.1 Model for Individual Polygon

In a regulated flow regime, growth and death processes determine river production in the varial zone. In a given river polygon, a particular site can either be in a state of growth (submerged) or a state of death (exposed), and these processes cannot occur simultaneously; rather there are consecutive periods of growth and death that vary with submergence in the river. Upon switching from either a state of growth or death, the final value of a response at the end of one period is the initial value for the next. A given river polygon can move between growth (submergence) or death (exposure) independently of all other river polygons at any time and the state of a river polygon submergence is entirely dependent upon the regulated flow. The Telemac model was used to determine the state of submergence on an hourly basis.

2.4.2.1.1 Growth Phase

Growth at a given time will occur between time $t = t_a \ldots t_b$, where time t_a and t_b represent the start of submergence and the time period where a polygon transitions from submergence to exposure, respectively. At the beginning of this time period, the initial response in a river polygon is $c_i(t_a)$, that may be zero or a positive number for any river polygon occurring within the maximum extents of the varial zone. This value will be peak production of the response in permanently submerged polygons.

At any point during this period we denote additional response growth by $c_i^g(t)$, that must equal zero at time $t = t_a$, the beginning of the period of growth. Thus:

(2) $$c_i(t) = c_i(t_a) + c_i^g(t - t_a)$$

At the end of this phase, the total amount of the response of this polygon is

(3) $$c_i(t_b) = c_i(t_a) + c_i^g(t_b - t_a)$$

2.4.2.1.2 Logistic Growth

At submergence, t_a, growth is initiated using a logistic growth function. The productivity response (e.g., abundance or biomass), $\mu_i(t_{a-1})$, is used to find the time on the growth curve, h_{a-1}

(4) $$h_{a-1} = xmid - ln\left(\frac{asym}{\mu_i(t_{a-1})} - 1\right) \cdot scal$$

Where $asym$, $xmid$ and $scal$ are the parameters of the logistics growth function: $asym$ is the asymptotic height or peak biomass, $xmid$ is the inflection point, or the time to achieve 50% peak biomass ($0.5 \cdot asym$) and $scal$ is the time to grow from 50% or $xmid$ to 75% peak biomass ($0.75 \cdot asym$).

Furthermore, $h_a = h_{a-1} + 1$, where h_a is the predictor time for the growth curve when the polygon is initially submerged. The relationship between h and t can be written as a function of t, $h(t) = (t - t_a) + h_a$. Thus, the total response in a river polygon i during the growth phase is

(5) $$c_i(t) = \frac{asym}{1+exp^{(xmid-h(t))/scal}} \cdot s_i \qquad \text{if } t_a \leq t < t_b$$

The parameters $asym$, $xmid$ and $scal$ for the same river polygon vary with season for periphyton, and not for invertebrates. If a time period $t = t_a \ldots t_b$ spans a change in season, growth will occur until the season peak biomass (asymptotic height) is reached. If the season peak biomass is greater than the following season, the biomass is reduced to the peak biomass for that season using the death curves.

2.4.2.1.3 Death Phase for an Individual Polygon

Death or loss within any given time period will occur between time $t = t_a \ldots t_b$, where time t_a represents the start of exposure and the time period t_b, where a polygon transitions from exposure to submergence. At the beginning of this time period, the initial response in this river polygon is $c_i(t_a)$, that may be zero or a positive number up to peak biomass.

At any point during this period we denote how much of the response was lost by $c_i^d(t)$, which must equal zero at time $t = t_a$, the beginning of the period of death. Thus:

(6) $$c_i(t) = c_i(t_a) - c_i^d(t - t_a)$$

At the end of the death or loss phase, the total amount of the response in this polygon is

(7) $$c_i(t_b) = c_i(t_a) - c_i^d(t_b - t_a)$$

We may rewrite this in terms of a percentage loss $\theta_i(t)$ for convenience:

(8) $$\theta_i(t) = \frac{c_i(t_a) - c_i(t)}{c_i(t_a)}$$

in which case

(9) $$c_i(t) = c_i(t_a) \cdot [1 - \theta_i(t)]$$

For periphyton, the start of the death or loss phase is offset by a fixed amount of time (starting values discussed above) that is dependent upon season, and this is easily incorporated by modifying the start time t_a used in these equations.

2.4.2.1.4 Exponential Decay

During the death phase, a response decays exponentially in time to an asymptotic value of $[c_i(t) \cdot A]$ such that the *total* amount of the response for a river polygon i during this period is:

(10) $$c_i(t) = c_i(t_a) \cdot \left\{A + [1 - A] \cdot e^{-\gamma \cdot (t - t_a)}\right\}$$

Where the decay constant γ and asymptote A are the same for every river polygon, such that the percentage loss is a river polygon-independent function of time only:

(11) $$\theta(t) = (1 - A) \cdot \left[1 - e^{-\gamma \cdot (t - t_a)}\right]$$

2.4.2.2 Full Production Model for All Polygons

At any given time there are river polygons which are both growing denoted with i, polygons which are saturated at peak biomass denoted with j, and polygons which are dying denoted with k. To find out the total overall response at any given time, we sum all the responses of all the individual river polygons since the beginning of the last time period at $t = t_a$:

(12) $$C(t) = \sum_i \left(\frac{asym}{1 + exp^{(xmid - h(t))/scal}} \cdot s_i \right) + \sum_j \left(\mu_p \cdot s_j \right) + \sum_k (c_k(t_a) \cdot [1 - \theta(t)])$$

2.4.2.3 Model Assumptions and Limitations

The following are a list of assumptions used to develop the derived functions for growth, death, and peak biomass:

1. Several assumptions are required for starting response values $c_i(t_a)$. For permanently submerged polygons within the river, we assume that peak production for that metric was achieved, whereas in varial zones where polygons are alternately submerged and exposed, the starting value is assumed to be zero until submergence occurs. The minimum time that can be considered in any given operational scenario must span the period necessary for peak production for that response.
2. All river cells are considered independent of all other river cells, meaning that growth, death or peak biomass in any cell have no direct effect on any other given river cell. Factors including invertebrate drift from natural migration or effects associated with flow regulation (via changes in velocity) are not accounted for.
3. As mentioned above, hourly is the most appropriate time period, and all associated functions have been derived assuming that production will be calculated on an hourly basis. We have assumed that for a given hour, a river polygon cannot change from a state of submergence to exposure and that starting conditions within that period will be maintained for the entire hour in question. Although this considers flow in a stepwise approach, this unit of time is sufficiently small to reduce substantial error in our determination of river productivity.

4. This model assumes that when a given river cell transitions from a state of submergence to a state of exposure, emigration to adjacent submerged cells does not occur and vice versa. It is acknowledged that emigration of invertebrates likely occurs and presumably emigration rates are species-dependent. Further, the ramping rates may affect emigration rates, where high ramping results in more rapid elevation changes within the river, reducing the ability of invertebrates to move, whereas lower ramping would increase movement potential. Despite this consideration, the clear relationship between submergence and production shown in the MCR (with its high associated ramping rates) suggests that emigration rates do not adversely influence predicted estimates of production responses within the proposed reach-wide models.
5. This model assumes that growth and death curves do not differ with weather or between years. High annual variation in growth was observed, but the specific reasons for the variability are not yet well understood. Other specific parameters that might be important include velocity, substrate, weather, and substrate stability. Both the peak biomass and the rate of growth to peak biomass have been observed to vary between years on the MCR.
6. Production is greater than zero upon the first hour of growth and is equal to the minimum predicted growth at hour 1 in logistic regressions for each season. This is necessary for logistic growth curves to be predicted as values cannot start outside of the range of production predicted by the model.
7. In cases where the previous production value is higher than the maximum predicted growth for a given season, production will exponentially decrease until it reaches the maximum predicted growth for that season. Currently, the same exponential decay death function for exposure is used to transition between seasons, and is probably more abrupt than what would occur naturally. Realistically, this process is governed by processes of natural slough, and we do not currently have any data to this transition. This process could be easily added to the reach-wide model to further develop seasonal transitions. Since seasonal transitions occurred on the first of the month, data was not analyzed spanning any month.
8. Da+- collected since 2007 for a variety of different projects on the Columbia River for both BC Hydro and Columbia Power Corporation (CPC) was used to develop the reach-wide productivity model. The data collected in these assessments was integrated into one data set and relies upon the full suite of work completed by CPC and BC Hydro. This dataset is primarily based on data from the LCR. The LCR has higher periphyton and benthic productivity than the MCR and also different periphyton and benthic community compositions. From this data set, predictive growth and death functions have been developed that are directly linked to submergence times. The predictive growth curves have been adjusted to better represent the productivity in MCR. However, no data was collected in the summer and winter in the MCR. Professional judgement was used to adjust the summer and winter curves. It is acknowledged that productivity estimates in these seasons have large uncertainties. High annual variation was observed on these systems, and the data was condensed to consider only one growth or death curve for each season. A full investigation of the potential consequences of dataset reduction like this was not considered, but is likely an important factor.

2.4.3 Growth and Death Curves

The following provides a summary of the periphyton and benthic invertebrate growth and death curves used in the reach-wide model of productivity. Periphyton chl-a and invertebrate biomass growth curves were generated and applied to the reach-wide productivity model using the same rationale as Schleppe et al. 2015. During the growth phase, production starts almost immediately upon submergence and continues until peak biomass is achieved. At peak biomass, growth still occurs, but is offset by rates of natural death or loss from physical factors including periphyton slough or invertebrate drift (Schleppe et al. 2015). The formula used for growth is represented as follows:

$$y = \frac{asym}{1 + e^{\frac{xmid - x}{scal}}}$$

where *y* is the response (productivity), *x* is the predictor (hours in the water), *asym* is the asymptotic height (peak biomass), *xmid* is the value of *x* that gives half the height of *asym* or the inflection point (i.e., the time to 50%), *scal* is the time to get from 0.5*asym to 0.75*asym, and e (natural log constant) is ~2.71828.

Fall and spring chl-a growth curves used in the original reach-wide model were adjusted using accrual data (Figure 2-5). Seasonal transitions were defined as March 1st and September 1st. MCR accrual data from 2011-2018 for T1 samples were used to adjust spring and fall growth curves for chl-a. Chl-a growth data was simulated using the above equation with the initially specified parameter values. A series of tests on fitted vs actual were performed until an optimum value for R-squared and MSE was achieved. The resulting asym, xmid and scal parameter values were then selected for the final chl-a growth curve. The chl-a growth curves were forced to a logistic curve by using chl-a samples that were incubated for six months as the horizontal asymptote. Winter and summer chl-a growth curves were not adjusted for this year's reach-wide model. The formula for each of the growth curves were as follows:

Chl-a

a. $Chla = \frac{1.171}{1+e^{(1200-hrs.in)/350}}$ Spring

b. $Chla = \frac{0.8}{1+e^{(579.939-hrs.in)/257.53}}$ Summer

c. $Chla = \frac{2.5}{1+e^{(1050-hrs.in)/350}}$ Fall

d. $Chla = \frac{1.173}{1+e^{(1174.26-hrs.in)/225.3289}}$ Winter

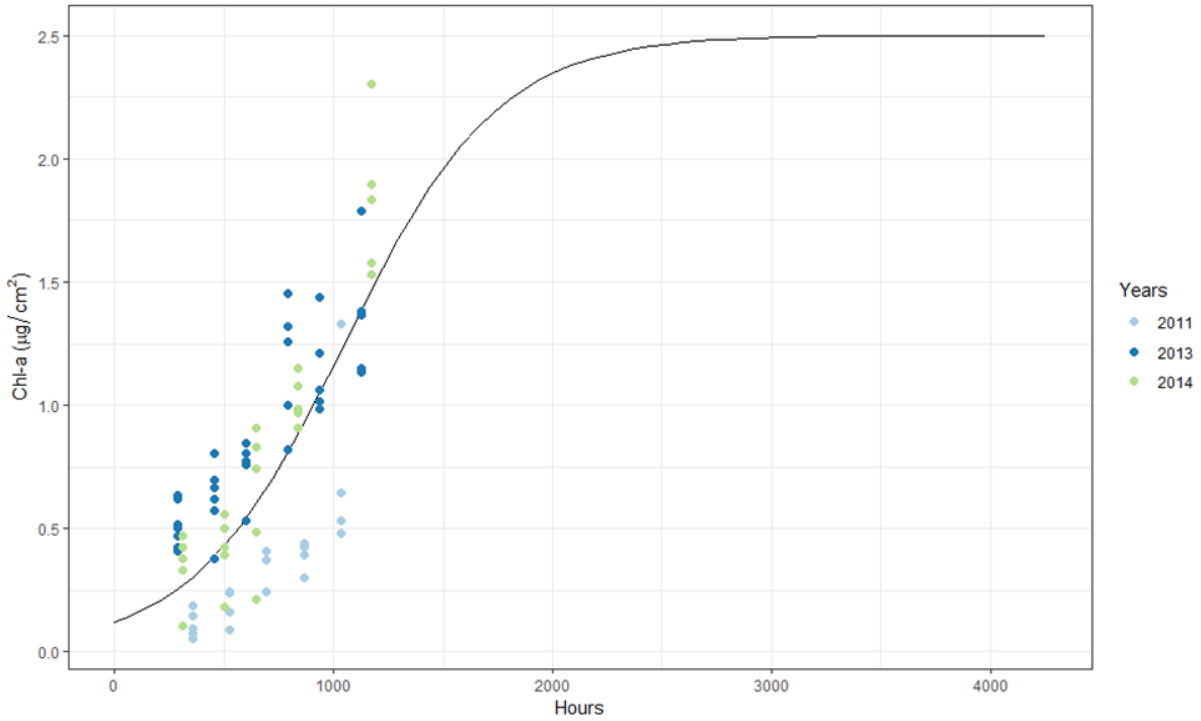


Figure 2-5: Growth curve for fall T1 chla time series data, mse= 0.0973.

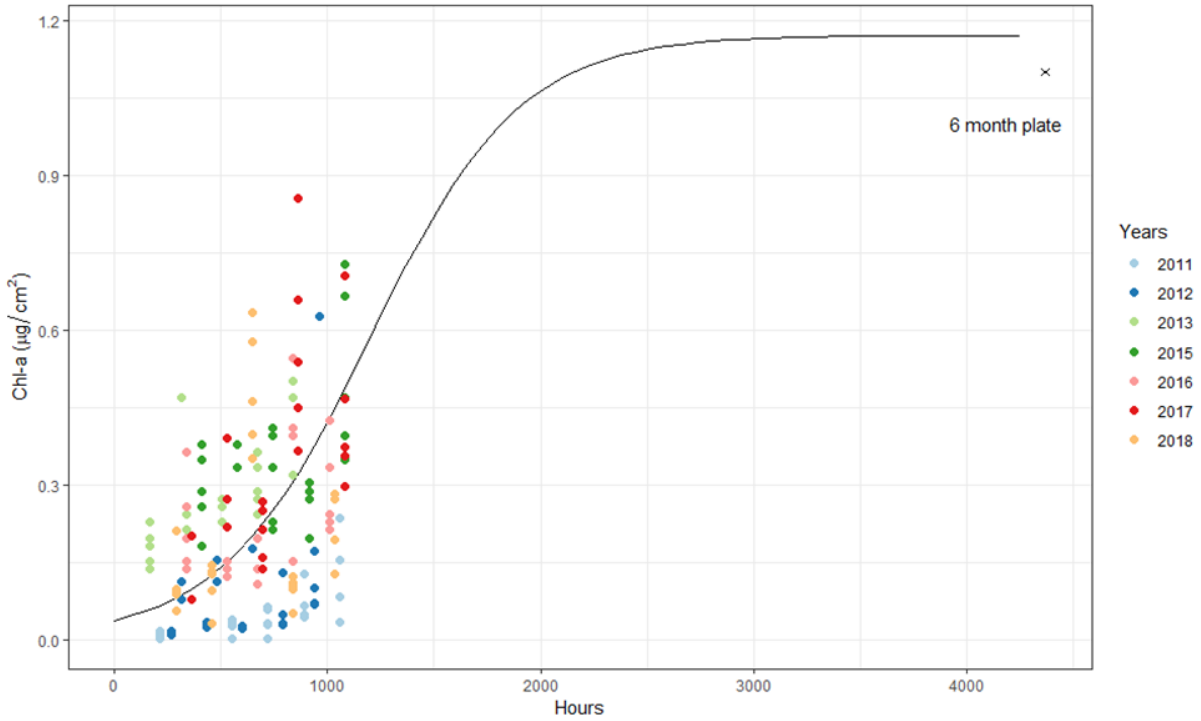


Figure 2-6: Growth curve for spring T1 chla time series data with six-month T1 plate, mse=0.290.

The invertebrate biomass growth curve was modified from Schleppe et al. (2015) for the LCR, and was used in all seasons (Figure 2-7). This growth curve measures the increase in invertbrate numbers through colonization drift processes and it does not account for growth or size increases of individual invertebrates. A different asymptote from the LCR biomass curve was used for the MCR biomass growth curve; this asymptote was based on the mean invertebrate biomass of only the permanently submerged sites. The MCR invertebrate biomass data (2007-2017) was used to calculate the mean biomass for all T1 sites; Big Eddy (BE) sites were not included in this calculation due to the small amount of depositional area in the MCR. The formula for the invertebrate biomass growth curve was as follows:

$$Biomass = \frac{11.3}{1 + e^{(490.413 - hrs.in)/104.907}}$$

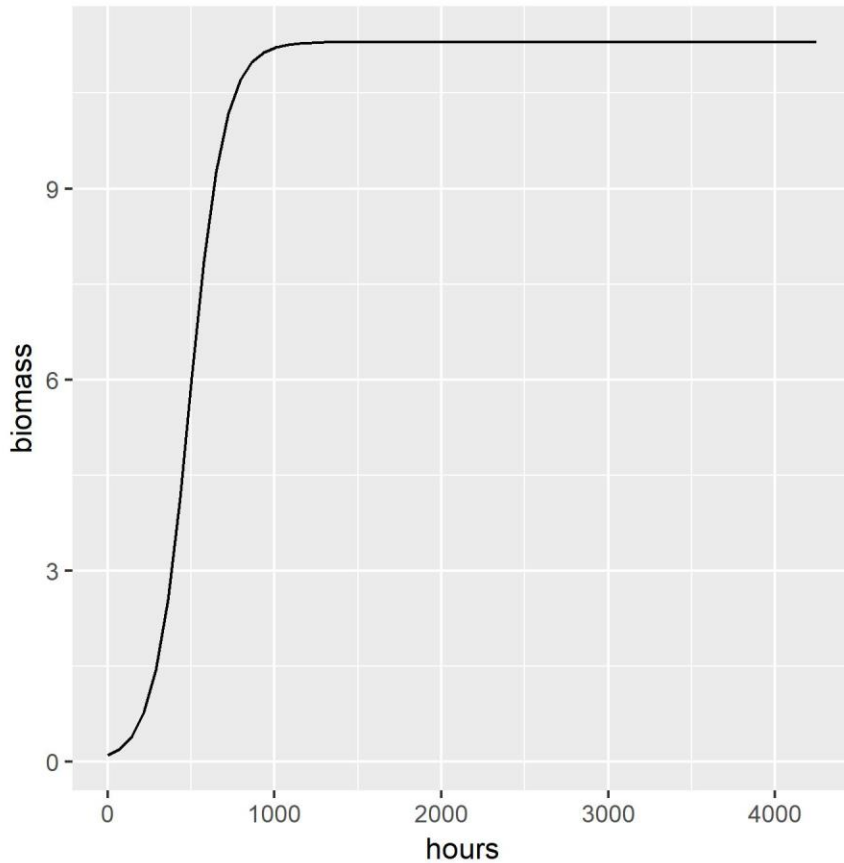


Figure 2-7: Growth curve for invertebrate biomass modified from Schleppe et al. 2015.

Death curves for both periphyton chl-a and invertebrate biomass used in the reach-wide productivity models are described in Schleppe et al. 2015. Winter and summer used the same invertebrate biomass death curve, whereas spring and fall also used the same death curve. The same chl-a death curve was used for all seasons (Schleppe et al. 2015).

The daily productivity of chl-a for R3 and R4 were estimated by taking the modelled productivity at 12 o'clock noon each day. The total productivity each reach was determined by summing all polygons at this time period.

Daily productivity estimates of each reach (R3 and R4) were compared before the implementation of minimum flows (2007-2010) and after implementation of minimum flows (2011-2018) using linear mixed effects models. Before and after implementation of minimum flows and month as well as their interaction were used as fixed effects in the model. The random effect was date nested within, before and after implementation of minimum flows. The mixed effects models were implemented in R package nlme version 3.1-131 (Pinheiro et al. 2017).

For both R3 and R4 models of periphyton chl-a, chl-a was log10 transformed to better meet linear mixed effects models assumptions. However, all four chl-a models violated the assumption of homoscedasticity (see Appendix C). The residuals within a given year were highly correlated from October to December. This high correlation is due to large annual differences in ALR elevations that causes different extents of backwatering in both R3 and R4.

2.4.4 Model Validation

The spatial location of spring 2018 MCR samplers were recorded using a Trimble Geo7X GPS. A spatial join in ArcGIS was conducted to determine which river polygon each sampler intersects. Each river polygon that intersected a 2018 spring sampler was selected to obtain productivity estimates on the day of sampler retrieval using the individual polygon model. The productivity models for chl-a and invertebrate biomass were started on April 11th and the productivity estimates that were used were from May 24th, 2018. The chl-a and invertebrate biomass models used the same parameters for growth and death curves that were used last year. An additional model for chl-a was run this year that used a modified growth curve. The predicted chl-a and invertebrate biomass were compared to the data collected in spring 2018.

3.0 RESULTS

3.1 Biophysical Characteristics of the Middle Columbia River

3.1.1 Light and temperature in submerged areas of MCR

Spring 2018 water temperature ranges were consistently lower and had fewer spikes than temperatures collected in spring 2010 through 2017 (Figure A1). Revelstoke Reservoir conditions upstream and temperature/flow of tributaries are the most probable factors affecting the daily variation in observed water temperature (Larratt et al. 2013; Olson-Russello et al. 2015). During the spring 2018 deployment, initial river ranged from 2 to 3ºC.

Temperatures of exposed plates in the spring usually exceeded water temperatures in MCR (Figure A1). On the LCR, winter river temperatures were more dependent upon the temperature of the upstream reservoir, while during the fall riverine temperatures were more dependent upon seasonal air temperature patterns (Olson-Russello et al. 2015). If similar trends exist on the MCR, springtime water temperatures would be more dependent on reservoir temperature, whereas fall water temperatures would be more dependent on air temperature, recognizing that cumulative summer weather determines the upstream reservoir temperature.

Figure A3 presents the spring light logger data when samplers were exposed to air. It shows the expected reception of far more light during dewatering compared to water-covered periods. The differences between the results at the various transect positions reflects a combination of aspect, riverbank shading and periphyton growth on the sensors.

Average light intensity during spring 2018 followed a similar trend to 2010 – 2017 but was higher at T1 – T4 sites and lower at T5 and T6 sites compared to 2010-2017 means (Figure A2). In accordance with the physics of light transmission through moving water with low suspended solids, light intensity on submerged samplers increased from deep T1 locations to shallow T6 locations in the spring. When samplers were in shallow water, they received more light that supported greater periphyton production, but these sites were also more likely to be exposed during the variable daily operating regime. Peak light intensities occurred around noon, a period when flows are usually high. Light intensities were much greater when samplers were exposed, and were highest at the T6 locations where exposure was the most frequent (Figure A2).

Light modelling was conducted in 2018 to determine if light should be integrated into the chl-a component of the RWP model. The total hours over 10 photons/m^2/sec was calculated for all MCR samplers and this metric confirmed that all MCR samplers were within the MCR photic zone. Fall daylength resulted in less hours over 10 photons/m^2/sec compared to the spring. In spring, all transects had a similar number of hours over 10 photons/m^2/sec (Figure 3-1). However, in fall the deeper transects (T1 and T2) averaged less hours of 10 photons/m^2/sec compared to T3-T6. Thus, it is possible that some periods of light limitation may occur during high flow, winter periods, when light intensities are lower and light penetration is not sufficient to support photosynthesis.

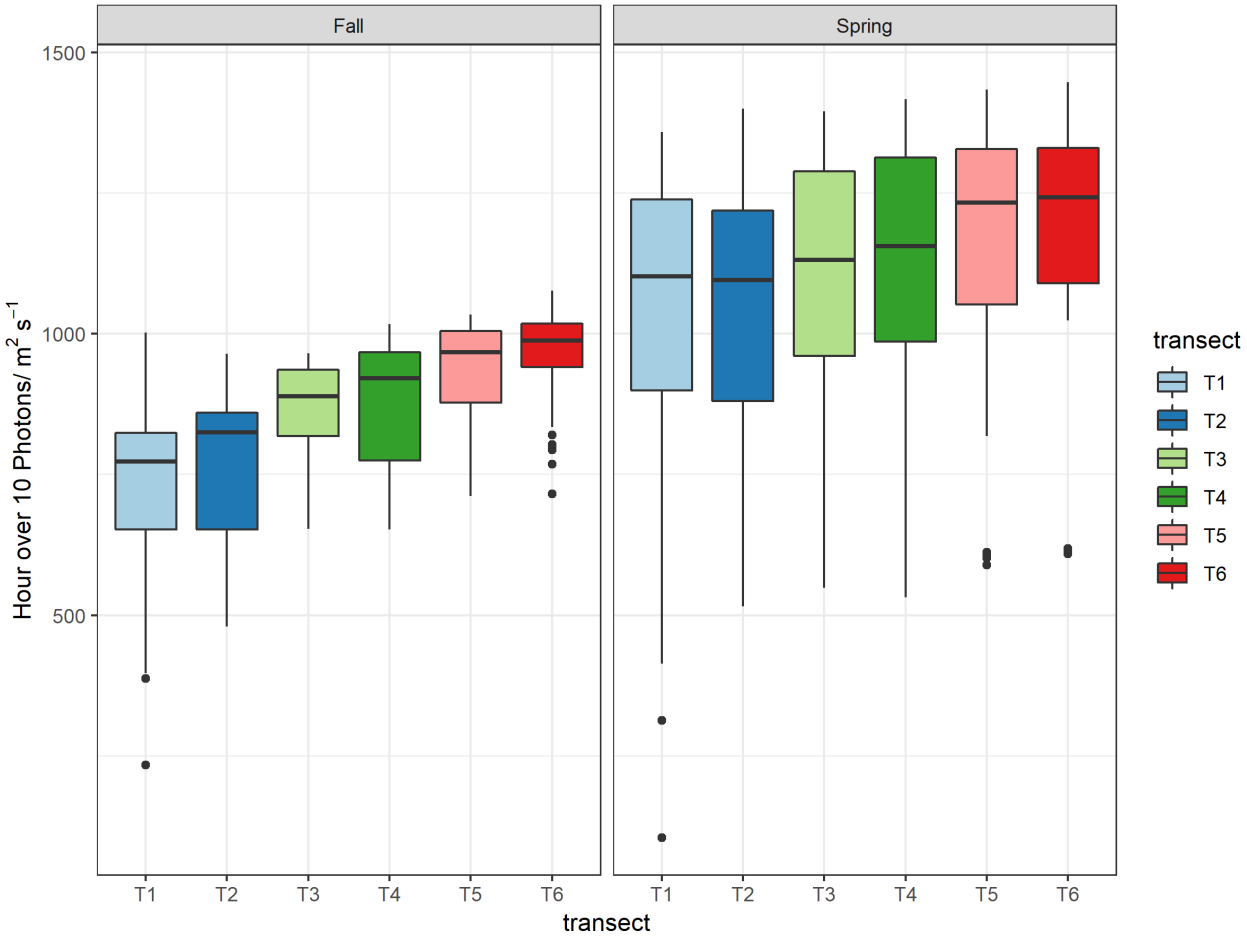


Figure 3-1: Hours over 10 photons for all fall and spring samplers from 2011-2018.

The euphotic depth is defined as the depth at which light in the photosynthetic active range (PAR) is attenuated to 1% of its surface value (Lee et al. 2007). Light attenuation in MCR was modelled using PAR profiles for sites S3 and S6 at both reaches. The modelled euphotic zone depth was 27±5.2 m (Figure 3-2). This metric is normally applied to lakes; however, it supports the 10 photons/m^2/sec metric results for MCR. Since the thalweg in R3 ranges from 2 to 8 m depth and the R4 thalweg from 2 to 7 m depth, all of the MCR channel substrates usually receive enough light for photosynthesis. However, primary productivity will be diminished in deep water locations of MCR.

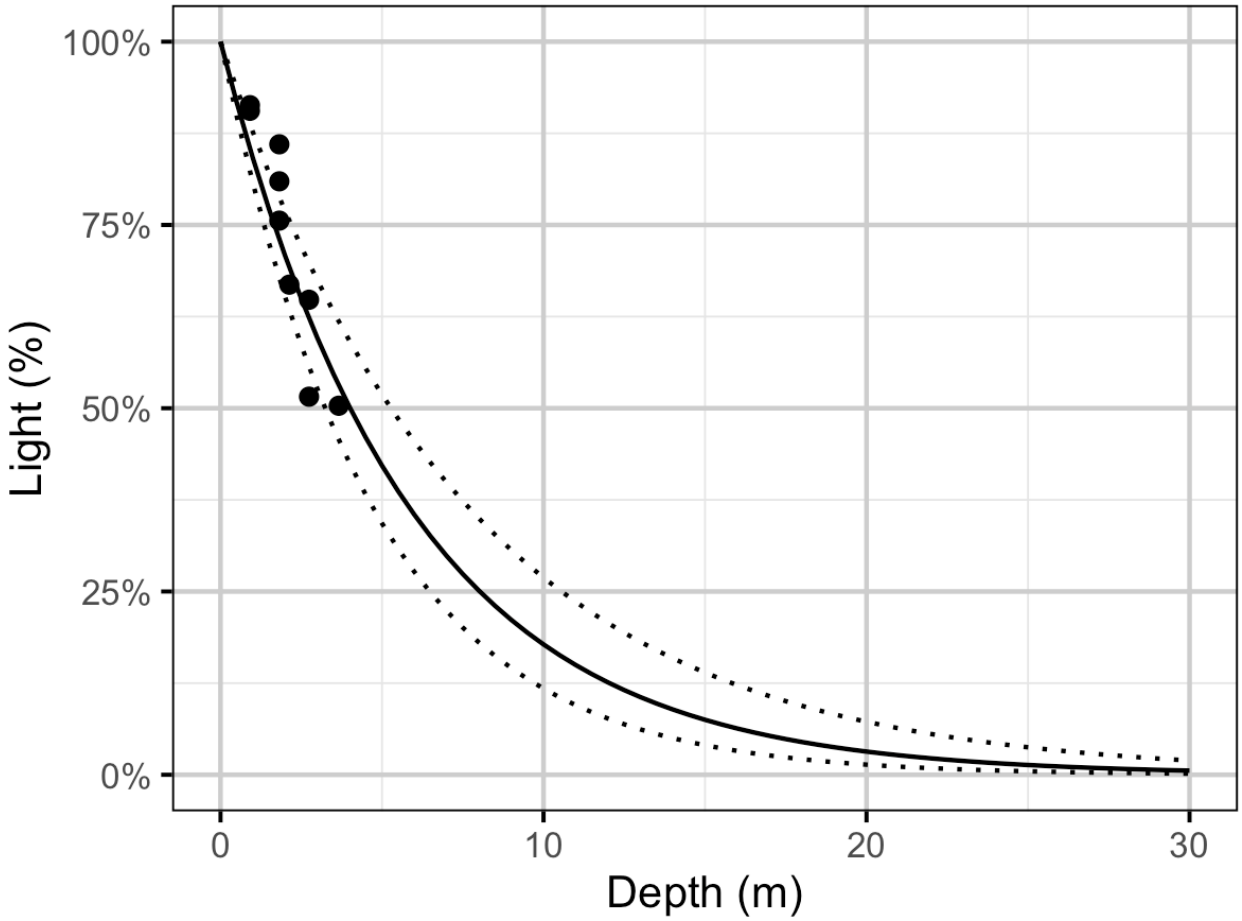


Figure 3-2: Light Attenuation by depth calculated from PAR profiles collected spring 2019.

Spring 2018 hourly light measurements were graphed against flow for all T1 samplers. As expected, hourly light measurements declined as hourly flow increased (Figure 3-3). However, even at flows greater than 2000 m^3/sec, light at the T1 samplers was above the 10 photons/m^2/sec threshold. Hours that had rain or fog had lower light measurements but were also above the 10 photons/m^2/sec threshold.

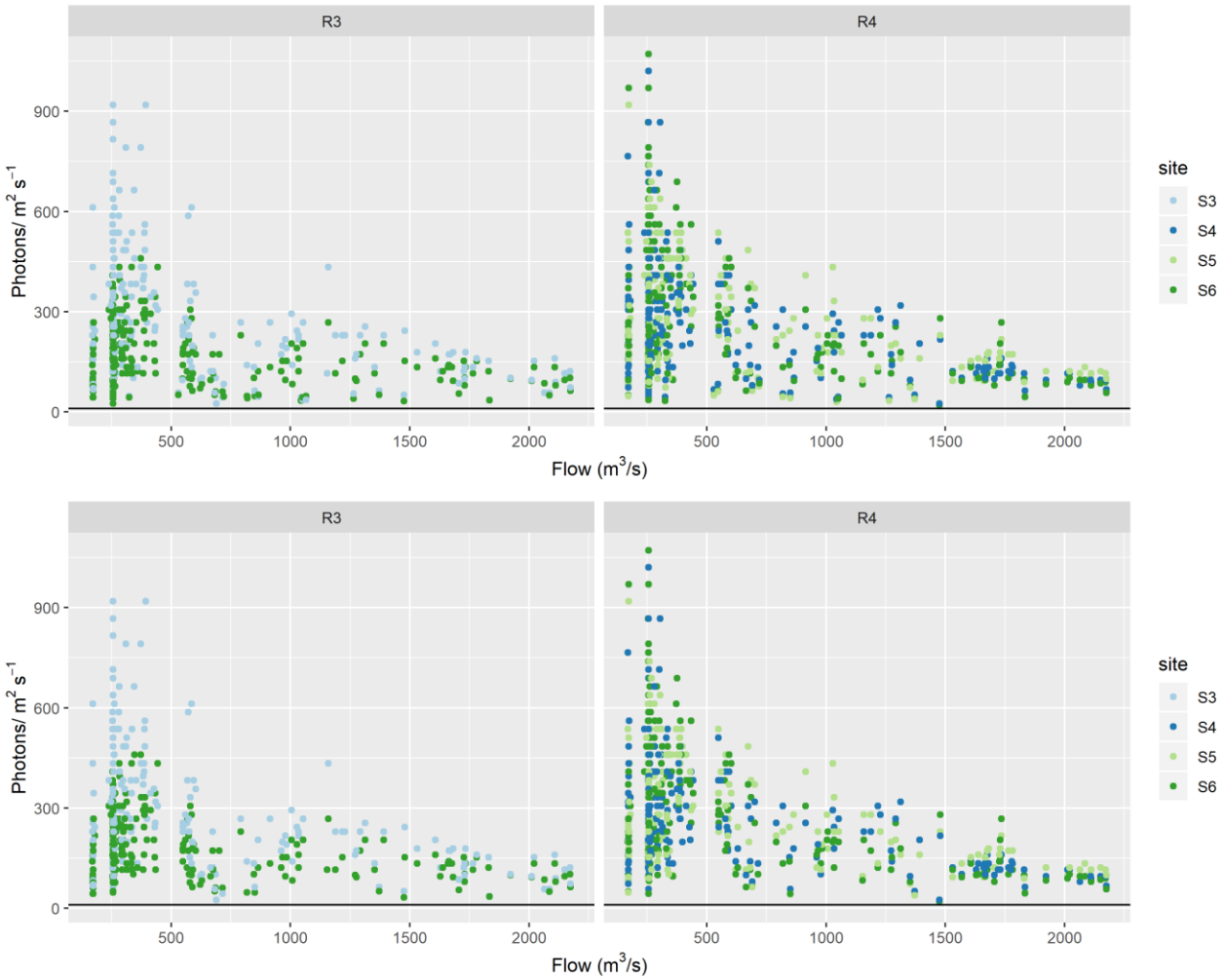


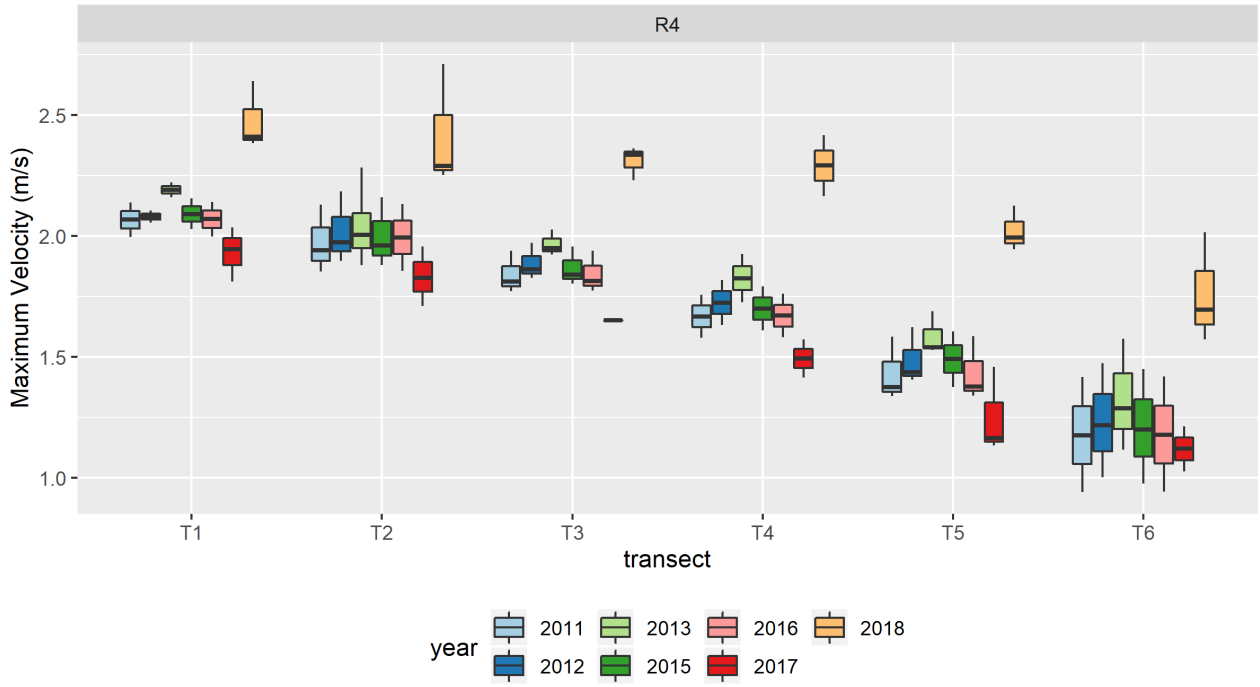
Figure 3-3: Hourly light intensity from 10:00-15:00 by reach and site at varying flows. The bottom plot excludes hours that had rain or fog.

3.1.2 Velocity and Flow in MCR

The hourly velocities for the spring 2018 samplers were extracted from the Telemac-2D model. These hourly velocities were regressed with hourly discharges to obtain sampler-specific velocity-discharge curves. Hourly discharge explained 93-99% of the variation of velocity at the R4 samplers, whereas discharge explained 62-91% of velocity at R3 samplers (Appendix D). The weakest site specific velocity-discharge relationship occurred at the R3-S3 samplers, likely because the R3-S3 site is the furthest downstream and was exposed to the most backwatering from ALR. Backwatering caused a complex, variable relationship between discharge and velocity.

Maximum modelled velocity had higher variability across transects at R4 sites compared to R3 sites. The maximum velocity at the R4 sites was the highest in spring 2018 and lowest in spring 2017 (Figure 3-4). At the R4 samplers, the sampling sessions with the highest maximum velocities correspond to the sampling sessions that had the highest discharge flow (Appendix D). In R4 during the spring deployment period, the maximum velocity of T1

samplers exceeded 2 m/s during most sampling periods and the maximum velocity was highest near the thalweg (T1-T2). The velocity in R4 generally decreased as distance from the thalweg increased (Figure 3-4). At some R4 sites, T2 samplers also had maximum velocities that exceeded 2 m/s. At the R3 samplers, the maximum velocity was affected by discharge and ALR backwatering. As a result, maximum velocities were less variable among sites and transects. In R3, the velocities from T1 to T4 were similar, which was expected given the wider channel cross section in this area. The T1 and T2 samplers in R3 had maximum velocities that did not exceed 2 m/s during the spring sampling sessions. However, velocities in R3 at the S6-T3 sampler did exceed 2 m/s during the spring sampling period.



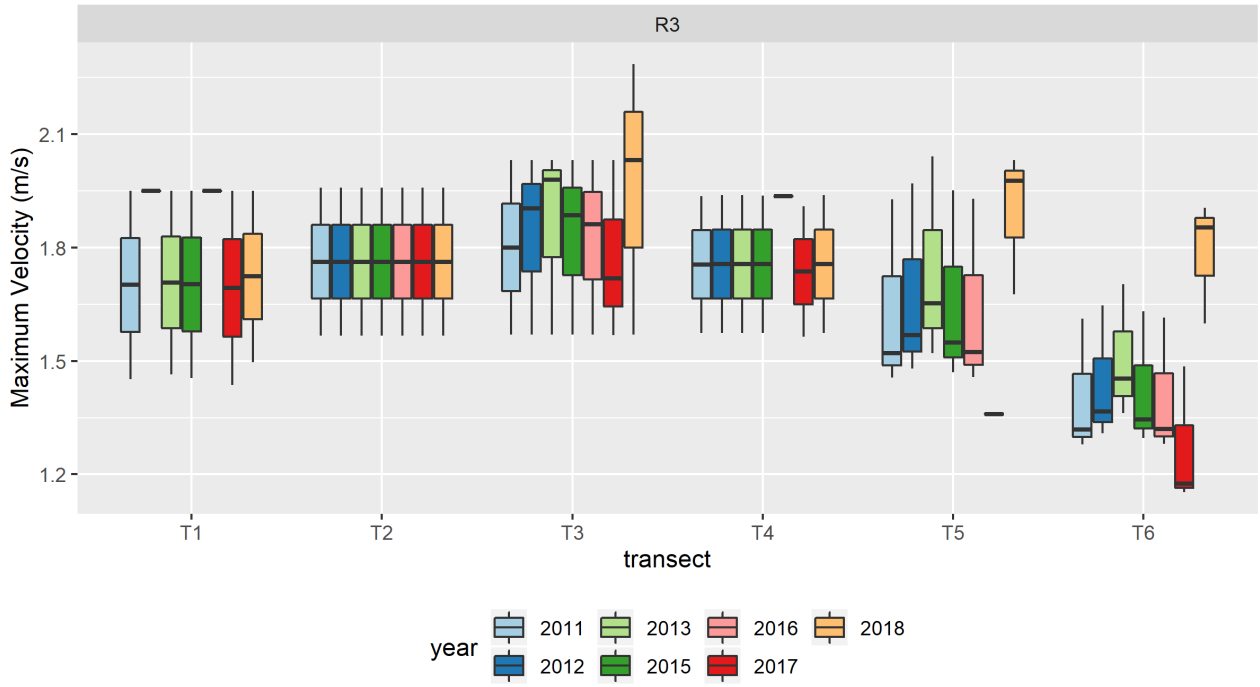


Figure 3-4: Predicted maximum velocity over spring sampling sessions by reach and transect.

3.1.3 Pattern of Flow in MCR

Several features of the MCR flow regime directly influenced productivity during the study period. These features are presented in approximate chronological order:

- Minimum flows of 142 m^3/s were maintained from 2011 onwards (refer to Schleppe et al. 2013 for analysis of 2011 and 2012 data).
- 2011, 2012 and 2017 were extremely high water years resulting from a combination of higher than normal snowpack and higher discharge from REV 5. Small morphological and biological channel changes were observed. For instance, in 2010 there was a noticeable fungal/bacterial black coloration on substrates in R4, and this was less apparent following the high water years.
- Very high flows exceeding 2000 m^3/s were concentrated in the winter months but also occurred in August of 2011, August and September of 2012, and May of 2018. The frequency of these events was greater in 2012 and 2018 than in 2011, 2013, 2014, 2015 and 2016. (Table A1).
- Flows followed a similar pattern between years, with low flows occurring during evening periods after midnight and high flows occurring during daytime periods from 10:00 until 19:00. At all other times, flows were either ramping up or down from high or low flow periods. An exception to this trend was seen in 2018 when peak flows occurred from 16:00 to 20:00. (Figure A4).
- Daily flow patterns were similar to previous years in spring 2018.
- The Arrow Lakes Reservoir (ALR) elevation can result in extensive back watering of R3 from early June through October, and can extend into R4 during the summer months (Figure A5). Backwatering effects have been considered through the submergence variables but these variables do not distinguish between submergence from backwatering and submergence from flows in the model analyses. During spring 2018, back watering occurred in R3 in the last couple of weeks of the spring deployment period.
- High variability in high, low, and ramping flow periods was observed between years and seasons.

Spring 2018 flows were similar to previous years (both pre- and post-implementation of minimum flows). However, there were higher maximum flows compared to previous spring sampling periods. Summaries of flow trends for daily or weekly comparisons are difficult because REV is designed to be a hydropeaking facility and the data is extremely variable.

3.2 Periphyton

Periphyton samples have been collected by Ecoscape during the fall (backwatering probable) in 2010 through 2014 for five sample sessions, and spring (minimal backwatering) in 2011 through 2018 for seven sample sessions. There were four fall sampling sessions collected by Golder from 2007-2010. The results to date are presented here, with emphasis on the parameters that inform the reach-wide productivity model for periphyton.

3.2.1 Overview of MCR Periphyton Biofilms

Periphyton consists of two broad groups of micro-organisms, photosynthetic (algae and some bacteria), and heterotrophic (decomposer bacteria and fungi). Algal periphyton production only grows while substrates are submerged and exposed to sunlight, while the bacterial biofilm component can grow in the dark (Lear et al. 2008). For both components, growth in the MCR slowed dramatically and mortality progressively increased during periods of desiccation. Drift of viable phytoplankton cells originating from the upstream Revelstoke Reservoir, and to a lesser extent, from Arrow Lakes Reservoir during back-watering, contributed to periphyton production and rate of recovery from desiccation events.

3.2.2 Periphyton Ash-Free Dry Weight

Collection of ash-free dry weight (AFDW or volatile solids) commenced in 2010. AFDW provides an estimate of all organic components of the biofilm plus detritus. Average MCR ash-free dry weight samples remained in the typical range for large rivers but with considerable variation from year to year. AFDW has averaged about 0.60 mg/cm^2 in both seasons, but with wider variation in the fall than in the spring. With both seasons and all years combined, AFDW remained consistent in the permanently submerged substrates from T1 through T4, and peaked at T5 in the lower varial zone before declining at T6 in the upper varial zone / floodplain (Table 3-1). T5 samples indicated it was a zone of organic accumulation or decomposition. Variable results from year to year are likely flow-driven and they highlight the volatility of conditions in MCR. Field observations of reduced black banding since 2011 suggest a decline in heterotrophic members of the biofilm in years with longer inundation of the flood plain areas (T5, T6). They are displaced by algae during periods of increased substrate submergence.

AFDW was not analysed for samples submitted in 2018 because of a lab error, therefore the table below represents only 2007-2017 data.

Table 3-1: Ash-free dry weight (mg/cm^2) averaged by season (spring/fall) and for both seasons in all study years (2007-2017).

Season	T1	T2	T3	T4	T5	T6
Spring	0.60 ±0.51	0.58±0.49	0.58±0.49	0.54±0.34	0.58±0.82	0.56±0.44
Fall	0.66 ± 0.66	0.53 ± 0.34	0.48 ± 0.22	0.48 ± 0.35	1.0 ± 3.66	0.37 ± 0.43
Spring & Fall	0.56 ± 0.45	0.56 ± 0.45	0.56 ± 0.45	0.56 ± 0.45	0.78 ± 2.54	0.48 ± 0.44

3.2.3 Characteristics of MCR Periphyton Algae

Like most large rivers, MCR species were dominated by diatoms representing up to 100% of the biovolume in all sample sites on both natural and artificial substrates (Schleppe et al. 2013). When all years of study to date are considered, diatoms accounted for 90 ± 15% of the fall biovolume and 93 ± 17% of the spring biovolume. The dominant MCR diatom species were either the low profile guild - rapid colonizing diatoms with firm attachment strategies, or large planktonic guild taxa imported from Revelstoke Reservoir that adhered to the

periphyton biofilm. Green algae accounted for 8 ± 15% in the fall with large filamentous species, and only 2.6 ± 11% in the spring samples where rigorous conditions including freeze-dry events eliminated all but the single-celled green types. The relative biomass contributions of flagellates ranged from 1.8 ± 4.7% in the fall to 3.1 ± 8.6% in the spring. Although cyanobacteria were functionally and numerically important, they only accounted for 0.55 ± 1.7% of total biovolume in the fall and increased to 1.6 ± 6.5% under spring conditions that favour species with rapid reproduction rates.

The taxonomic structure of all river periphyton communities tends to be predominated by a small number of taxa. The MCR had 5 - 52 species per sample, with all microflora taxa included. Among the true algae, mean taxa richness was 18 ± 6 in the spring and 20 ± 6 taxa in the fall. These results suggest that species richness in the MCR was lower than is typical for unregulated large rivers of similar latitude.

The range of river habitats investigated was expanded to include backwater, Big Eddy and bedrock in 2011, but still found many of the same taxa found at mainstem sites. Over the years of study on the MCR habitats, ten dominant taxa accounted for 9 –93% of abundance (71 - 99% of total biovolume) in the fall and 2 – 97% of abundance (73 - 99% of biovolume) in the spring.

3.3 Drivers of MCR Periphyton Communities

The identified drivers directing the growth and diversity of MCR periphyton are discussed separately below, although several of them operate in concert.

3.3.1 Effects of Reservoir Donation

The donation of Revelstoke Reservoir planktonic diatoms is very important to MCR periphyton production metrics and to recovery rates following dessication. Donations were highly variable from year to year, and this variability relates to production dynamics within the reservoir versus the timing and depth of releases. These diatoms accounted for 0 - 84% of biovolume in fall samples and 0 - 80% of biovolume in spring samples to date. The planktonic guild was prominent in mainstem samples and not in the backwater and Big Eddy samples. This may be from greater exposure of substrates to drifting algae along the mainstem. Similarly, more planktonic drift taxa were found in R4 than R3 fall samples because the reservoir algae cells progressively settle out under typical flows (Figure A11). During high flows, the planktonic diatoms tended to remain suspended and settlement was lower and more even between R3 and R4.

3.3.2 Effects of Flows

Year-round implementation of 142 m^3/s minimum flows and full operation of REV 5 were initiated on December 20, 2010. Fall samples collected across the channel before and after REV 5 are compared in Table 3-2 and Figure 3-5. While species diversity was unchanged, many fall periphyton growth metrics were lower after the flow regime change, with fall 2012 having the lowest periphyton metrics and the highest flows to date. Both abundance and biovolume decreased significantly while chl-a did not, implying that a shift to fast-growing very small taxa occurred. Tiny (<20 micron) components of the biofilm can be utilized incidentally when invertebrates are foraging larger periphyton taxa.

Table 3-2: Range of periphyton metrics in MCR R4 and R3 (all depths combined) in 2007 – 2018

Fall	abundance cells/cm²	biovolume um³/cm²	chl-a ug/cm²	n
Pre REV 5	$6.55 \pm 4.57 \times 10^5$	$3.78 \pm 3.09 \times 10^{8*}$	1.04±0.75	105
Post REV 5	$5.10 \pm 3.14 \times 10^5$	$2.98 \pm 2.87 \times 10^8$	1.05±0.96	187
% difference	-22%	-21%	0.7%	
Spring				
Post REV 5	$3.34 \pm 2.30 \times 10^5$	$1.58 \pm 1.57 \times 10^8$	0.44 ± 0.38	295

** biovolume not available before 2011, thus only one year's data in this metric*

As expected, the the modelled velocity from discharge and Telemac-2D velocities indicated that maximum velocities correspond to the highest discharge flows, with back-watering causing a more variable relationship between dicharge and velocity, particularly in R3.

Increased fall filamentous green algae growth was observed in R4 and R3 after 2010 under the new flow regime. These slow-growing algae can form visible mats in the summer under ideal conditions where shear is low under stable, lower flows. Less favorable conditions include high flows when their mats are dislodged and desiccation when their filaments are destroyed. The area remaining wetted by minimum flows should retain short growths that could re-populate dewatered substrates. Filamentous growth in the R4 T2-T4 zone may continue to gradually increase over the years since minimum flows were implemented. Filamentous green algae were also prevalent in the spring 2012 samples but were uncommon (>4% abundance and biovolume) during all subsequent spring sampling sessions. This review of filamentous green algae distributions supports the assumption that flow management exerts a powerful influence on the MCR periphyton community.

When the fall T1 thalweg samplers are considered in isolation, only small differences were detected between pre and post minimum flows (Table 3-3). Small increases occurred in periphyton chl-a, biovolume and in % planktonic taxa and overall diversity indexes that may be attributable to the permanent wetted area created by implementation of minimum flows. Small decreases occurred in periphyton abundance that may be affected by increased maximum velocities with the REV5 flows

Table 3-3: MCR T1 thalweg samplers mean and standard deviation for pre and post implementation of minimum flows.

T1 Fall Periphyton metric	Pre Rev 5, min flows	Post Rev 5, min flows
chl-a (ug/cm^2)	1.13 ± 0.6234	1.42 ± 0.89
Effective # sp	7.2758 ± 2.693	8.82 ± 2.52
% planktonic (biov)	35.04 ± 12.05	41.34 ± 17.76
Simpson Index	0.7833 ± 0.09374	0.82 ± 0.06
Abundance cells/cm^2	6.95x10^5 100± 4.59x10^5	6.88x10^5 ± 3.72x10^5
Biovolume um^3/cm^2	3.82 X10^8 ± 2.86x10^8	3.88X10^8 ± 3.09 X10^8

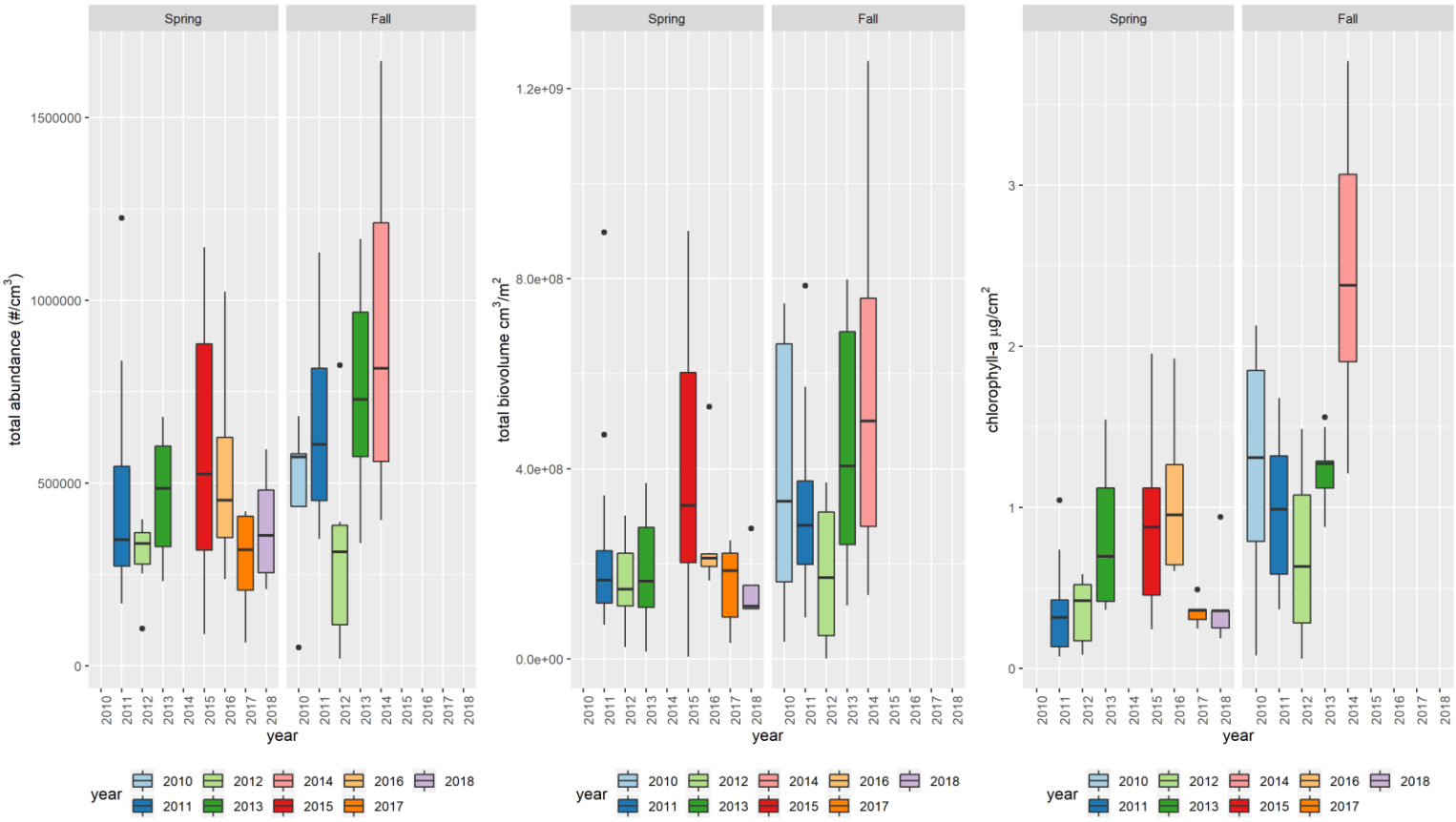


Figure 3-5: Periphyton productivity by year and season in R3 and R4 in the Thalweg (T1) zone. spring 2015, fall 2011 and fall 2012 had higher flows than average (Table A1).

Fall 2012 was the highest fall flow sampling session studied to date with a mean daily flow of 875 m^3/s and the highest number of hours that exceeded 1800 m^3/s. The spring sampling session with the highest mean daily flow was spring 2015 (Table A1). However, spring 2018

had the highest number of hours that exceeded 1800 m^3/s. Thalweg T1 periphyton metrics dropped significantly in 2018 at both reaches compared to years with a lower range of flows (Figure 3-5). In the fall thalweg data, R4 showed a greater difference than R3 between 2012 and typical flow years, possibly because water velocities would have been higher in the narrower R4 channel. Overall, both R3 and R4 had lower productivity metrics across the river transects with high flows in fall 2012.

In high-flow spring 2018 and fall 2012, the chl-a and biovolume at T1 samplers were 37-56% lower compared to previous spring and fall sampling sessions. The 40 hours of flows over 1800 m^3/s during the spring 2018 deployment and the 27 hours over 1800 m^3/s in fall 2012, likely caused high shear stress that resulted in a loss of periphyton (Figure 3-5).

Linear mixed effect models were used to determine if high velocities during the deployment period resulted in loss of periphyton. Biovolume had a negative association with maximum velocity in R4 samples but not in R3 (Figure 3-7). Abundance and chl-a in both R3 and R4 models had no associations with maximum or median velocity.

Year by year, productivity in R3 and R4 showed the same patterns in all growth metrics, however in both the spring and fall samples, R4 generally showed greater reactions to flows and growing conditions, while R3 reactions indicated greater periphyton stability despite variable flows and growing conditions.

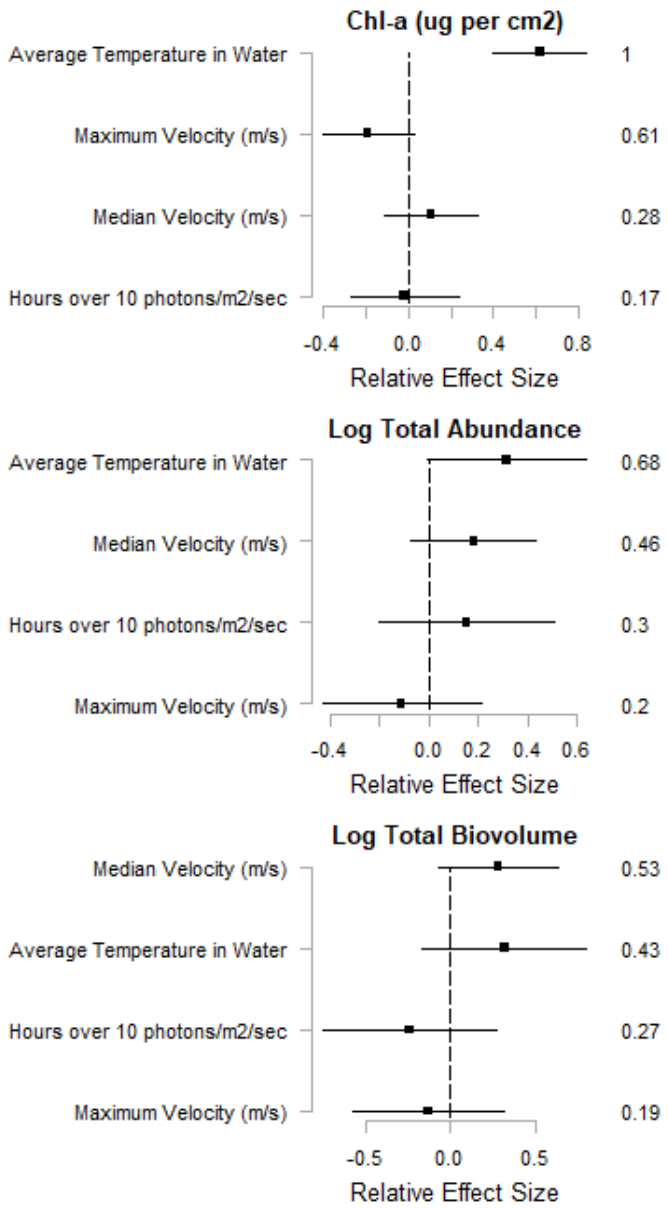


Figure 3-6: The coefficients and their 95% confidence limits (CLs) of standardized explanatory variables of periphyton production for mostly submerged R3 riverine samples for spring. Coefficients were standardized to allow comparisons of the direction and size of effects, noting that variables with CLs that do not cross zero have an effect on the response variable. Key explanatory variables are those that have a relative variable importance (RVI) of greater than 0.6-0.7; the RVI is shown on the right-hand side of each figure.

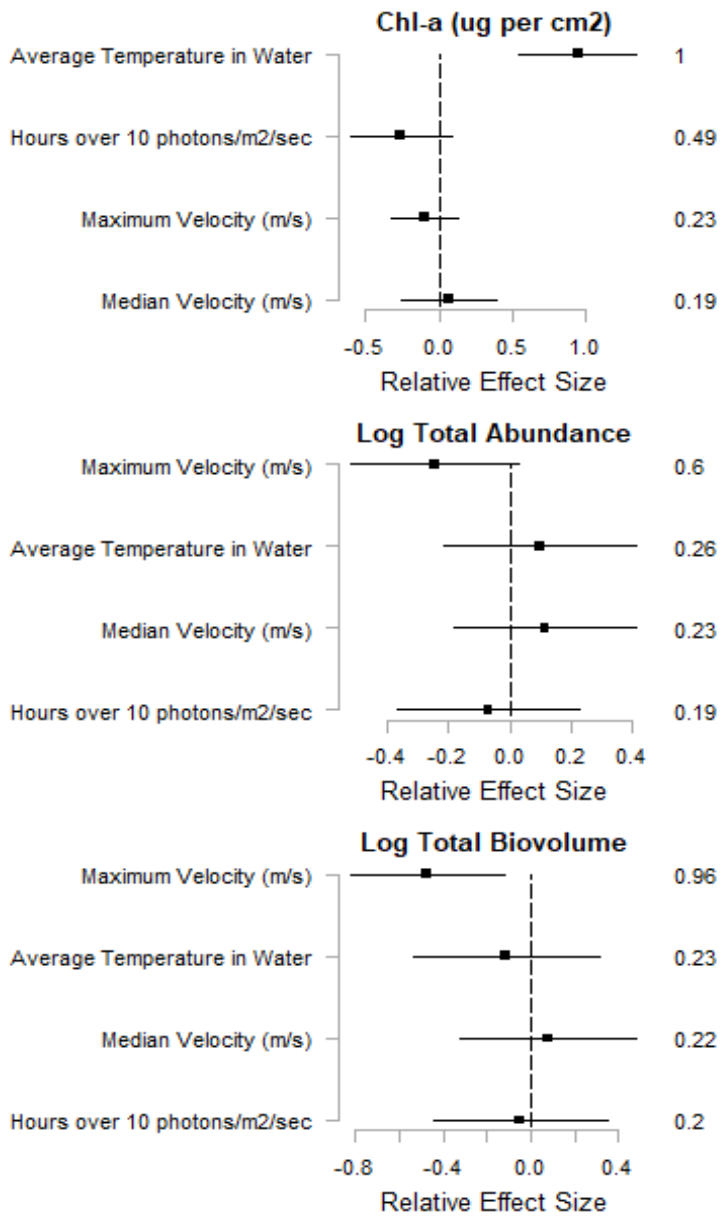


Figure 3-7: The coefficients and their 95% confidence limits (CLs) of standardized explanatory variables of periphyton production for mostly submerged R4 riverine samples for spring. Coefficients were standardized to allow comparisons of the direction and size of effects, noting that variables with CLs that do not cross zero have an effect on the response variable. Key explanatory variables are those that have a relative variable importance (RVI) of greater than 0.6-0.7 and the RVI is shown on the right-hand side of each figure.

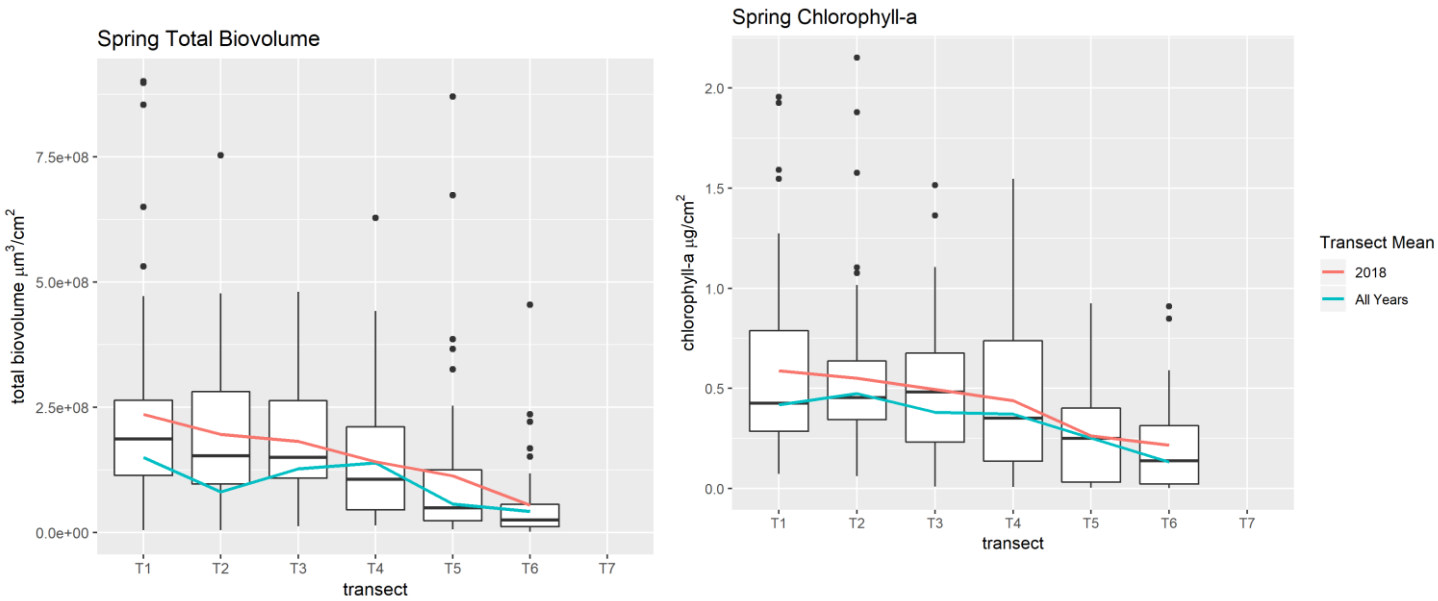


Figure 3-8: Total biovolume of MCR periphyton and chlorophyll-a in spring for 2010 to 2018 by sampler location (T1 deepest in thalweg to T7 shallowest on floodplain). The highest spring flows occurred in 2015

Flows should also affect the distribution of periphyton guilds, where high flows bias the MCR towards the small low-profile types and away from the large high profile and motile guilds. In terms of diatom abundance, the low profile guild averaged 41±20%, while high profile and motile guilds averaged 28±17%, and 8.1±9.4%, respectively. For perspective, these results are very different from the turbid, slower moving Peace River where the large diatom and motile guilds were more important (Schleppe et al. 2019).

Linear mixed effects models for percent high and low profile guilds were used to better understand the effects of physical habitat parameters on periphyton community composition in R4. Average water temperature was the most important predictor for the observed percentages of high and low profile algal guilds. The percent high profile guild was negatively associated with water temperature, whereas the percent of low profile guild taxa was positively associated with water temperature (Figure 3-9). Spring 2017 had the highest mean percentage of high profile guild taxa at the T1-T3 samplers and the lowest maximum flow of 1529 m^3/s compared to other spring sampling sessions (Figure A55). However, spring 2016 also had a low maximum flow of 1681 m^3/s but had low percent of high profile guild. Spring 2016 had the warmest water temperatures of all spring deployment periods, whereas spring 2017 and 2011 had the coldest water (Figure A55).

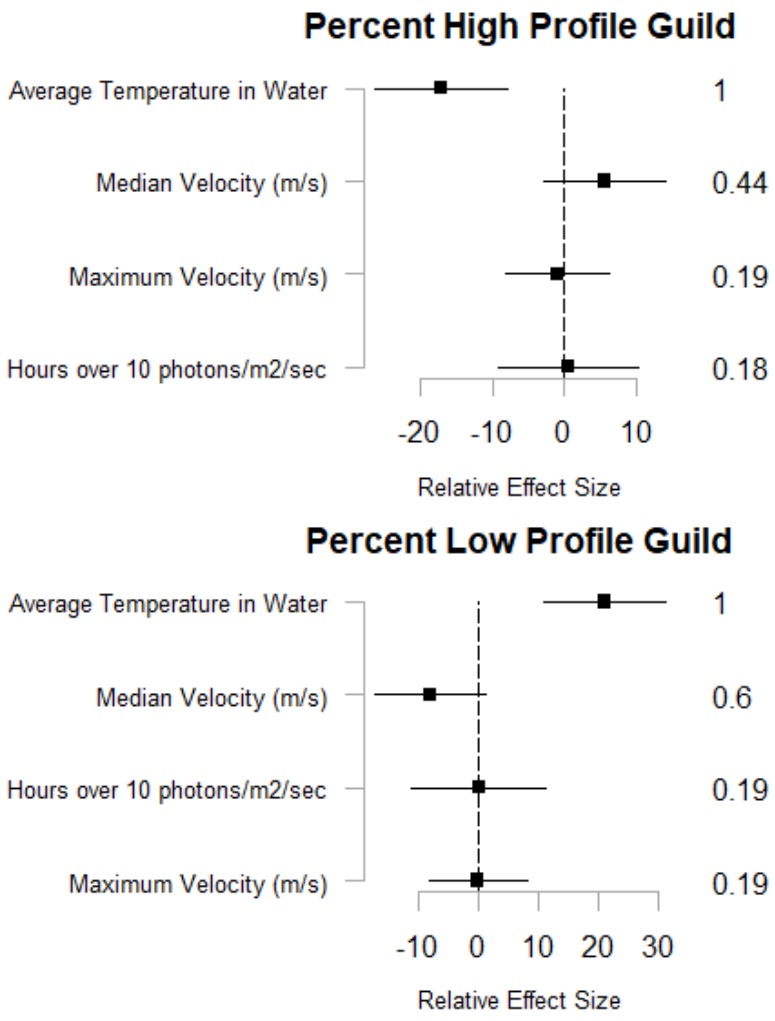


Figure 3-9: The coefficients and their 95% confidence limits(CLs) of standardized explanatory variables of periphyton production for mostly submerged R4 riverine samples for spring. Coefficients were standardized to allow comparisons of the direction and size of effects, noting that variables with CLs that do not cross zero have an effect on the response variable. Key explanatory variables are those that have a relative variable importance (RVI) of greater than 0.6-0.7; the RVI is shown on the right-hand side of each figure.

3.3.3 Effects of Water Depth

Throughout MCR and in both seasons, samplers in the permanently wetted and lower varial zone T1 through T3 had greater autotrophic periphyton production, while frequently exposed samplers showed increasing heterotrophic dominance and lower autotrophic production. Most of the organic material at heterotrophic-dominated sites was decomposer microflora and non-viable organic materials including dead diatoms, leaf litter and detritus. The distribution of algae groups through the range of transect depths was consistent between years and seasons, with declining diatom density but increasing flagellate, cyanobacteria and green algae density through the varial zone, at T3 through T6 positions.

When all biovolume measurements were compared to chlorophyll-a (chl-a) results, similar curves emerged (Figure 3-8). Average periphyton productivity decreased with increasing exposure from T1/T2 through T5/T6. For the transect depths that were consistently covered by minimum flows (T1/T2), or adjacent to the wetted edge (T3), algae cell biovolume was stable. The frequently dewatered T6 and T7 locations had the lowest biovolume and chl-a, particularly in R4 because few periphyton species can tolerate frequent desiccation. There were similar patterns of abundance and productivity among depths between spring and fall, but with lower overall production in the spring. In general, substrates that were wetted for periods greater than 9 hours per day experienced rapid periphyton growth (Schleppe et al. 2012).

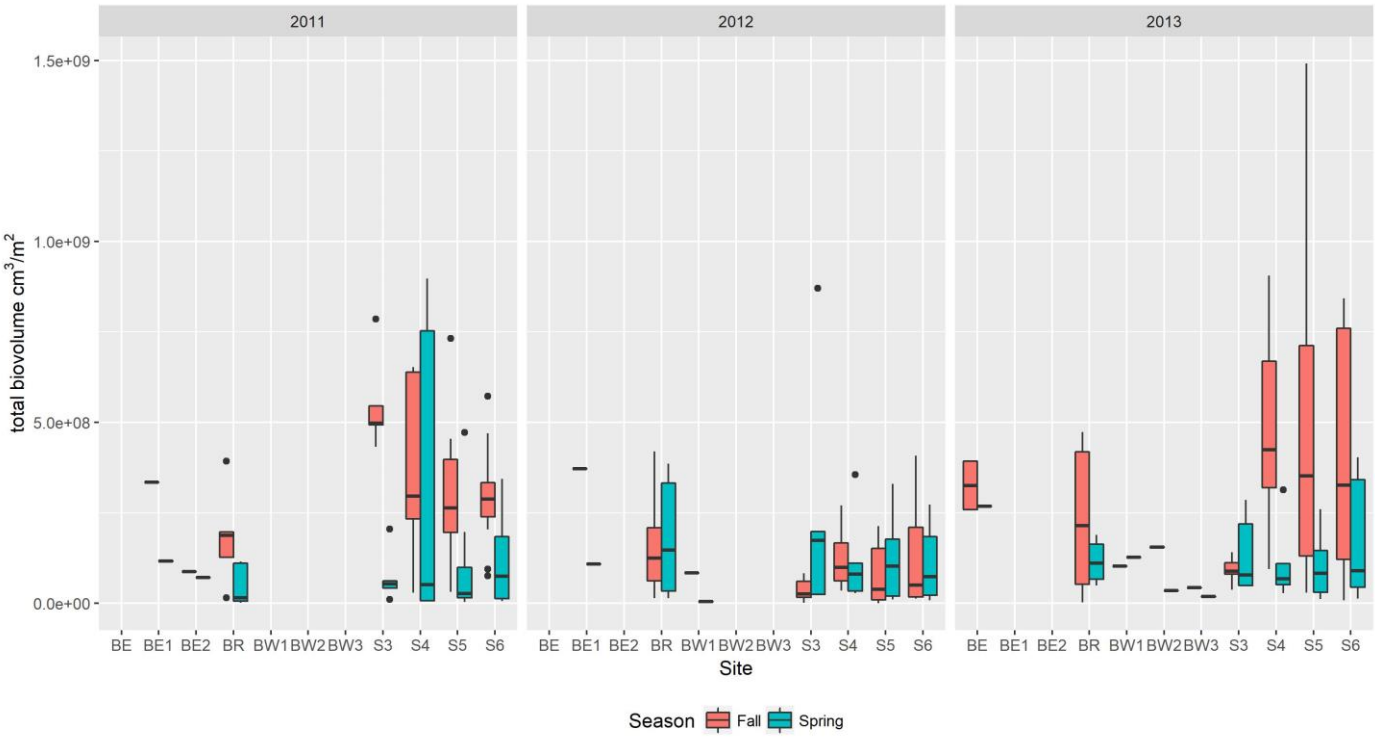


Figure 3-10: MCR Periphyton seasonal responses by site, 2011 to 2013 abundance and chl-a are presented in Appendix C.

3.3.4 Effects of Season

There were seasonal shifts in the dominant periphyton taxa in the MCR, likely in response to flows, light regime, water temperature and freezing conditions. In all spring samples, the same diatoms dominated the periphyton, along with large concentrations of rapidly reproducing single-celled algae. In fall samples, similar diatoms dominated and there was a greater contribution made by filamentous green algae. Spring samples had lower average species richness of 12 (T6) to 17 (T2) species/sample compared to fall samples at 15 (T6) to 23 (T2) species/sample.

Summary statistics for all spring sample periods are provided in Appendix B Table A3-4 and summarized in Table 3-4. Spring periphyton growth metrics were stable and low. Abundance ranged from 2.52 – 4.76 x 10^5 cells/cm^2. Chlorophyll-a ranged from 0.16 – 0.19 ug/cm^2 chl-a in the first three years, but more than doubled to 0.33 - 0.75 ug/cm^2 in the subsequent years, with 2015 and 2016 having the highest average chl-a. Spring 2015 and 2016 had warmer water temperatures from milder winters (Figure A53). Average water temperature explained more variation of chl-a in R4 compared to R3 in linear mixed effects models (Table A34 and Table A35). These warmer spring water temperatures increased periphyton growth in 2015 and 2016.

In all spring sample periods, average species diversity metrics were stable at 0.71 – 0.81 Simpson's Index and at 13 – 21 taxa. Average effecitve number of species was also stable in the spring sampling periods at 6.7-8.9. Productive spring seasons tended to have low contributions of reservoir algae to the periphyton mat. Overall, spring means and spring maxima among growth metrics were usually significantly lower than fall samples from the same year (Figure 3-10). Fall periphyton total abundance, chl-a, and total biovolume were significantly higher than spring periphyton productivity metrics in paired t-tests ($p<0.001$, Appendix C).

The fall sampling sessions demonstrated a range of mean abundance from 2.73 to 12.5 x 10^5 cells/cm^2, a range of mean biovolume of 0.98 – 6.05 x 10^8 microns^3/cm^2 and a range of mean chl-a of 0.49 to 1.76 ug/cm^2. For all fall growth metrics, the lowest year was 2012, the highest flow year to date. In all fall samples, the same diatoms were dominant, but with a significant filamentous green component. There was 3.0±7.9% nuisance algae Didymo in fall samples.

Table 3-4: Range of periphyton metrics in MCR (R4 and R3) by season, 2007 – 2018

Fall (all depths)	abundance cells/cm^2	biovolume um^3/cm^2	chl-a ug/cm^2	AFDW mg/cm^2	species richness	Simpson's Index
2007 – 2010	7.10 x10^5	3.78 x10^8	1.01	0.499	17.2	0.695
2012	2.76 x10^5	1.11 x10^8	0.47	0.400	21.6	0.704
2011 – 2014	5.10 x 10^5	3.45 x10^8	1.03	0.581	22.3	0.703
Spring (all depths)	**abundance cells/cm^2**	**biovolume um^3/cm^2**	**chl-a ug/cm^2**	**AFDW mg/cm^2**	**species richness**	**Simpson's Index**
2011 – 2018	3.34 x 10^5	1.58 x10^8	0.44	0.57	17.7	0.78

The spring sampling sessions demonstrated a range of mean abundance from 2.52 to 4.76 x 10^5 cells/cm^2, a range of mean biovolume of 0.97 to 2.79 x 10^8 microns^3/cm^2 and a range of mean chl-a of 0.16 to 0.75 ug/cm^2 – all ranges were lower than the corresponding fall sample sessions.

Like the full transect results, when the T1 samplers that are permanently wetted by minimum flows are considered, spring was significantly less productive than fall, but had similar community composition metrics (Table 3-5). These results also suggest that the resevoir donations were more important in spring composing 49% of periphyton, compared to 40% in fall samples.

Table 3-5: MCR T1 (Thalweg) periphyton productivity metrics in fall and spring.

T1 Periphyton Metric	Fall	Spring
chl-a (ug/cm^2)	1.28 ± 0.78	0.59 ± 0.46
Effective # sp	8.08 ± 2.70	8.12 ± 1.94
% planktonic (biov)	40.5 ± 17.1	49.36 ± 17.28
Simpson	0.80 ± 0.079	0.80 ± 0.10
Abundance cells/cm^2	$6.91 \times 10^5 \pm 4.12 \times 10^5$	$4.40 \times 10^5 \pm 2.65 \times 10^5$
Biovolume um^3/cm^2	$3.83 X10^8 \pm 2.85 X10^8$	$2.35 X10^8 \pm 2.01 X10^8$

There was minimal nuisance algae Didymo (<0.01% biovolume) in some spring sample sessions (e.g., 2017 and 2018), while other spring samples that had significant Didymo growth (8% biovolume in 2016).

In summary, seasonal conditions including weather, flows, light and water temperature all contributed to the observed spring and fall periphyton growth patterns observed in MCR.

3.3.5 Reach Effects

Many growth metrics were higher in R3 than R4 over the years of study, depending on factors including flows, back-watering and weather. When spring sample sessions were compared by reach, R3 had 18% higher cell abundance, 7% more biomass and 116% higher chl-a than R4 averages. When all fall samples to date were compared, R3 had the same abundance and biovolume as R4, but with 36% higher chl-a than R4. The large reach difference in spring chl-a was often driven by the occurrence of filamentous green algae in R3 samples but not R4 samples. Thus, spring was the season with the greatest difference between R3 and R4 periphyton productivity.

Substrate changes between R4 and R3 were reflected in shifts among periphyton dominants. For example, species that were planktonic or adherent (non-motile) were more common in R4 samples (e.g. *Synedra ulna, Achnanthidium minutissima*), while species that were stalked or motile increased in R3 samples (e.g. *Didymosphenia geminata, Navicula spp.*). These taxa changes were probably driven by substrate changes. R3 has greater sand concentrations, while R4 has more cobble and bedrock.

Reach effects including local water velocity, substrate type and duration of backwatering may alsoinfluence the distribution of the high-profile guild that shows an overall biovolume decline from the top of R4 to the bottom of R3 (Figure A10) in the fall data. The percent planktonic guild showed the reverse trend in the fall biovolume data. The spring periphyton growth metrics were lower than fall metrics and did not show distinct reach effects.

Although species composition changed between reaches, there was no observable difference in the Simpson's index (0.79) and effective number of species and only a negligible 5% difference in species diversity (19.7 – 18.8) between reaches. There are numerous mechanisms that account for similarities in species distribution in large rivers like the MCR. These include flow events that can either shield (backwatering) or move (high flow events) benthic species to new substrate locations. Additionally, the T1/T2 area that remained wetted by minimum flows and continuously received drifting algae from Revelstoke Reservoir, can function as a source of organisms to re-colonize exposed habitat areas with the same suite of taxa after catastrophic flow events.

3.3.6 Effects of Backwatering

A final aspect of MCR flow regime affected by both BC Hydro releases and by watershed hydrology is back-watering of Arrow Lakes Reservoir (ALR). This seasonal water cover reduces desiccation on substrates that would otherwise be exposed by low flow releases, particularly in the fall. It should also increase the opportunity for limnoplankton suspended in the ALR water column to settle onto MCR periphyton. In most years, sampler deployments in spring occurred at the lowest Arrow Lakes Reservoir levels and ended when backwatering was just starting in R3, while fall deployments commenced as backwatering declined in R3 and R4 (Figure A5). Both seasonal deployments can be affected by backwatering with R3 receiving the greatest effect. Since the hydrologic regime in the preceding week is always of greater importance to periphyton production than events that occurred further in the past (Schleppe et al. 2013), fall data should provide the best insight into the effects of backwatering on R3 productivity because of the recent loss of backwatering cover on the substrates (declining limb of hydrograph). The data summarized in Figure 3-5 illustrates the benefits of back-watering on periphyton, and this was confirmed by statistical modelling in previous years (Schleppe and Larratt 2016).

The R3 upper varial zone is the most variable region for periphyton productivity in the MCR. With continuous backwatering, it can exceed the productivity of deeper areas but in seasons without backwatering, it can have minimal productivity. For example, without backwatering, upper varial zone abundance dropped by about 30% and biovolume by 70% in fall 2013, while in fall 2014, the upper varial zone was continuously covered by back watering, resulting in far greater periphyton growth throughout the R3 upper varial zone (Figure 3-5).

High flows are another important influence on the R3 upper varial zone. Very high flows without backwatering (spring 2012) apparently curtailed productivity, while high flows with back watering into R3 (spring 2015) allowed moderate productivity. These effects of backwatering are accounted for in the statistical models and the reach-wide productivity model because they consider duration and timing of submergence.

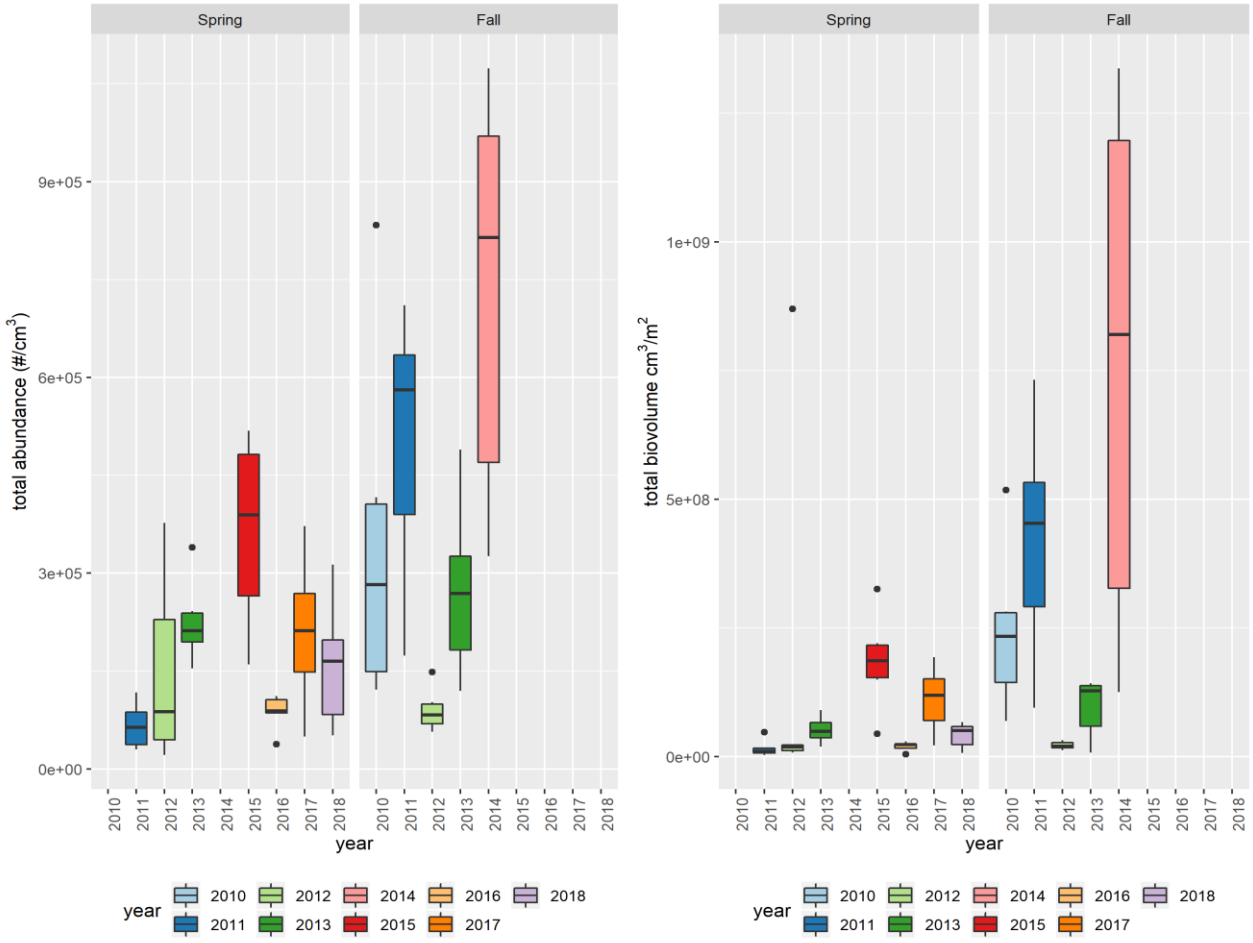


Figure 3-11: Upper varial zone (T5,T6) periphyton productivity in R3, 2010 – 2018 by year and season. All sampling periods were affected by some backwatering except spring and fall 2013 (Table A-1).

3.3.7 Death of Chl-a Before Implementation of Minimum Flows

Determining the effect of the implementation of minimum flows during the spring was difficult because no pre-spring data was collected.The influence of minimum flows on periphyton production is likely stronger in spring compared to fall because ALR backwatering protects R3 from extensive dewatering during the fall sampling sessions. In addition, freezing air temperatures in spring can cause higher periphyton death rates during dewatering compared to moderate fall temperatures. To better understand the effects of minimum flows a theortical exercise was conducted with chl-a death curves and historical discharge data. The number of consecutive hours below minimum flow (below 142 m^3/s) was used to calculate the percent loss of chl-a. The 2007-2010 data were used to calculate the theoretical percent loss of chl-a. The most frequently observed duration that flows that were below minimum was four to seven hours (Figure 3-12). Flows were rarely below minimum flow for longer than 10 hours and the maximum duration that flows were below minimum was 22 hours.The calculation of percent loss assumed that a drop below minimum flows resulted in exposure below the minimum flow line. After four to seven hours of exposure,

11-59% of chl-a can be lost through mortality (Figure 3-12). Using the conservative death rate which is feasible for spring and fall in the MCR, the percent loss of chl-a was 11-19% for four to seven hours of exposure.

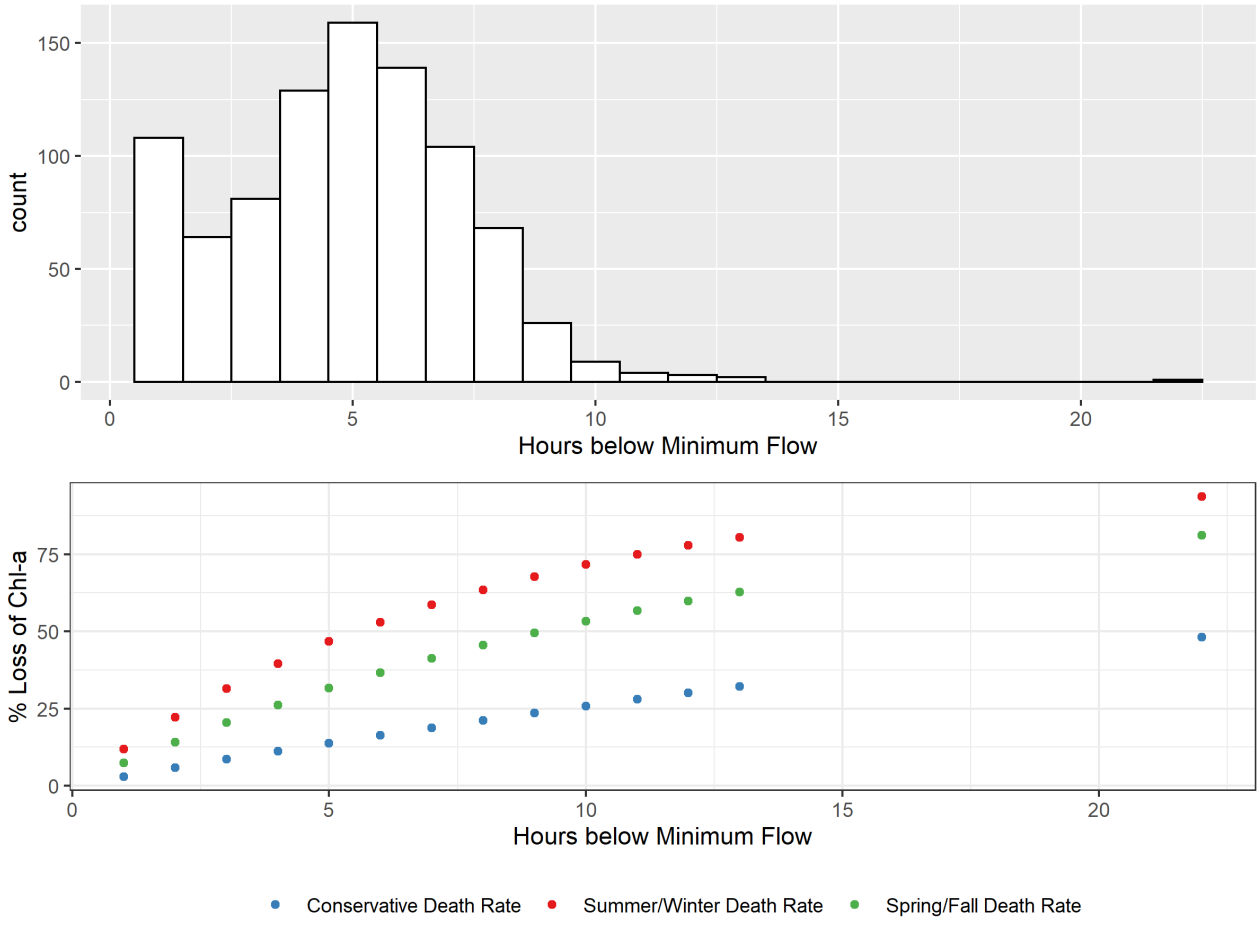


Figure 3-12: Histogram of consecutive hours below minimum flow for 2007-2010 and% loss of chl-a using variable death rates.

3.3.8 Periphyton Reach-wide Productivity Model Validation

The reach-wide productivity model (RWP model) was developed in 2017 and revised in 2018 with better growth curves. Predicted chl-a was compared to actual 2018 spring chl-a data in a RWP model validation exercise (Figure 3-13). If the point on the graph intersects the line with a slope of 1 and intercept of 0, the predicted value from the model is equivalent to the measured value. Using the first RWP iteration, most of the samplers, T1-T4, had overpredicted chl-a, with the exception of some of the T6 samplers where predicted chl-a values were accurate. The accurate T6 chl-a predicitons suggested that the death curve used in RWP was reasonable.

The spring growth curve was modified in 2018 and was used to improve the second iteration of the RWP model. The updated reach-wide model still overpredicted most of the chl-a

concentrations of the 2018 spring samplers (Figure 3-13), but the overpredictions were lower than in the original reach-wide model.

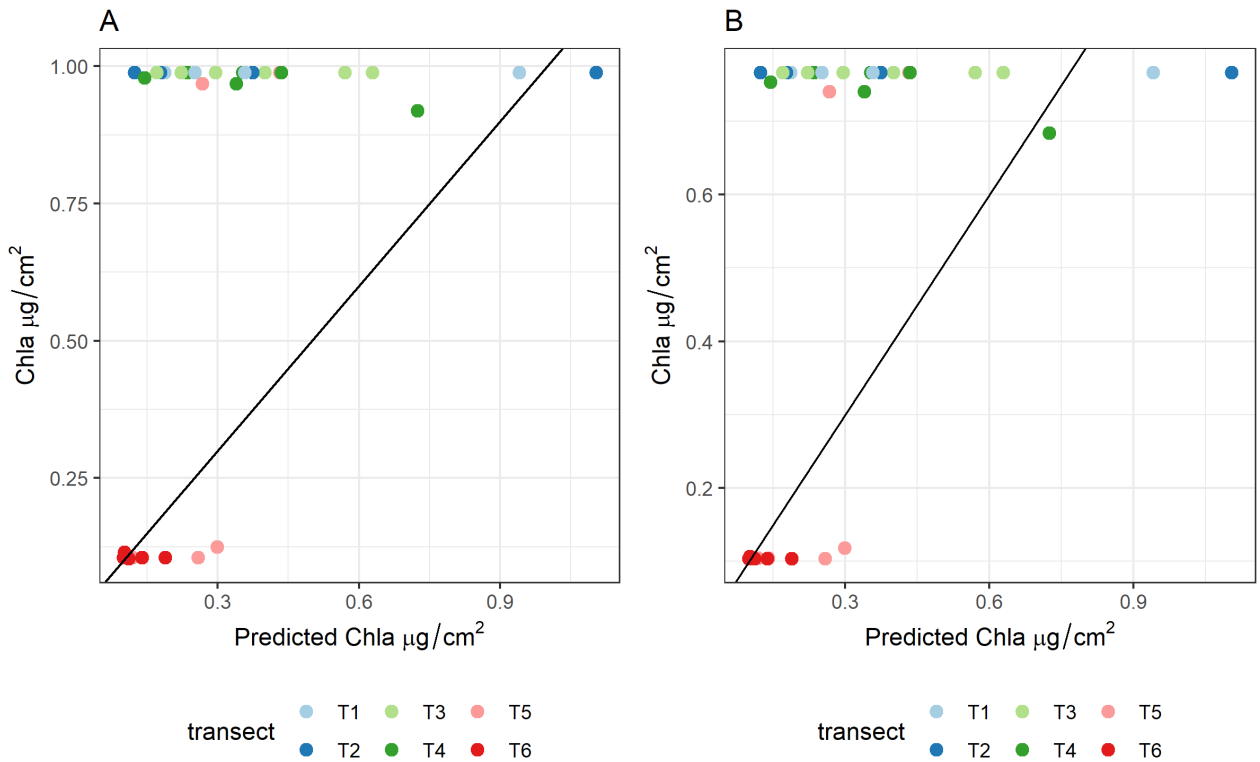


Figure 3-13: Comparison of predicted chl-a values from reach-wide model and 2018 spring chl-a. The black line has a slope of 1 and intercept of 0. A) Original reach-wide model B) Adjusted reach-wide model.

3.3.9 Periphyton Reach-Wide Productivity Model

A hydrologic model was used to determine the wetted history of R3 and R4 and the reach-wide productivity model was used to estimate periphyton chl-a as a function of growth and death using patterns of submergence. Daily periphyton chl-a estimates for 2007-2018 of R3 and R4 were compared used linear mixed effects models (Figure 3-14). The effect of minimum flows was first tested by comparing daily productivity without considering monthly differences. The second linear mixed effects model considered the effect of month and its interaction with the implementation of minimum flows.

The effects of minimum flows on periphyton chl-a in R3 and R4 were significant in both statistical models. When month was not included in the reach-wide productivity model, the effect of minimum flows on periphyton chl-a in R3 was significant (m=-0.016, p<0.001). The effect of minimum flows in R3 was stronger when month was added as a fixed effect with an interaction (m=-0.056, p<0.001). Month and its interaction with the implementation of minimum flows were also significant, meaning that an effect was more prevalent in some months than others. Similar to R3, the effect of implementation of minimum flows on R4 periphyton chl-a was stronger when month was included as an interaction term. The slope of the implementation of minimum flows was -0.028 (p<0.001) for the model without the

interaction term, whereas the model with the interaction term had a slope of -0.038, $p<0.001$. The larger negative slope with the interaction term included suggested that the implementation of minimum flows has variable effects on chl-a depending on the month.

The periphyton chl-a model indicated that implementation of minimum flows had a stronger effect on R4 chl-a than on R3 chl-a when the influence of month was not included. After the implementation of minimum flows, daily productivity was higher in February and March in both R3 and R4. The mean daily productivity of R4 was higher in October and November in 2011-2018 compared to 2007 and 2009-2010. October and November of 2008 was the only year before the implementation of minimum flows that had similar chl-a to 2011-2018. High chl-a productivity in October and November 2008 resulted from extensive R4 backwatering (Figure A5; Figure 3-14). Prolonged backwatering increased the wetted habitat area and obscured the benefits of minimum flows on reach-wide productivity.

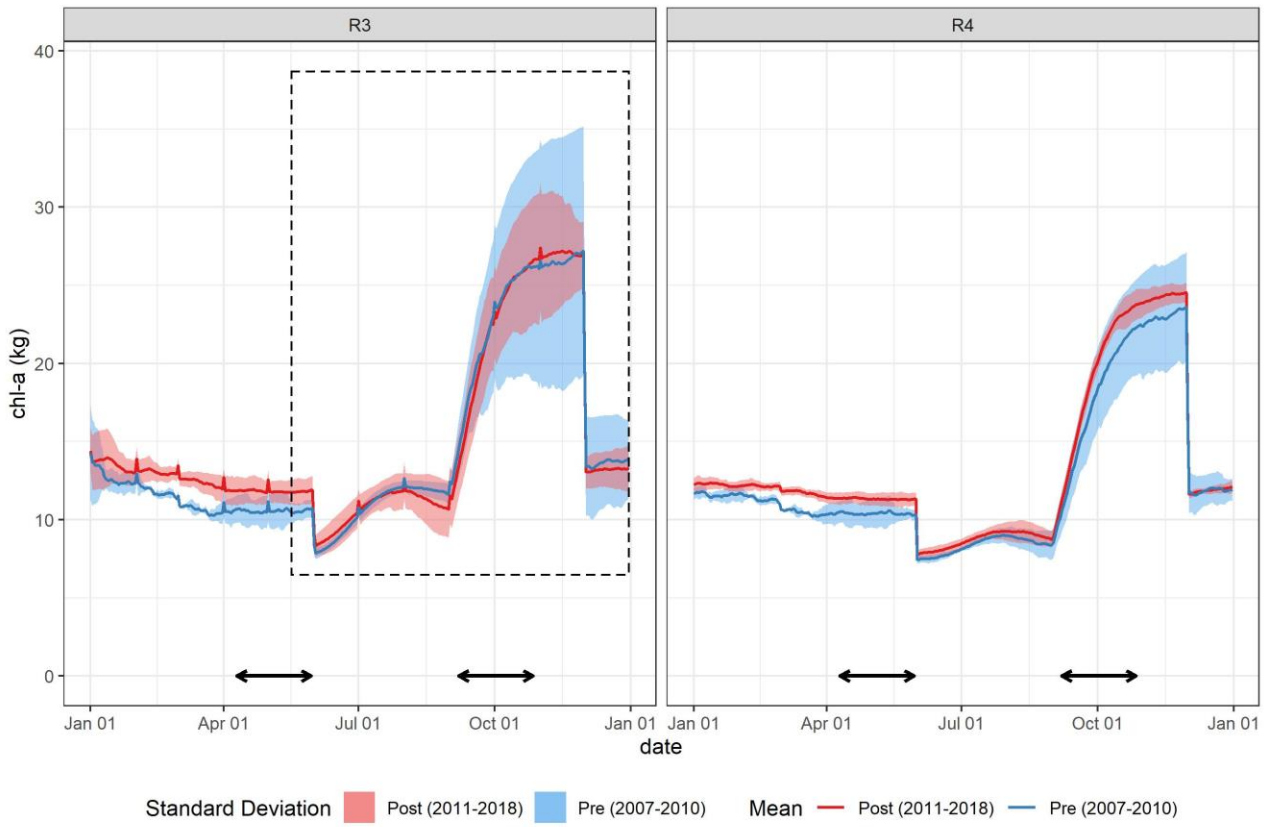


Figure 3-14: Comparison of Pre-Post Implementation of minimum flows for periphyton chlorophyll-a. The dotted box represents when R3 is typically backwatered from ALR and the arrows represent the typical range of spring and summer deployment periods.

3.4 Benthic Invertebrates

The results from previous NMDS analyses using the 2007-2015 data indicated that annual differences and implementation of minimum flows explained some community variation (Schleppe and Larratt 2016). However, separating natural annual variability in community structure from differences induced by operations or by implementation of minimum flows is challenging. Analyses for community groupings of benthic have not been analyzed since 2015 and past years' reports summarized the key findings. The biggest community differences observed originate from annual variability. Future consideration of community structure could assess species-specific responses.

Analyses in previous years used benthic production models to understand the underlying processes affecting invertebrate production. In 2017 and 2018, benthic production models were not run because the focus was shifted to the development and validation of the reach-wide productivity model using data from all study years. In previous years, the most important variable found to influence invertebrate production (abundance, biomass, EPT+D) was increasing submergence (Schleppe and Larratt 2015). Other variables including velocity, water temperature and substrate size were also identified as top predictors in different iterations of the RWP model. For this reason, submergence in either the day or night is still considered the most important factor affecting food for fish but other important physical variables that interact with flow are also important drivers of the whole benthic community.

3.4.1 Yearly Comparisons of Benthic Invertebrate Sampling

Relative biomass and relative abundance of benthic invertebrates varied between years at the lowest taxonomic levels of identification (family to genus). Members of *Hydra* sp., chironomids, and small tubificid worms were usually the most abundant, accounting for up to 75% of the total abundance in all years and seasons studied. Although not as numerically abundant, percent EPT measured as relative abundance was consistent across years. These trends were consistently observed in both spring and fall data. In most samples, 10 taxa made up over 85% of the total abundance at any sampling location.

Like periphyton, benthic invertebrate abundance and biomass tended to be slightly greater in R3 than R4 during most years and seasons, with standard deviations within a given year/season usually higher than the mean. Invertebrate species richness also varied among years with the lowest values in fall months occurring in 2010. Species richness was greater in R3 than R4 samples because R3 had more Ephemeroptera families including Baetidae, Ephemerellidae and Heptageniidae than R4 (Appendix B).

Percent EPT, Simpson's Index, and Hilsenhoff index metrics were much more consistent among years and seasons than invertebrate biomass and abundance. Percent Chironomidae and Diptera gradually increased throughout the study period in the permanently submerged and lower varial zones. Dipteran taxa were higher in spring 2017 and 2018 compared to previous spring samples. Benthic invertebrates were usually more abundant in the fall than in spring, however no effects of flow, season, or year were observed. The fall and spring sample pairs for benthic invertebrate abundance, biomass and fish food metric confirmed productivity is significantly higher in the fall compared to the spring ($p<0.01$).

Chironomidae were much more prevalent than EPT taxa, and accounted for 29-90% of the total abundance in the spring or fall at all sites. EPT taxa were most prevalent in 2012-2014, when they accounted for 2.5-5% of the total abundance in the fall and spring. Greater abundance of EPT taxa was associated with increased submergence of substrates within varial zones. Although the Jordan River was not sampled in recent years, existing data show it is an important source of invertebrates for areas within R3, noting mayflies are commonly found in drift (Anderson and Lehmkul, 1968). This partially explains the increased diversity and mayfly richness observed in R3 sites compared to R4 sites and these results are similar to other studies (Kennedy et al. 2016).

Abundance, biomass, species richness, percent Diptera and percent Chironomidae were highest from the mid channel to the lower varial zone (T1-T3) and declined with decreasing depth and increased exposure in the mid to upper varial zone (T4-T7). This supports the importance of submergence identified in previous years' models across several different production metrics.

3.4.2 Fall Pre and Post Implementation of Minimum Flows Comparison

Benthic invertebrate total abundance and biomass at fall T1 samplers were similar before and after implementation of minimum flows. Total invertebrate abundance at the T1 samplers had the highest variation in fall 2008 when ALR backwatering was extensive (Figure 3-15). Invertebrate biomass and fish food index were the highest in fall 2013 but similar in all other sampling sessions (Figure 3-16 and Figure 3-17). The productive fall 2013 season benefitted from low ALR elevations and from high 2012 flows that likely increased instar survival throughout the MCR, resulting in a higher colonization rate of permanently submerged habitat in 2013. The low ALR elevations in fall 2013 also reduced backwatering in R3 which provided favourable habitat for EPT taxa.

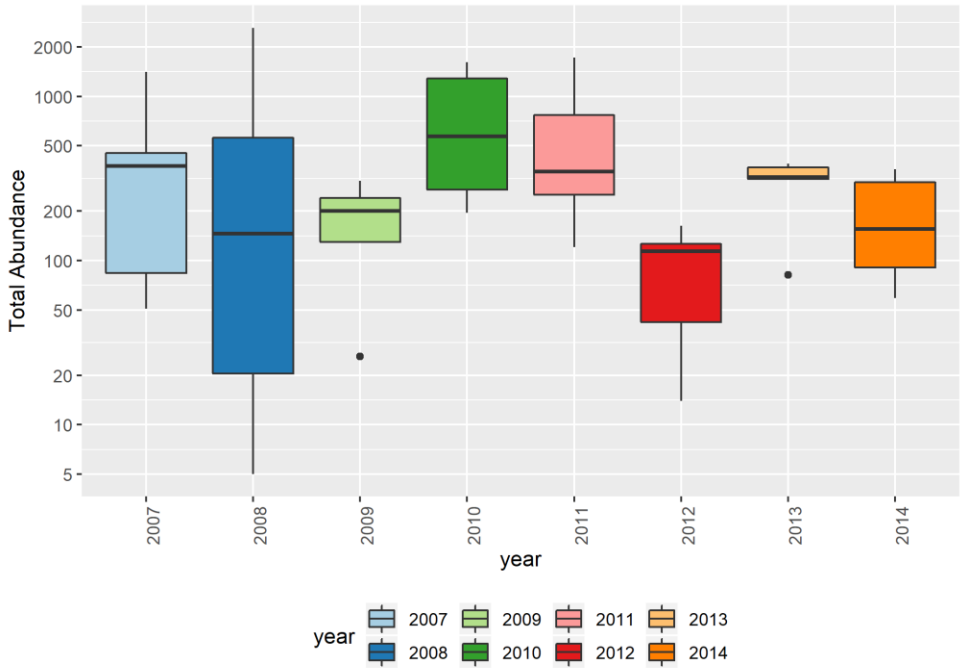


Figure 3-15: Invertebrate abundance for fall T1 samplers for R3 and R4 S3-S7 sites.

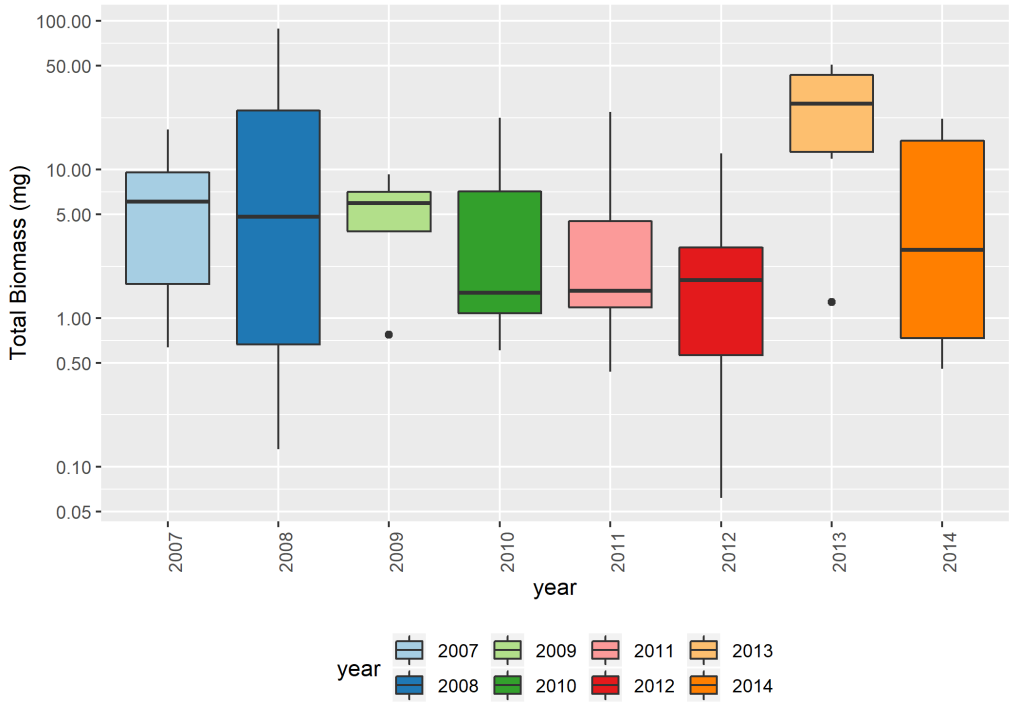


Figure 3-16: Invertebrate biomass for fall T1 samplers for R3 and R4 S3-S7 sites.

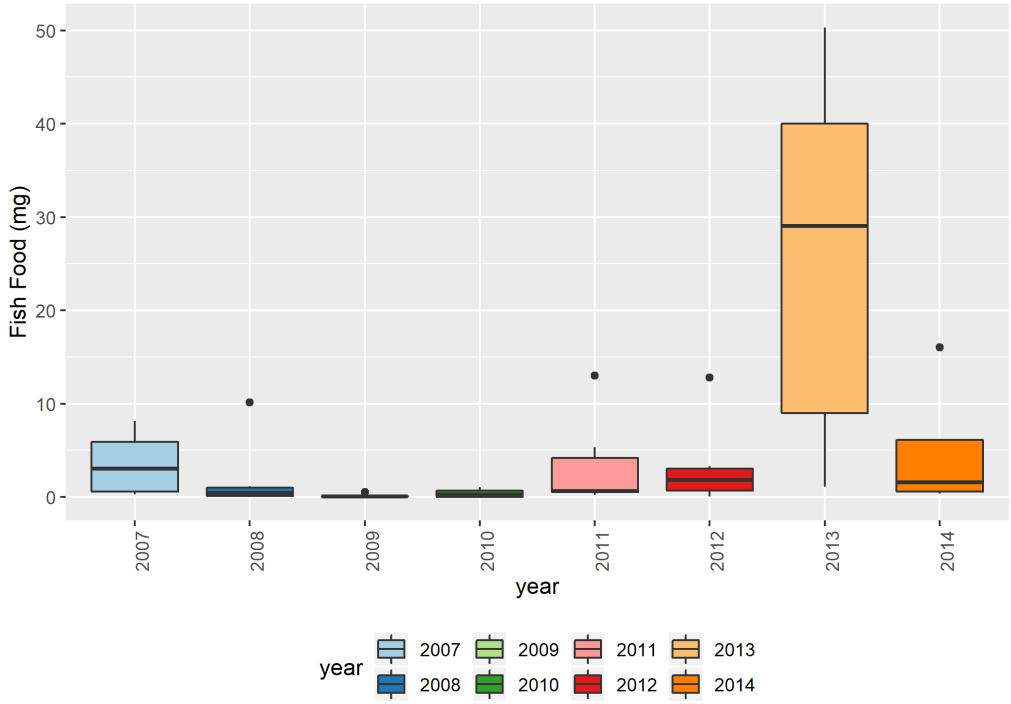


Figure 3-17: Fish food for fall T1 samplers for R3 and R4 S3-S7 sites.

Invertebrate community composition and diversity exhibited small differences before and after the implementation of minimum flows at fall T1 thalweg samplers. The mean percentages of EPT at the T1 samplers were similar in fall 2007, 2008, 2011-2014 (Figure 3-18). Fall 2009 and 2010 had lower percentages of EPT than other fall sampling sessions but also had lower sampler retrieval success. Diversity metrics (mean effective number of species) in fall 2011-2014 were higher than in fall 2007-2010 (Figure 3-19). Fall 2012 was the only year after the implementation of minimum flows that had an effective number of species comparable to fall 2007-2010. Very high flows occurred in August 2012 and fall 2012 that changed the habitat conditions and made the T1 samplers less favourable for invertebrate colonization.

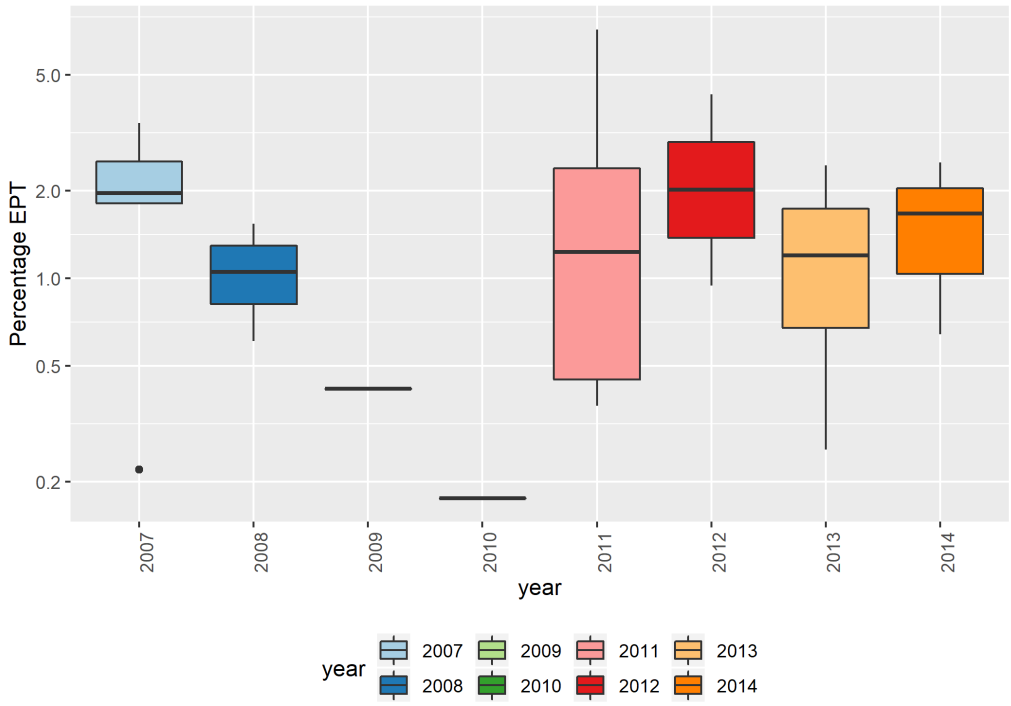


Figure 3-18: Percentage of EPT for fall T1 samplers for R3 and R4 S3-S7 sites.

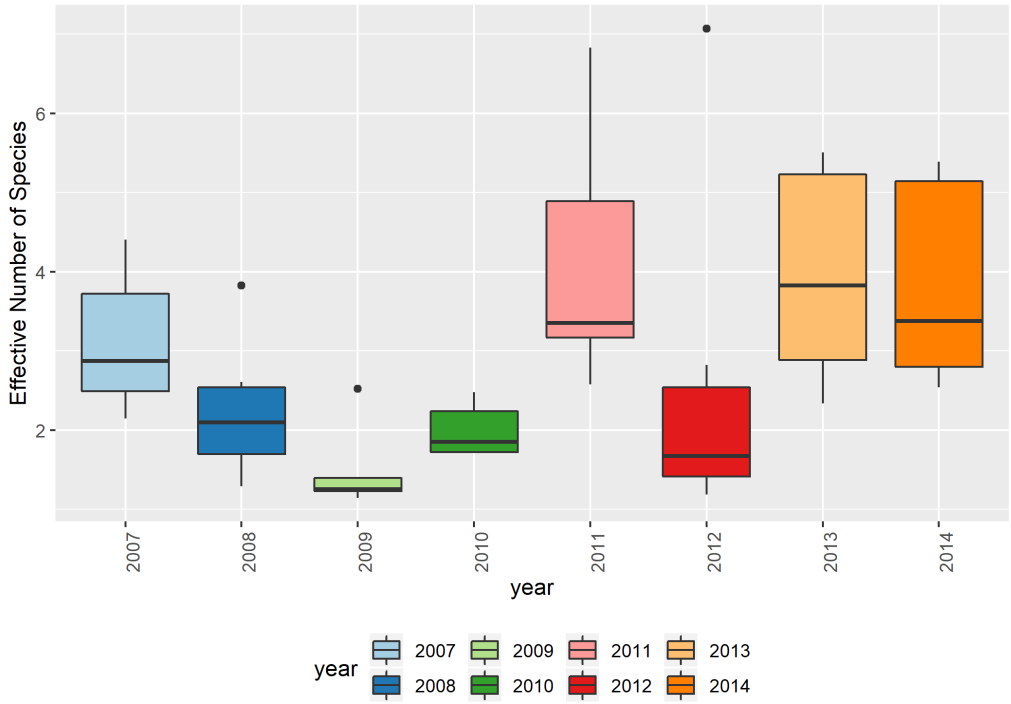


Figure 3-19: Effective number of species for fall T1 samplers for R3 and R4 S3-S7 sites.

3.4.3 Benthic Invertebrate Production Models

Benthic invertebrate production linear mixed effects models were used to test the effect of predicted velocity on invertebrate biomass, abundance and fish food index. Only samples that were submerged 95% of the time were included in the models. Separate linear mixed effect models were run for each reach because effects were expected to be reach-specific.

Velocity had a stronger influence on the invertebrate production metrics of abundance, biomass and fish food in R4 than in R3 (Figure 3-20 and Figure 3-21). Median velocity, maximum velocity and average water temperature explained 0-5% of variation in invertebrate production metrics of R3 (Table A36). In R4, maximum velocity explained the most variation in invertebrate abundance compared to the other invertebrate metrics (Table A37). Maximum velocities ranged from 0.94-2.7 m/s in R4 and 1.15- 2.3 m/s in R3 during spring deployment periods. The median difference in maximum velocities between R3 and R4 was 0.2 m/s. Maximum velocity also had a significant negative association with fish food and invertebrate biomass.

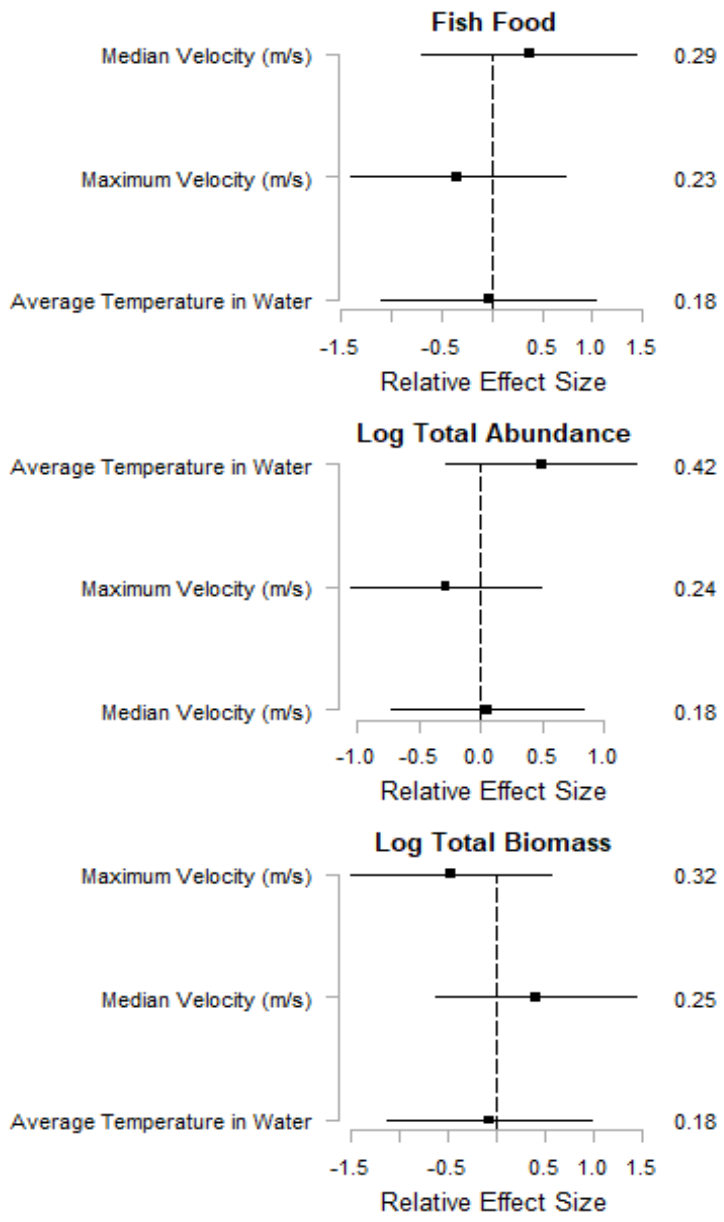


Figure 3-20: The coefficients and their 95% Confidence limits (CLs) of standardized explanatory variables of benthic invertebrate production for mostly submerged R3 riverine samples for spring. Coefficients were standardized to allow comparisons of the direction and size of effects, noting that variables with CLs that do not cross zero have an effect on the response variable. Key explanatory variables are those that have a relative variable importance (RVI) of greater than 0.6-0.7 and the RVI is shown on the right-hand side of each figure.

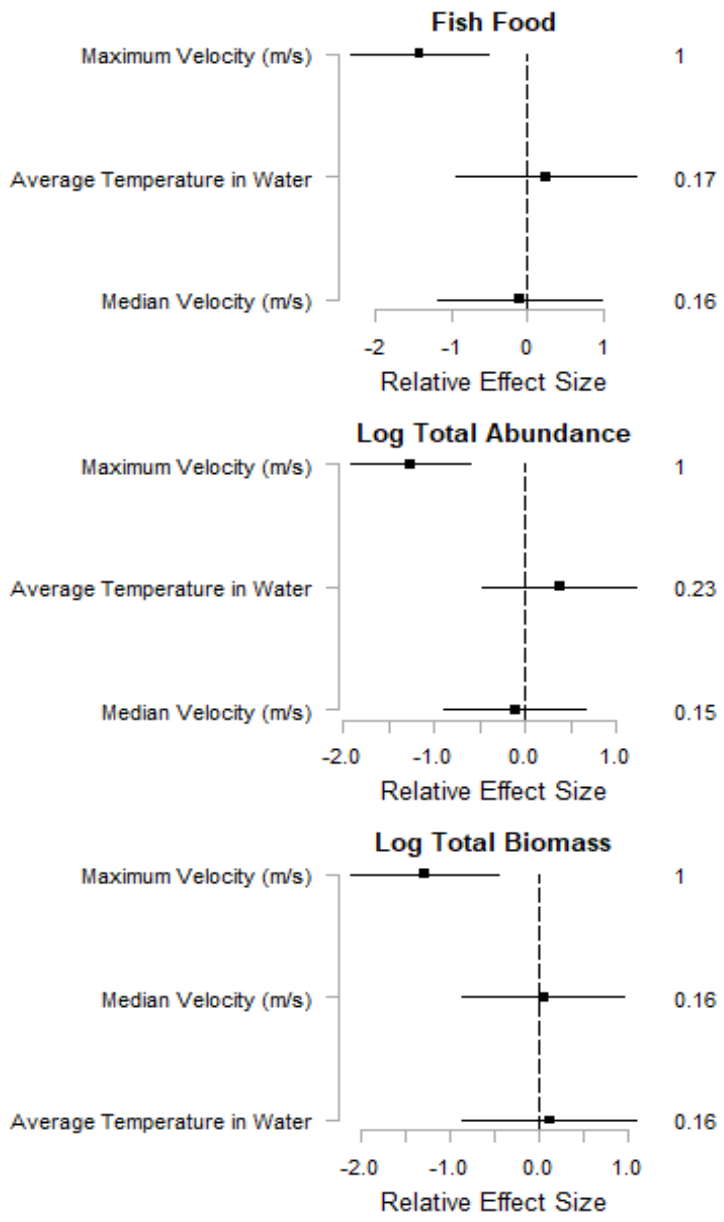


Figure 3-21: The coefficients and their 95% Confidence limits CLs of standardized explanatory variables of benthic invertebrate production for mostly submerged R4 riverine samples for spring. Coefficients were standardized to allow comparisons of the direction and size of effects, noting that variables with CLs that do not cross zero have an effect on the response variable. Key explanatory variables are those that have a relative variable importance (RVI) of greater than 0.6-0.7 and the RVI is shown on the right-hand side of each figure.

3.4.4 Benthic Invertebrate Reach-wide Productivity Model Validation

The reach-wide model was used to predict total benthic invertebrate biomass for samplers that were retrieved in spring 2018. The invertebrate biomass of T6 samplers were underpredicted by the model, whereas the biomass of all T4 samplers were overpredicted (Figure 3-22). Most of the T1 and T2 samplers also had overpredicted invertebrate biomass by the reach-wide model. The consistent underprediction of T6 sampler biomass suggested that the slope of the death curve is too steep. The death curves were derived from Trichopterans and Simuliidae because this was the only data available, yet these invertebrates were not among the MCR dominants that included desiccation-resistent chironomids, Hydra and small tubificid worms (Jones 2013).

The invertebrate biomasses of two T3 samples were underpredicted by the reach-wide model. These two T3 samples also had higher biomasses compared to all other 2018 samples because the R3-S6-T3 sampled contained one *Megarcys sp (springflies).* that weighed 102.9 mg, whereas the R4-S5-T3 sample had one *Clistoronia* (caddisfly) that weighed 44.5 mg.

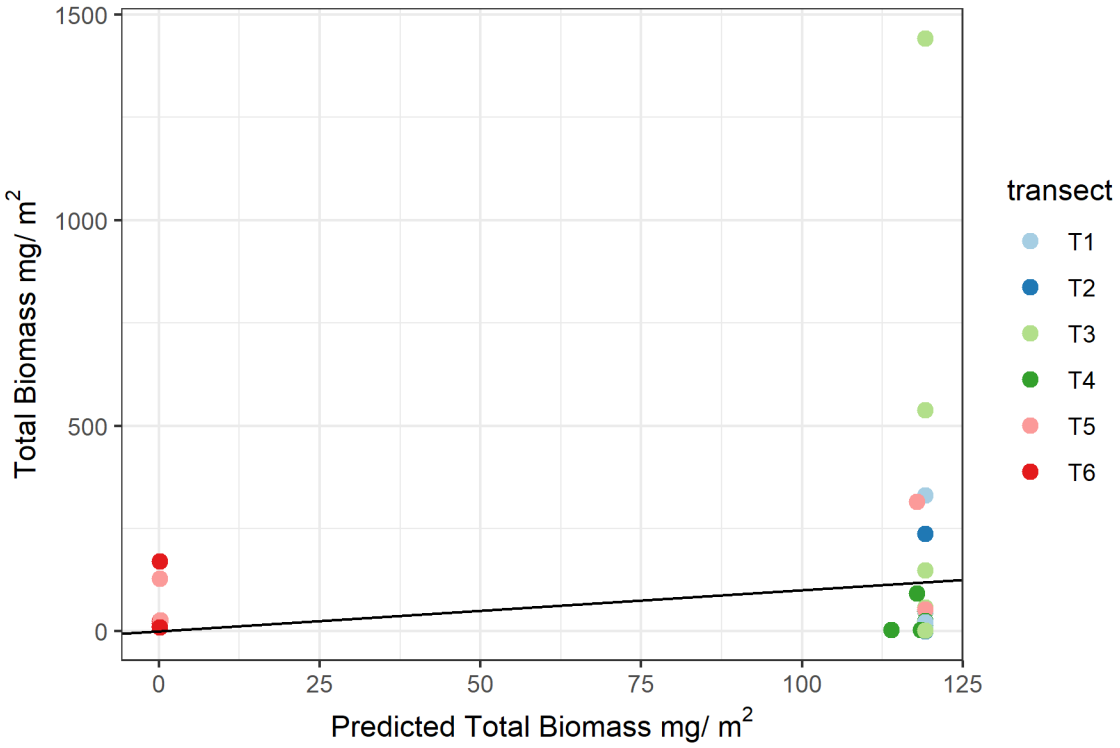


Figure 3-22: Comparison of predicted invertebrate biomass values from reach-wide model and 2018 spring invertebrate biomass. The black line has a slope of 1 and intercept of 0.

4.0 DISCUSSION

As in all regulated rivers, periphyton and benthic invertebrate components of the MCR benthic communities are sensitive to changes in habitat conditions and are good indicators of hydrologic disturbance (Biggs and Close 1989; Blinn et al. 1995). The 12-year monitoring program to determine the effects of minimum flows and REV 5 flows on MCR periphyton and benthic invertebrates is nearing completion. The main objective of the 142 m^3/s minimum flow strategy is to enhance the productivity and diversity of MCR benthic communities by increasing the permanently wetted area by an estimated 32–37% (Golder 2012). This discussion summarizes the findings from the 2007 to 2018 field surveys and subsequent analyses.

This study seeks to answer the Management Questions for MCR. They are:

> Q.1. What is the composition, distribution, abundance and biomass of periphyton and benthic invertebrates in the section of MCR subjected to the influence of minimum flows?
>
> Q.2. What is the effect of implementing minimum flows on the area of productive benthic habitat?
>
> Q.3. What is the effect of implementing minimum flows on the accrual rate of periphyton biomass in the MCR? Is there a long-term trend in accrual?
>
> Q.4. What is the effect of implementing minimum flows on the total abundance, diversity and biomass of benthic organisms in the section of the MCR subjected to the influence of minimum flows? Is there a long-term trend in benthic productivity?
>
> Q.5. If changes in the benthic community associated with minimum flow releases are detected, what effect can be inferred on juvenile or adult life stages of fishes?

These five Management Questions on the effects of minimum flows and REV 5 flows on MCR productivity are addressed in the following discussion sections.

Overview of flow effects In the MCR, peak flows occur during the day while low flows are more prevalent at night, corresponding with peak power production and usage in BC. Within this general pattern, flows are highly variable on a day-to-day and month-to-month basis, where some seasonal patterns are present. Natural variation from freshet flows and storm events augment regulated flows and can create periods with unusually high flows like the freshet of 2012. Extreme events (flows in excess of 1800 m^3/s, or minimum flows of 142 m^3/s that extend beyond 48 hours) occur regularly and can create habitat conditions that affect community structure and productivity, even to the point of large-scale die-off of benthic communities during longer periods of exposure during warmer weather. Based on the research conducted to date, we conclude that extreme events, coupled with routine BC Hydro operations, ultimately determine the area of productive habitat and the benthic community structure within the MCR.

4.1 Q.1. What is the composition, distribution, abundance and biomass of periphyton and benthic invertebrates in the section of MCR subjected to the influence of minimum flows?

Like most large rivers, MCR periphyton communities were dominated by diatoms representing between 82 and 98% of the biovolume at all sample sites. Other taxa including filamentous green algae were more prevalent near the edge of permanently wetted areas (T2), and in the lower varial zone (T3/T4) where stable substrates were present. The small-celled flagellates, cyanobacteria, and colonial greens were numerous but rarely exceeded 1.5% of the biovolume in MCR samples. Finally, in upper varial zone (T5/T6), periphyton communities transitioned from producer to consumer organisms, as indicated by the Autotrophic Index at T5/T6 locations. AFDW (volatile solids) results have oscillated over the years and seasons indicating continual adjustments in the balance of producers and consumers, probably in response to habitat drivers, principally flows.

MCR benthic invertebrate communities were also dominated by taxa that are more tolerant of disturbance, such as chironomids (Tonkin et al. 2009). These taxa are often over-represented in flow-managed rivers (Bunn and Arthington 2002). EPT taxa and chironomids were more abundant in samples collected along the edge of minimum flow (T2) or in the lower varial zone (T3), and was also suggested by our modelling of permanently submerged habitats (Schleppe et al. 2014).

Although the major taxonomic group contributions of periphyton and benthic taxa remained the same among the three zones, the dominant species varied with a number of determining factors including: operations, weather conditions, physical habitat constraints and the interaction between life history strategies.

This question is addressed in more detail by submergence zones in sections 4.1.1 to 4.1.8

4.1.1 Permanently Submerged Areas

Permanently submerged areas were sampled at T1 (thalweg, mid channel) and T2 (channel edge at minimum flow) transect locations. Similar to most large rivers, MCR periphyton production in permanently wetted areas was negatively correlated with velocity and substrate embeddedness, but positively correlated with increasing light intensity and substrate size (Schleppe and Larratt 2016). Peak production occurred near the edge of the permanently wetted channel at T2 locations where shear stress was less, light penetration was greater, substrates were stable, and the effects of scour and saltation were not as pronounced as they were near the thalweg at T1 locations. Time series data suggested that extreme high flow events with velocities exceeding 2 m/s coincided with periphyton thinning in the T1 thalweg zones. These high velocities were theoretically sufficient to cause shearing of filamentous algae (Flinders and Hartz 2009), and to mobilize sand particles that cause periphyton thinning through abrasion (Gregory et al. 1991; Goudie 2006; Luce et al. 2010).

Similarly, high thalweg water velocities likely reduced invertebrate biomass through scour, although some benthic invertebrate taxa have specific preferences for high velocity sites due to feeding styles (Sagnes et al. 2008; Jowett et al. 2003). The area permanently wetted by minimum flows supported the most productive and diverse benthic invertebrate communities. Overall, the permanently wetted zone productivity is within the range expected for oligotrophic or stressed large rivers (Table A38).

Like the full transect results, when just the deepest T1 thalweg samplers that are permanently wetted by minimum flows are considered, spring was significantly less productive than fall, but had similar community composition dominated by rapidly reproducing diatoms and phytoplankton from Revelstoke Reservoir. This finding confirms the importance of Revelstoke Reservoir in supporting MCR productivity, and suggests that flows control the deposition of phytoplantkon on the river substrates.

Spring thalweg samples were not collected prior to the implementation of minimum flows, but fall samples were. When all fall T1 thalweg sampler data before and after implementation of minimum flows are compared, only small differences were detected. Prior to implementation, the periods where the area covered by minimum flows commenced drying were often brief and occurred most often at night. None the less, small increases occurred in periphyton abundance and biovolume that may be attributable to the permanent wetted area created by implementation of minimum flows. This benefit is offset by increased REV5 maximum velocities that may have caused the observed small decreases in % planktonic taxa.

4.1.2 Lower Varial Zone (mid-channel)

The second habitat condition that exists in the mid-channel area of MCR was much more variable and dynamic. It occurred above the boundary of the permanently wetted habitat in what is termed the lower varial zone, typified by T3 and T4 sampler locations. The fluctuations between submergence and exposure usually occurred at night and resulted in less desiccation than the equivalent exposure period in daylight hours (Self and Larratt, 2013; Vincent 2007). Further, these areas were submerged during moderate flow events (between 600 to 800 m^3/s) that occurred more frequently than higher flow events. The heterotrophic components of the biofilm can continue growing in damp substrates in the dark, while the photosynthetic components cannot, resulting in greater heterotrophic contributions to overall production in this zone. The invertebrate community underwent periods of growth and decline depending on how the recent operating regime coincided with their life cycles. The variable hydrologic conditions of MCR tended to select for rapid colonizers and rapid reproducers.

The lower varial zone is productive and an important component of the overall productivity of the MCR. However, the time series chl-a accrual rate at T3 positions was significantly lower than T1 positions during most seasons and years, likely influenced by mechanisms of exposure (Schleppe and Larratt 2016). In the LCR, the total time spent in variable submergence before a more permanent submergence has also been shown to increase the time required to achieve peak biomass (Olson-Russello et al. 2015). Statistical modelling provides further support of this because factors including daytime submergence and substrate exposure were crucial predictors of both periphyton and benthic invertebrate community development in the lower varial zone (Schleppe and Larratt 2016). Research below the hydropeaking Glen Canyon Dam in Colorado show similar results, where abundance and diversity of EPT were reduced by daily, post-dusk, flow reductions immediately following egg deposition of substrate-dependant species (Kennedy et al. 2016). Overall, increasing EPT taxa were associated with increased substrate submergence within the varial zones and at times, frequently wetted substrates were as productive as those that were permanently wetted.

4.1.3 Upper Varial Zone

The frequently de-watered upper varial zone was typified by T5 and T6 locations, and included some samples from T7 located in the floodplain. It was less productive than the lower varial zone because these substrates experience regular daytime fluctuations between submergence and exposure. These conditions resulted in a benthic community that underwent brief periods of growth and frequent collapses determined by the timing and duration of exposures and how they intersected benthic invertebrate life cycles. Although the upper varial zone periphyton community had a similar structure to deeper zones, reduced species diversity and accrual rates indicated stress, particularly to the photosynthetic microflora. Periphyton production commenced and rapid growth occurred after the substrates were wetted during daylight hours for periods of >9 hours (Schleppe et al. 2012). Periphyton production halted when the substrates were dewatered during the day because normal cell processes could not proceed and desiccation stress reduced survival in both invertebrates and periphyton. The upper varial zone became more heterotrophic as the frequency or duration of drying events increased. This finding is also supported by modelling data for the periphyton autotrophic index in previous years that identified the frequency of 12-hour submergence events and total incubation time in the water and light, as important factors (Schleppe et al. 2013).

Benthic invertebrate productivity in the upper varial zone was dependent on a combination of operations and annual variability. Higher spring flow years 2015 and 2018 had higher invertebrate abundance and biomass of fish food organisms compared to other years that had lower flows. Higher flows keep the upper varial zone wetted for longer periods, resulting in less invertebrate death.

Chironomids and oligochaetes were the dominant invertebrates in the upper varial zone in MCR fall and spring samples. However, the percent abundances of chironomids, oligochaetes, hydrozoans and EPT showed high variability between years and between sites within the upper varial zone. Both chironomids and oligochaetes can withstand frequent substrate dewatering and high flows and as a result, these invertebrates thrive in MCR during high flow years (Schleppe et al. 2019).

The floodplain zone (T7) commenced beyond the upper varial zone and it was wetted only in very high flows and was not a significant contributor to MCR productivity. It did not produce true aquatic species, but rather it supported a riparian microflora community including aerial cyanobacteria, fungi, and heterotrophic bacteria. The floodplain did donate terrestrial detritus during flows exceeding 1700 m^3/s, but these floodplain benefits occurred infrequently and were mostly associated with allochthonous nutrient input rather than production originating from benthic community development. Infrequent floodplain contributions to river productivity are typical of larger rivers (Doi 2009).

4.1.4 Varial Zone Boundary Conditions

The boundaries between the productivity zones in MCR were dynamic. Based on MCR and LCR time series accrual data, these boundary positions depended upon the average flow regime during the preceding 30-70 days (Olson-Russello et al. 2015). Growth within these zones occurred rapidly during a 6-month period, when appropriate conditions for benthic community development occurred. The width of the productive lower varial zone expanded during stable flows in the 400 to 800 m^3/s range.

4.1.5 Benthic Community Determinants, Composition and Diversity

Statistical modelling results previously identified submergence as the top predictor of benthic production and diversity (Schleppe and Larratt 2016). In previous years, benthic invertebrate diversity models explained limited variation. This could be a result of uniform diversity among sites and transects. The effect of hydropeaking on benthic diversity has not been well studied. However, all studies generally found benthic diversity was lower and less variable below a dam, and included taxonomic shifts (Hasting 2014; Ellis and Jones 2013; Mihalicz et al. 2019). These studies also identified variable impacts on invertebrate density that had a seasonal component.

Physical parameters including velocity and substrate type were important determinants of periphyton and invertebrate community establishment in permanently submerged habitat areas (Schleppe and Larratt 2016). In 2018, the effect of maximum velocity on productivity was investigated and is discussed further in Section 4.2. During hydropeaking operations, complete dewatering of river-edge substrates used exclusively by some Ephemeroptera and Trichoptera egg-layers could cause their extirpation (Kennedy et al. 2016). Large peaks in flow on other regulated rivers have induced decreases in invertebrate species density, diversity and biomass (Robinson et al. 2004) and caused shear stresses sufficient to thin algal communities (Flinders and Hartz 2009). Overall, MCR benthic invertebrate productivity indicates that MCR is a stressed system compared to other river systems of similar size (Table A39).

4.1.6 Effects of Flow Ramping

The rate of substrate de-watering (ramping) events influenced the mode of periphyton and benthic invertebrate recovery and interacted with the life history of different taxa. In large rivers, rapid water loss through ramping down of hydro releases restricted in-situ benthic recovery and caused recovery to be driven by recolonization (Stanley et al. 2004; Kennedy et al. 2016). Periphyton originating from the Revelstoke Reservoir are expected to be important to periphyton recovery while drift of invertebrates from tributaries is expected to be important to benthic invertebrate recovery in the MCR, similar to studies conducted on other regulated rivers (Kennedy et al. 2016). However, since the full suite of environmental data including detailed submergence predictor variables was not studied before Rev 5 flows, a statistical model to test the importance of ramping is not possible.

4.1.7 Benthic Recovery from Dewatering

The ever-changing hydrologic patterns in the MCR varial zone induced a benthic invertebrate community that was in a constant state of recovery following periods of exposure of >24 to 48 consecutive hours (Schleppe et al. 2012). Recovery rates were variable among the MCR benthic communities. MCR periphyton recovery was usually faster than invertebrate recovery because periphyton reproduction rates are faster and because bacteria and cyanobacteria form organic coatings that pre-condition dewatered substrates, allowing faster recolonization (Stockner 1991; Wetzel 2001, Robson 2000). Our desiccation/re-wetting experiments (2010) indicated that resumption of growth occurred faster for species capable of rapidly producing desiccation-resistant structures such as akinetes or extracellular mucilage. Even with these strategies, the rate of desiccation can exceed the rate at which these structures can be produced, particularly during daytime substrate drying in warm or freezing weather (Stanley et al. 2004). Periphyton species that

do not have strategies capable of allowing them to withstand repeated exposure would presumably become eliminated from the varial zones of the MCR, resulting in the observed homogeneity of the periphyton community structure throughout the varial zone. The low MCR periphyton diversity is dominated by resilient diatoms and by phytoplankton taxa.

Periphyton biofilm recovery is dependent on the reproduction rates of its constituent taxa together with upstream donation rates. Biofilm bacteria are capable of division every 20-30 minutes and cyanobacteria every 7 – 34 hours (Yang et al. 2010). Five hours of saturating light per day can support a diatom division every 1-3 days in summer and every 3-6 days in winter (Capblanco and Decamps 1978; Biggs, 1990; DeRuyter van Steveninick et al. 1992; Gosselain et al. 1994). As a result, bacteria can colonize natural and artificial surfaces within a few hours (Gerchakov et al. 1976; Fletcher, 1980; Dempsey, 1981), while diatoms and other microbes immigrate onto substrates within a day to several weeks (Cundell and Mitchell 1977; Colwell et al. 1980; Hoagland et al. 1993). Environmental conditions including water temperature influence periphyton recovery because high profile guild taxa do not benefit from warmer water temperatures as much as the rapidly reproducing low profile guild taxa do. This could mean that periphyton recovery in cold water periods will be slower and biased against the low profile guild taxa.

Invertebrate recovery after a catastrophic event could take several weeks or more (if at all; taxa may become extirpated) and was dependent upon the life-stage of the invertebrates at the time of the event (Kennedy et al. 2016). Species with specific riverside substrate-dependent egg-laying strategies such as EPT species are more vulnerable to the effects of hydro-peaking than species that use a different strategy like the Dipterans (Kennedy et al. 2016). These pressures on invertebrate and periphyton communities are common to all large rivers, however, BC Hydro operations create a larger, more dynamic varial zone in the MCR than would otherwise be expected, and these operations can have a greater effect on populations than those observed in a natural system. Invertebrate life cycles also vary by species, with some laying eggs multiple times per season, whereas others may only emerge once a year that may further affect recovery/colonization rates (Kennedy et al. 2016). In summary, the effects of desiccation on either periphyton or invertebrates are function of species-specific desiccation tolerance, and how life history and reproductive strategies intersect with the timing and duration of dewatering.

4.1.8 Seasonal Growth Patterns

Benthic communities followed annual and seasonal growth patterns. Periphyton production metrics measured in the spring deployments were usually less than half of the fall deployments. We expect this is because night outages in the spring exposed both the upper and lower varial zone substrates to freezing temperatures, and because low water temperatures reduce enzymatic activity and slow growth even in the rapidly reproducing bacterial biofilm (Wetzel 2001). Additionally, taxa subsidies from upstream Revelstoke Reservoir were lower in spring except at T1 locations. Early and warmer spring weather resulted in higher periphyton productivity during spring sampling sessions. Spring samples were not collected prior to the implementation of minimum flows, preventing a before/after comparison for that season. When all fall T1 thalweg sampler data before and after implementation of minimum flows are compared, only small differences were detected.

Similarly, benthic invertebrate production and fish food availability were higher in fall compared to spring. In natural river systems, invertebrate production peaks in early fall and similar trends have been reported in the LCR (Giller and Twomey 1993; Plewes et al. 2017). We conclude the MCR benthic community structure is stable but is still subject to seasonal variation.

4.2 Q.2. What is the effect of implementing minimum flows on the area of productive benthic habitat?

The intent of minimum flows is to increase the spatial area of wetted habitat to improve benthic community function by maintaining a permanently wetted perimeter. All MCR data indicate that productive benthic habitat was controlled by submergence parameters, including duration and timing of flow events. The productivity data from 2007 through 2018 demonstrates that submergence metrics are the most important determinant of benthic communities in the MCR, most notably abundance, biomass, and food for fish.

Work on a reach-wide productivity model commenced in 2017 and was updated for this report (Schleppe et al. 2018). The RWP model provides a simplified approach to modelling periphyton and invertebrate production while accounting for hourly flow fluctuations. The simplified approach assumed that periphyton and invertebrate productivity were a function of the wetted history only. This is justified because substrate submergence has been consistently identified as the most important parameter controlling invertebrate and periphyton productivity in the MCR (Schleppe and Larratt, 2016). While the simplicity of the RWP model results in inaccuracies when determining the absolute reach-wide productivity for a given season or year, it can address relative differences within a given season to answer management questions regarding minimum flow.

The RWP model found that the implementation of minimum flows caused an increase in periphyton chl-a in MCR R3 and R4. The effect of minimum flows on chl-a in R4 was stronger than in R3 in all months. The daily chl-a estimates for R3 were higher after the implementation of minimum flows during months when R3 did not backwater. Similarly, the RWP model for benthic invertebrate biomass found that the effects of minimum flows were stronger in R4 than in R3. Additionally, the magnitude of the minimum flow effect on benthic invertebrate biomass was variable across different months and was most apparent in February and March. The greater influence of minimum flows on R4 productivity than on R3 productivity is likely the result of increased water cover on R3 varial zones from periodic ALR backwatering.

Invertebrate and periphyton production in the upper varial zone were the most accurately predicted by the RWP models. The upper varial zone samples had the best predictions because the primary factor that determined productivity of T6 samplers was desiccation from frequent substrate dewatering. However, the invertebrate biomass model underpredicted biomass in the upper varial zone. These modelled underpredictions are a result of invertebrate taxa that had different rates of survival to dewatering. The death curves were based on Simuliidae and Trichoptera which are less resistant to desiccation than the dominant taxa in MCR that include chironomids and oligochaetes (Calapez et al. 2014).

The RWP modelled chl-a values of most 2018 samplers in permanently submerged and the lower varial zones were overpredicted. Overpredictions are expected because the reach-wide productivity model does not consider the influence of velocity-induced shear, light attenuation, or invertebrate grazing. During the spring 2018 deployment period, there were

flows exceeding 1800 m^3/s for 40 hours. These high flows likely reduced periphyton production in spring 2018.

RWP modelling of benthic invertebrate production was challenging because there were complex interactions between substrate, velocity and invertebrate drift from tributaries that direct benthic invertebrate communities. For example, invertebrate colonization is affected by the magnitude of flows that increase chironomids and oligochaetes in drift (Irvine and Henriques, 1984) and by important contributions of invertebrate drift from upstream areas such as the Jordan River in R3.

The RWP modelled invertebrate biomass of 2018 samplers in the permanently submerged zone were also overpredicted because the model cannot account for velocity-induced drift and foe unsuitable habitat conditions (Jones, 2013). Other parameters not considered by the reach-wide model include site-specific factors such as donations from the Jordan River (invertebrates) or from Revelstoke Reservoir (more so for periphyton). In areas close to the thalweg, lower benthic invertebrate abundance ocurred because velocity and substrate conditions are less favourable habitat for dominant invertebrate taxa in MCR (Jones 2013). High thalweg water velocities not only reduced invertebrate biomass through scour, it also may have caused artificial losses as sample baskets were raised through the water column.

Increasing the accuracy of the RWP model for periphyton and invertebrate biomass and chl-a requires the addition of parameters that account for differences in physical habitat. A focus of this year's analysis was to test if these parameters should be considered in the model. Parametrizing any RWP model that incorporates light, velocity, water temperature and drift will increase the predictive accuracy but cause greater computational overhead.

Light modelling was conducted in 2018 and it was not necessary to include light in the RWP model. Available light can limit periphyton production in turbid riverine systems such as the Peace River (Schleppe et al. 2019). However, MCR modelled light attenuation and light logger data demonstrated that most of the wetted habitat area of MCR remained in the photic zone even during periods of high flow due to its low turbidity.

Average velocities were extracted from the hydraulic model in 2018 to determine if this parameter should be integrated into the RWP models. There was no detectable effect of velocity on periphyton productivity metrics in R3 spring data because velocities at R3 samplers rarely exceeded the 2 m/s threshold where shearing of the algae mat is expected (Flinders and Hartz 2009; Schleppe and Larratt 2016) due to ALR backwatering. R4 samplers experienced less backwatering and as a result had velocities greater than 2 m/s along the thalweg during periods of high flows. The spring R4 samples had reduced periphyton biovolumes, indicating that velocities were sufficient to generate shear stress and sloughing of larger periphyton such as filamentous green algae. However, velocity did not prove to be an important predictor of chl-a in the R3 and R4 statistical models, nor was maximum velocity an important predictor of the predominance of high and low profile guilds.

Statistical modelling and sampler-specific velocities from the TELEMAC-2D model for spring 2018 confirmed that at discharges exceeding 1800 m^3/s, there are very few areas in the MCR that have velocities high enough to cause shearing of low profile types and reduction of chl-a. The inclusion of hourly velocity in the RWP model is unlikely to significantly improve the accuracy of chl-a predictions.

Higher spring water temperatures were associated with large increases in periphyton production in other rivers (Kazanjiian et al. 2018). R4 water temperatures were driven by

the temperature of Revelstoke Reservoir releases and by air temperatures. MCR water temperatures influenced the abundances of high and low profile guilds. Similar to other studies, the percentage of the periphyton community in the high profile guild in R4 decreased with increasing temperature (da Silva et al. 2019). The high profile types are typically outcompeted by the low profile algal taxa at higher water temperatures (Passy, 2007).

Spring water temperatures were an important driver of chl-a. The inclusion of water temperature as parameter in the RWP model would improve the accuracy of chl-a predictions. However, riverine temperatures are not heavily influenced by flow regulation of the MCR. This means that inclusion of this parameter in a reach-wide model would increase the accuracy of predictions but would not necessarily increase our ability to determine the effects of minimum flows on the MCR.

Similar to periphyton, the invertebrate mixed effects models only detected an effect of velocity on R4 invertebrate production and not on R3 production due to lower velocities at the later. Higher R4 velocities decreased invertebrate abundance and biomass through habitat inhospitable to dominant taxa and to and losses to drift (Irvine and Henriques, 1984; Kang et al. 2017).

Maximum velocity was a better predictor of invertebrate abundance than invertebrate biomass because it explained more variation. Invertebrate abundance was more responsive to higher velocities than invertebrate biomass because the velocity-sensitive dominant chironomids and oligochaetes are small and contribute less to biomass than EPT taxa. The use of velocity in the invertebrate RWP model is best accomplished through the use of taxa-specific relationships with velocity, however, they are complex and would substantially increase computational overhead. Further, inclusion of velocity in the RWP model is unlikely to result in a better answer to the management questions, but rather a better ability to estimate the absolute value of productivity in the MCR over the study period.

In summary, MCR operating regimes influence benthic community abundance and diversity in areas subjected to minimum flows because these flows increase the wetted history - the most important determinant of overall benthic productivity. However, other parameters including duration of daytime submergence were also important but more challenging to model spatially. The reach-wide model confirmed that the ALR elevation plays an important role. When the ALR elevation is high, the benefit of minimum flows on the spatial area of productivity are lessened by the effects of backwatering throughout R3 and to a lesser extent in R4. Thus, the total area of productive habitat in the three MCR submergence zones depends upon more than just minimum flows. Despite difficulties in determining the exact benefits of minimum flows to spatial area of productive habitats, we can conclude that minimum flow increased the spatial area of productive habitat for at least portions of the year because it provided a minimum wetted habitat area that is more productive than pre-minimum flows.

4.3 Q3. What is the effect of implementing minimum flows on the accrual rate of periphyton biomass in the MCR? Is there a long-term trend in accrual?

Establishment and accrual of periphyton communities in the MCR occurred at slow rates similar to other large oligotrophic rivers (Table A38). The combined time series data collected across year, season and river depth indicated that accrual on MCR continued linearly to the end of the 46-51 day deployment period (Schleppe and Larratt 2016).

Therefore, incubation periods exceeding 46 days are required to achieve peak periphyton biomass in MCR and may require more than 6 months for full development, based on limited MCR long-term data (Wu et al. 2009; Biggs 1989).

The effect of minimum flows on the accrual rate of periphyton biomass in MCR was dependent on the spatial area under consideration, the environmental conditions, annual patterns of operations, and ALR backwatering. The MCR periphyton accrual rate is the net sum of gains - a product of growth rate and periphyton immigration from upstream areas and losses - a product of death rate, invertebrate grazing, scour and sloughing. The introduction of minimum flows had a minimal effect on the periphyton growth rate because it is sensitive to seasonal and annual variations in water temperature and light. The implementation of minimum flows also had a minimal effect on scour and sloughing because sloughing of high-profile periphyton only occurs at very high flows that are unrelated to minimum flows. However, implementation of minimum flows reduced periphyton losses because it decreased the spatial area that was periodically dewatered.

Implementation of minimum flows should have the largest effect on periphyton death rates in areas below and just above the minimum flow line that remain permanently submerged. Before the implementation of minimum flows these areas were periodically dewatered for four to seven hours, inducing an average percent chl-a loss of 11-19%. However, the death rate is highly variable and dependent on environmental conditions. Before the implementation of minimum flows, the death rate was likely lower than 11-19% because BC Hydro avoided daytime dewatering. Periphyton likely did not start dying in the first couple hours of exposure because most substrates drain and dry slowly at night. Other conditions such as ALR backwatering, rain or high humidity, and cool air temperatures ranging from 5-10 ºC can decrease periphyton death rates on exposed substrates (Stanley et al. 2004). Conversely, dry weather with air temperatures below 0 ºC (spring) or exceeding 15 ºC to 20 ºC (fall) can increase the death rate of periphyton on exposed substrates.

In the lower varial zone that is immediately above the minimum flow line, accrual rates increased as a result of the implementation of minimum flows. Higher average flows from minimum flow implementation resulted in shorter exposure (drying) periods for portions of the lower varial zone. The conclusion that minimum flows benefit the area directly above or adjacent to the wetted edge at minimum flows was supported by sampler data because peak production occurred at the lower varial T2 and T3 positions.

The rate of periphyton recovery and accrual rates was influenced by seasonal differences in growth and by peak flows. Minimum flows were particularly advantageous during the fall when periphyton recovery were highest, while the benefits were less evident in the spring with slow periphyton recovery rates and high peak flows. Velocity modelling suggested that peak flows associated with the REV 5 turbine resulted in the loss of periphyton biovolume but not chl-a in R4 near the thalweg.

Channel areas covered by minimum flows are not the only areas of MCR that can maintain and act as sources of species to aid recovery. Shallows including backwaters and back-eddies are a source of recruitment and maintenance of some planktonic and periphytic species (Reynolds and Descy 1996; Butcher 1992). These areas are more abundant in R3 than in R4, and may enable R3 periphyton to recover faster after catastrophic flow events. Many of these areas may also act as impoundments to fish, resulting in mortalities, inferring that trade-offs are probable and should be considered in any flow management decisions.

Patterns of periphyton accrual and recovery in the MCR are further complicated by drifting limnoplankton exported by flows from Revelstoke Reservoir. Phytoplankton that becomes trapped in the periphyton matrix (Middleton 2010) can subsidize the population for many kilometers below a dam (Doi et al. 2008; Larratt et al. 2013). In the MCR, this subsidy is important to standing crop and accrual rates. Contributions of phytoplankton to MCR periphyton may also occur from the ALR to R3 during backwatering, but the results of plankton hauls suggested the ALR phytoplankton was impoverished, likely by turbidity (Schleppe et al. 2012). Species contributed by Revelstoke Reservoir appeared to account for a significant proportion of the MCR periphyton, particularly in the summer/fall and at R4. This means phytoplankton events occurring in Revelstoke Reservoir and the timing and depth of reservoir releases exerted an influence on MCR periphyton accrual and recovery rates, as well as community structure.

In summary, the study data to date indicate that in some areas MCR periphyton communities benefit from the implementation of minimum flows. However, the magnitude of that benefit is difficult to determine because it is dependent on a wide range of physical factors that have high seasonal and annual variability. Using field data and theoretical knowledge, we conclude that minimum flows are most beneficial to periphyton accrual when 1) the lower varial area above or adjacent to the edge wetted by minimum flows when there is no ALR backwatering and physical conditions would induce rapid desiccation and 2) the area below minimum flows during dry weather in summer and winter.

4.4 Q.4. What is the effect of implementing minimum flows on the total abundance, diversity and biomass of benthic organisms in the section of the MCR subjected to the influence of minimum flows? Is there a long-term trend in benthic productivity?

The responses of MCR benthic invertebrates to minimum flows were very similar to periphyton responses. Productive habitat occurred in permanently submerged habitat and areas in the lower varial zone adjacent to the edge wetted by minimum flows. Like periphyton, benthic invertebrate communities were directly dependent upon submergence and physical conditions of MCR for survival.

The area of the varial zone that is productive invertebrate habitat is bounded by minimum flows and its upper limit determined by the recent daily submergence. However, MCR invertebrate models explained less variation than periphyton models, limiting our ability to understand trends (Schleppe and Larratt 2016). This is because many factors could not be accounted for in our analyses including: patchy distribution of invertebrate communities in space and time; potential sampling biases associated with use of rock baskets retrieved from depths of 5 m at high velocities; a low sample size to habitat area ratio when compared to periphyton; the occurrence of microhabitat factors and finally, daily hydropeaking timing on species-specific life history and reproductive strategies.

There were small differences between invertebrate diversity and community composition before and after the implementation of minimum flows. The fall invertebrate data collected to date suggested the benthic invertebrate community became more diverse in the areas subjected to minimum flows, possibly through protection of rare MCR taxa that were sensitive to dewatering. Daytime exposures have been shown to reduce the abundance of sensitive EPT taxa and favour tolerant taxa such as chironomids (Mihalicz, et al, 2019). The implementation of minimum flows provide a permanetly wetted area that functions as a

source of benthic organisms to re-colonize previously exposed habitat areas after extensive low flow events lasting longer than 24 hours in MCR.

MCR fall invertebrate abundance data collected to date was similar before and after the implementation of minimum flows, indicating that minimum flows did not affect the invertebrate abundances in the area below the elevation wetted by minimum flows. Before the implementation of minimum flows,substrate dewatering only occurred for 4-7 hours at night. The most abundant invertebrates, chironomids and oligochaetes, can likely withstand this nightime dewatering.

Annual differences in fall invertebrate biomass were not related to the implementation of minimum flows and were more related to ALR backwatering. Fall 2013 had high invertebrate biomass in areas subject to minimum flows relative to all other fall sampling sessions, but this was attributable to factors including higher survival of instars from the previous year and no backwatering resulting in faster velocities that are favourable for EPT colonization.

4.5 Q5. If changes in the benthic community associated with minimum flow releases are detected, what effect can be inferred on juvenile or adult life stages of fishes?

Our data from 2013-2016 suggested that the abundance, biomass, and overall availability of fish food (Fish Food Index in 2013 and EPT+Diptera responses in 2014-2016) were directly dependent upon submergence. The overall fish food availability was greatest at T1 through T3 locations and coincided with the areas identified as being the most productive benthic habitats in our statistical models (Schleppe & Larratt 2016). For these reasons, we conclude minimum flows increased fish food availability, but other critical influences on productivity including frequency and duration of daytime submergence events, and timing of insect life history events must also be considered. Substrates submerged for 450 – 500 hours (10 – 11 hours/day during the sampling duration) during daytime hours had the greatest availability of preferred fish food items. Similarly, EPT+D biomass was greatest in areas submerged for at least 500 – 1000 hours over >46 days (Schleppe & Larratt 2016).

The implementation of minimum flows has increased the area of productive invertebrate habitat in the MCR. An overall increase in wetted habitat area resulted in more availability of fish food organisms, especially EPT taxa. Inferring the effect of changes in fish food availability was complicated because fish species and their life stages have different feeding preferences and habitat requirements. Fish species that are drift feeders such as adult Rainbow Trout (*Oncorhynchus mykiss*) were likely more affected by increased EPT productivity because some EPT taxa have a high propensity to drift (Rader 1997). However, juvenile Rainbow Trout feed on smaller invertebrates including zooplankton and chironomids that are less sensitive to river changes caused by minimum flows. Finally, bottom feeders including Mountain Whitefish (*Prosopium williamsoni*) may also be less affected by increased EPT availability brought on by minimum flows because they feed on more sediment dwelling invertebrate including chironomids (Scott and Crossman 1973).

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APPENDIX A DATA TABLES AND FIGURES

Light and Temperature Figures

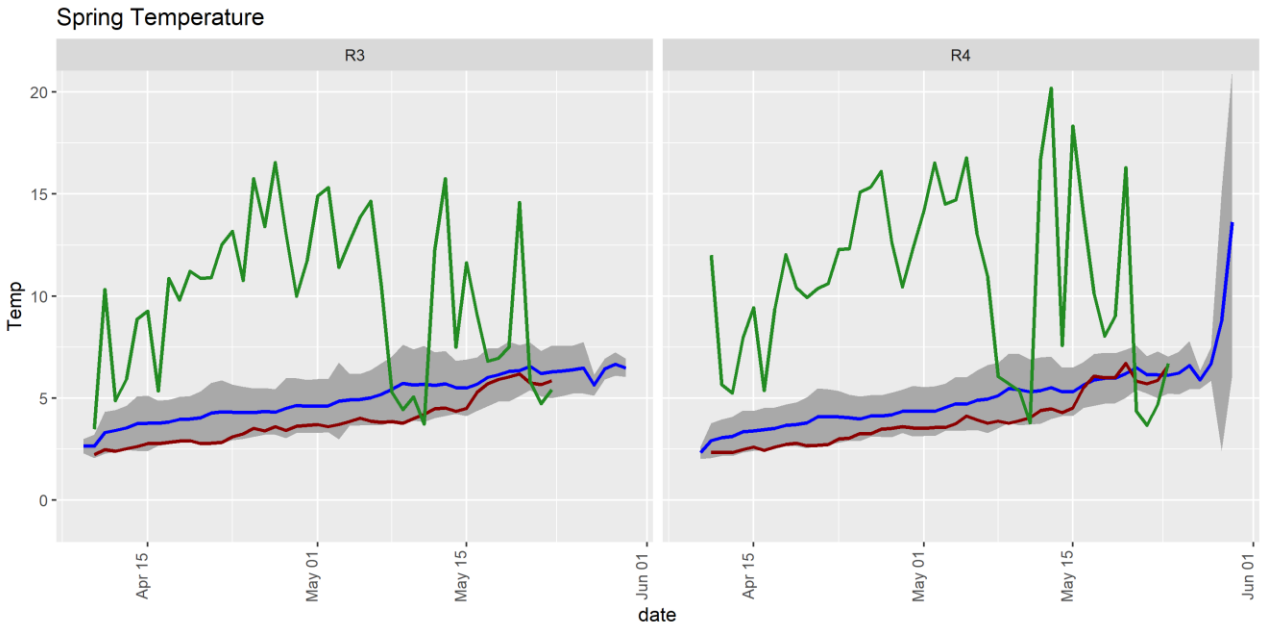

Figure A1 The pattern of daily water temperature in MCR by reach during the spring study period. The blue line represents the mean from 2011 to 2018 (spring) and red represents the mean water temperature in 2018 from all submerged samplers. The green line represents the average temperature of exposed sites in spring 2018. Data were pooled for spring periods between 2011 – 2018 (±SD in grey).

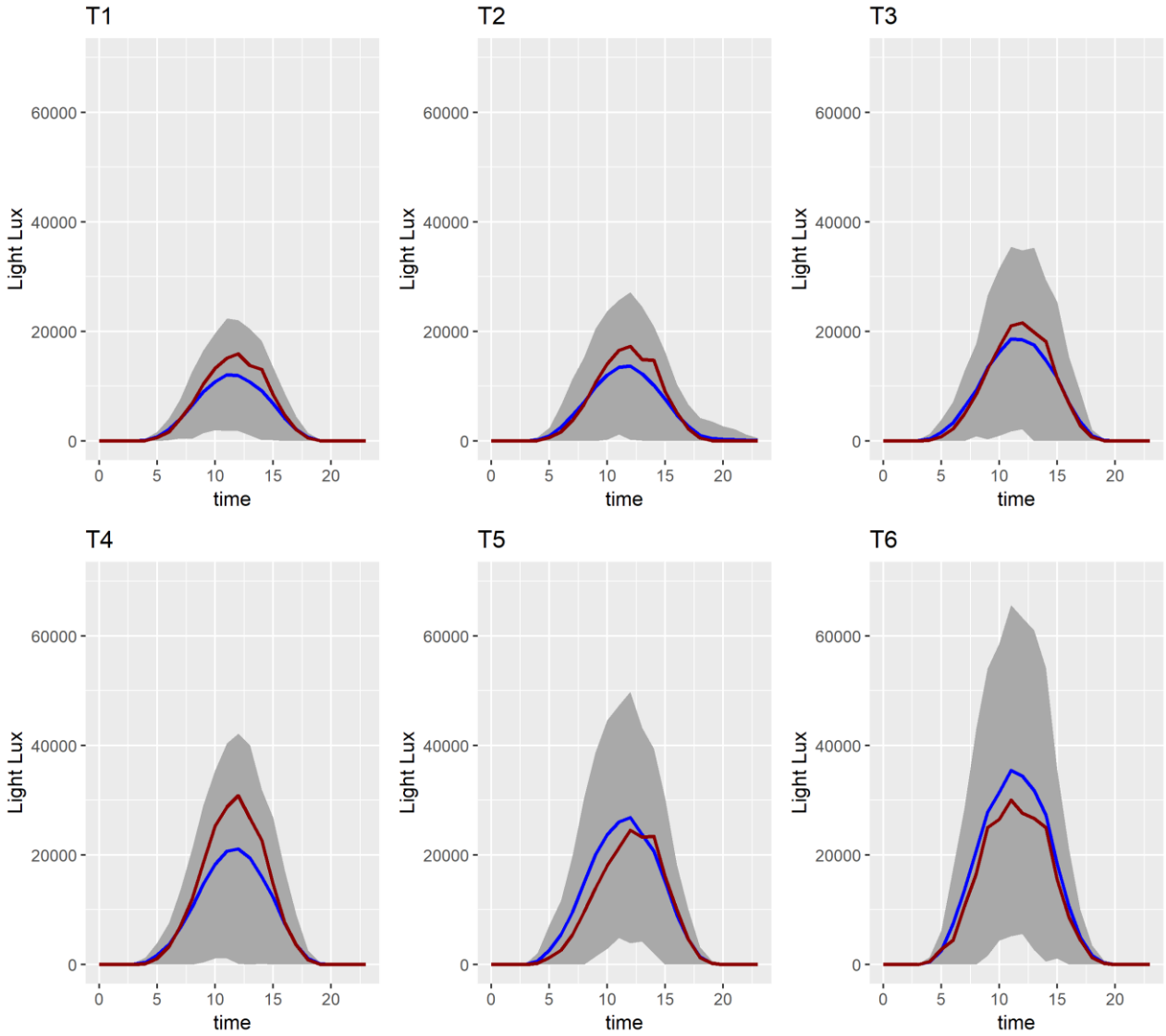

Figure A2 Spring daily pattern of light intensity (lux) while samplers were submerged in the MCR at varying depths, where T1 is the deepest and T6 is the shallowest for samplers. The blue line represents the mean from 2011 to 2017 (±SD in grey) and red represents the mean 2018 spring data from all submerged samplers. The x-axis is time in hours of the day (0:00 to 24:00).

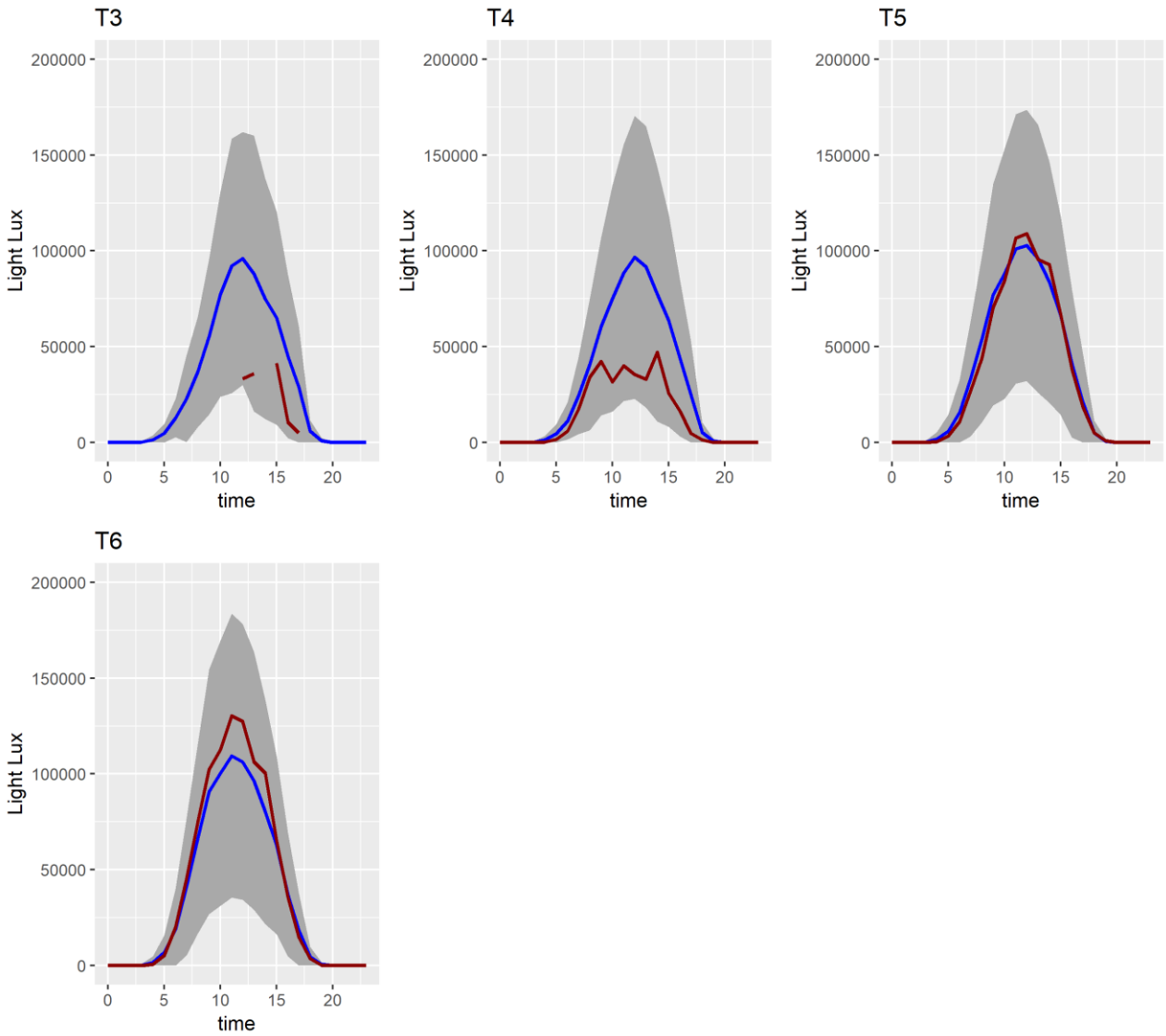

Figure A3 Spring daily pattern of light intensity (lux) in the MCR when samplers were exposed (out of the water). T3 is the deepest and T6 is the shallowest for samplers. Noting T1 and T2 were continuously submerged so are not included in the above figure. The blue line represents the mean from 2011 to 2017 (±SD in grey) and red represents the mean spring 2018 data from all exposed samplers. The x-axis is time in hours of the day (0:00 to 24:00).

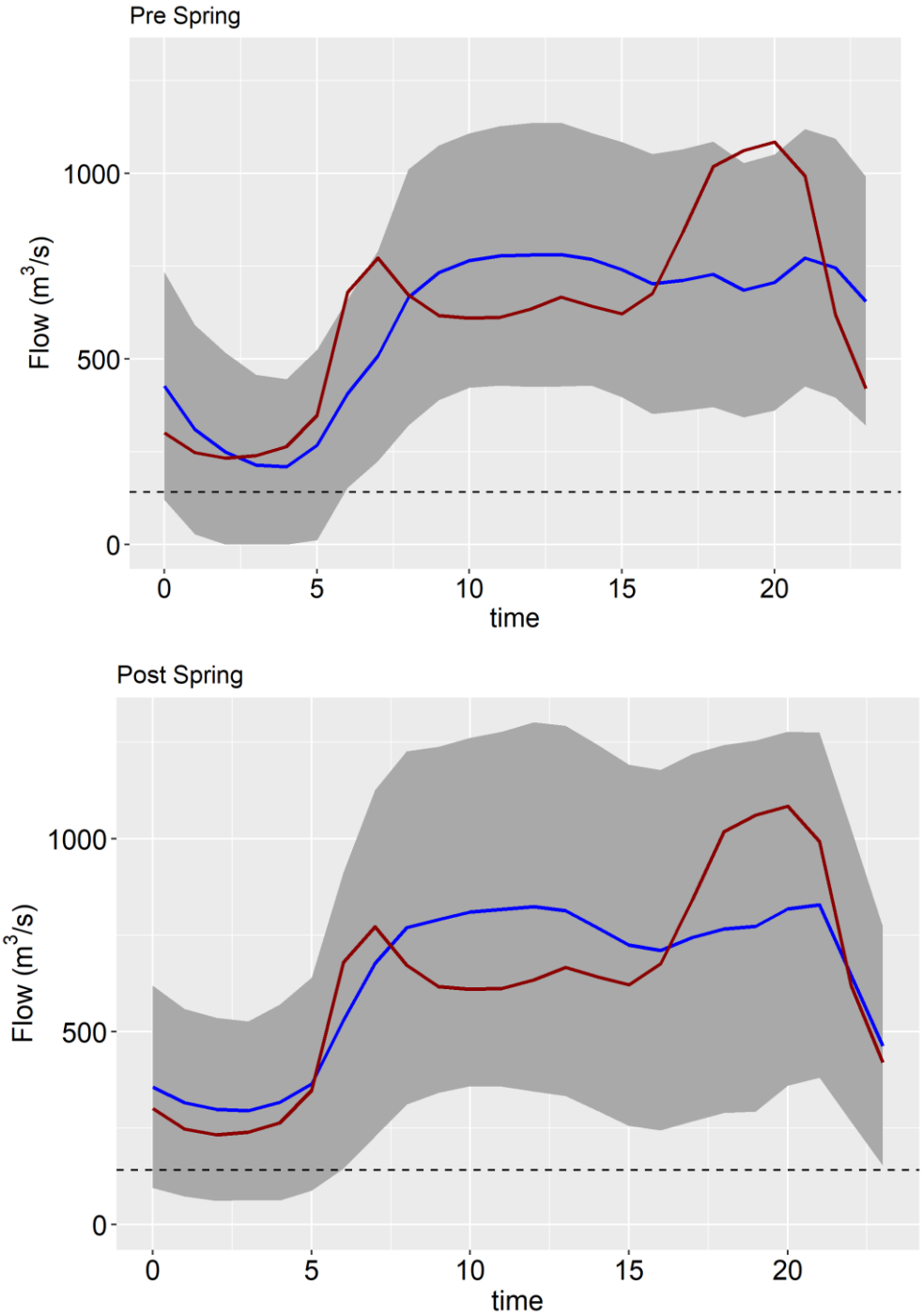

Figure A4 The pattern of daily flow in the MCR during the spring study periods in pre (2007-2010) and post implementation (2011-2017) of minimum flows. Average hourly flows from 2018 (spring) are shown in red, while the average of all data pooled (2010-2018) is shown in blue. The standard deviation of average hourly flow across all years pooled is shown in grey. The minimum flows are shown as a black dotted line.

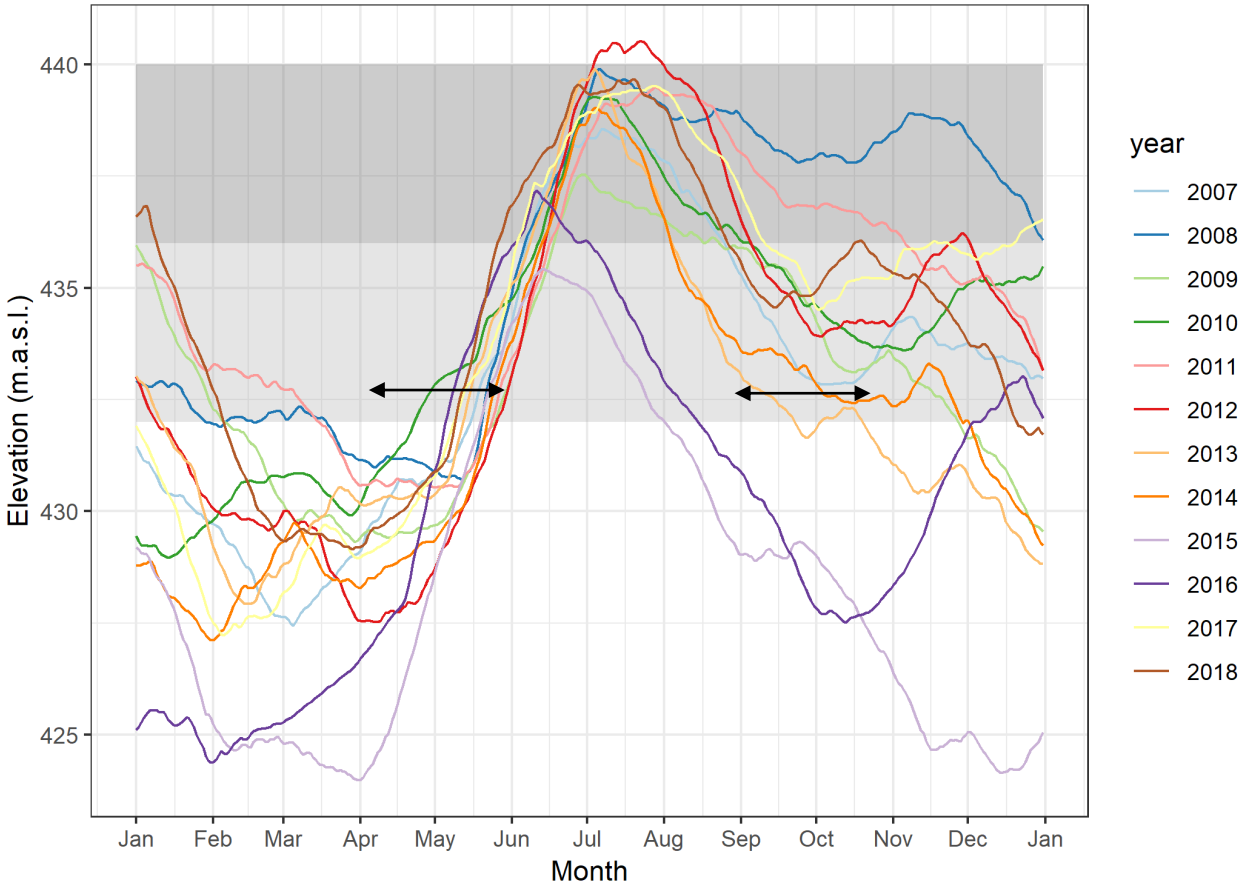

Figure A5 Backwatering of Arrow Lakes Reservoir (ALR) into MCR R3 and R4 with typical spring and fall deployment periods occurring between the arrows. The vertical axis shows elevations in the normal operating range of ALR. Light grey shading denotes when R3 was backwatered; dark grey shading denotes when R3 and R4 were backwatered.

Table A1 Flow summary table for each deployment period, summary statistics are calculated from mean daily flows.

		flows (m^3/s)								
Year	Season	minimum	1st Quantile	Median	Mean	2nd Classification	Maximum	Flow Class	Backwatering	Hours over 1800 m^3/s
2010	Fall	192.90	360.26	508.66	497.58	618.32	908.67	average	yes	0
2011	Fall	356.00	627.66	819.72	801.76	955.60	1177.14	high	yes	2
2012	Fall	323.81	630.06	924.44	875.74	1096.95	1437.37	high	yes	27
2013	Fall	156.05	385.69	682.61	651.90	842.00	1193.78	average	no	0
2014	Fall	316.19	477.71	591.06	652.68	858.88	1181.22	average	yes	4
2011	Spring	153.07	308.60	480.26	500.35	670.66	987.73	average	yes	0
2012	Spring	178.31	386.30	520.76	584.64	799.43	1037.33	average	yes	0
2013	Spring	222.74	376.14	553.25	575.83	749.36	1105.54	average	no	1
2015	Spring	487.74	986.56	1120.24	1108.17	1250.47	1474.57	high	yes	0
2016	Spring	185.64	353.59	533.49	577.41	754.62	1223.21	average	yes	0
2017	Spring	350.08	605.66	732.69	731.67	893.40	1076.91	average	yes	0
2018	Spring	194.38	306.18	494.98	606.66	794.26	1548.62	high	yes	40

APPENDIX B DIGITAL DATA TABLES AND FIGURES

APPENDIX C SUPPLEMENTAL METHODS AND RESULTS

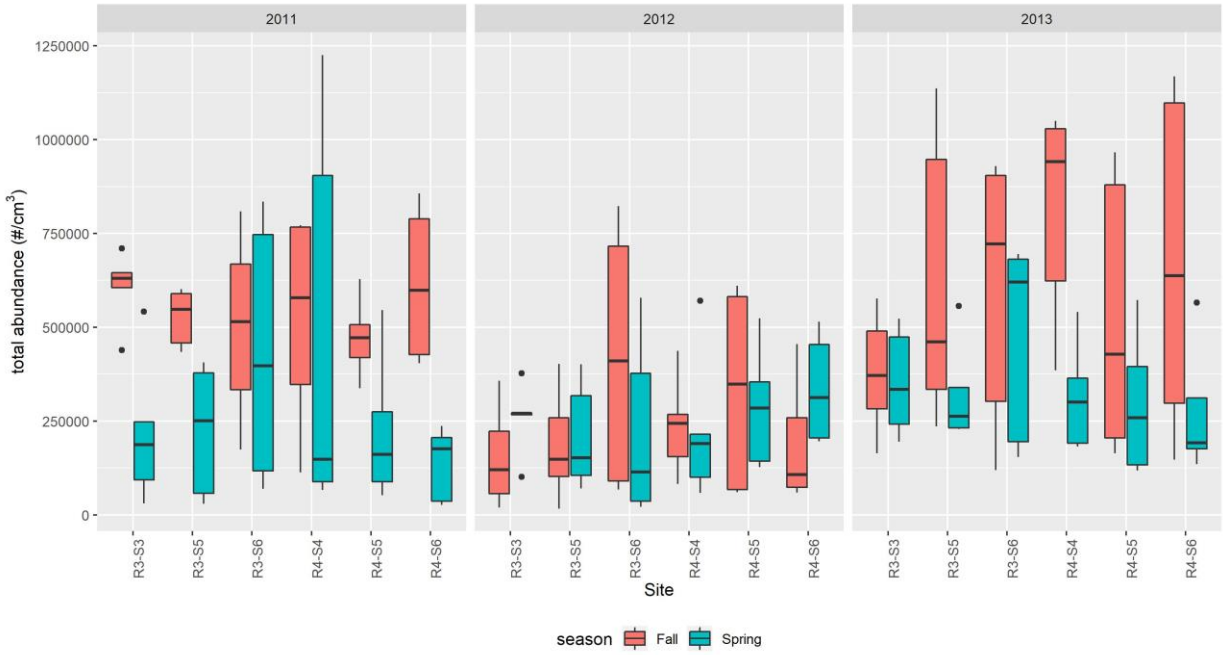

Figure A6 Periphyton total abundance by season and site 2011-2013.

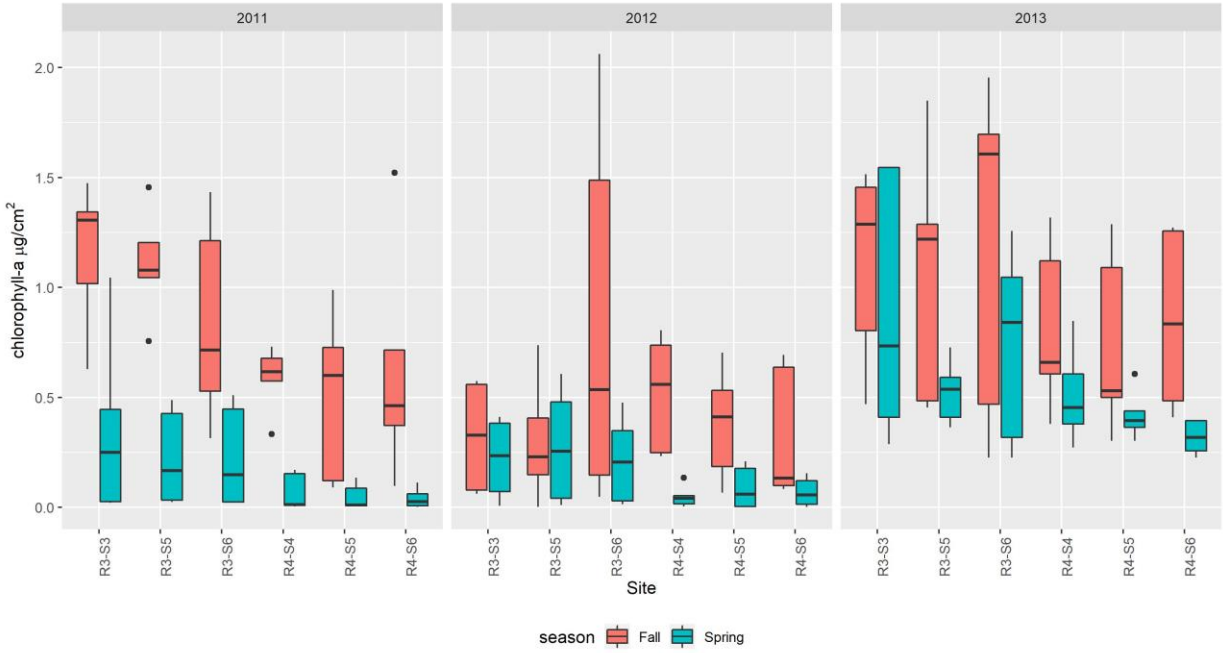

Figure A7 Periphyton chl-a by season and site 2011-2013.

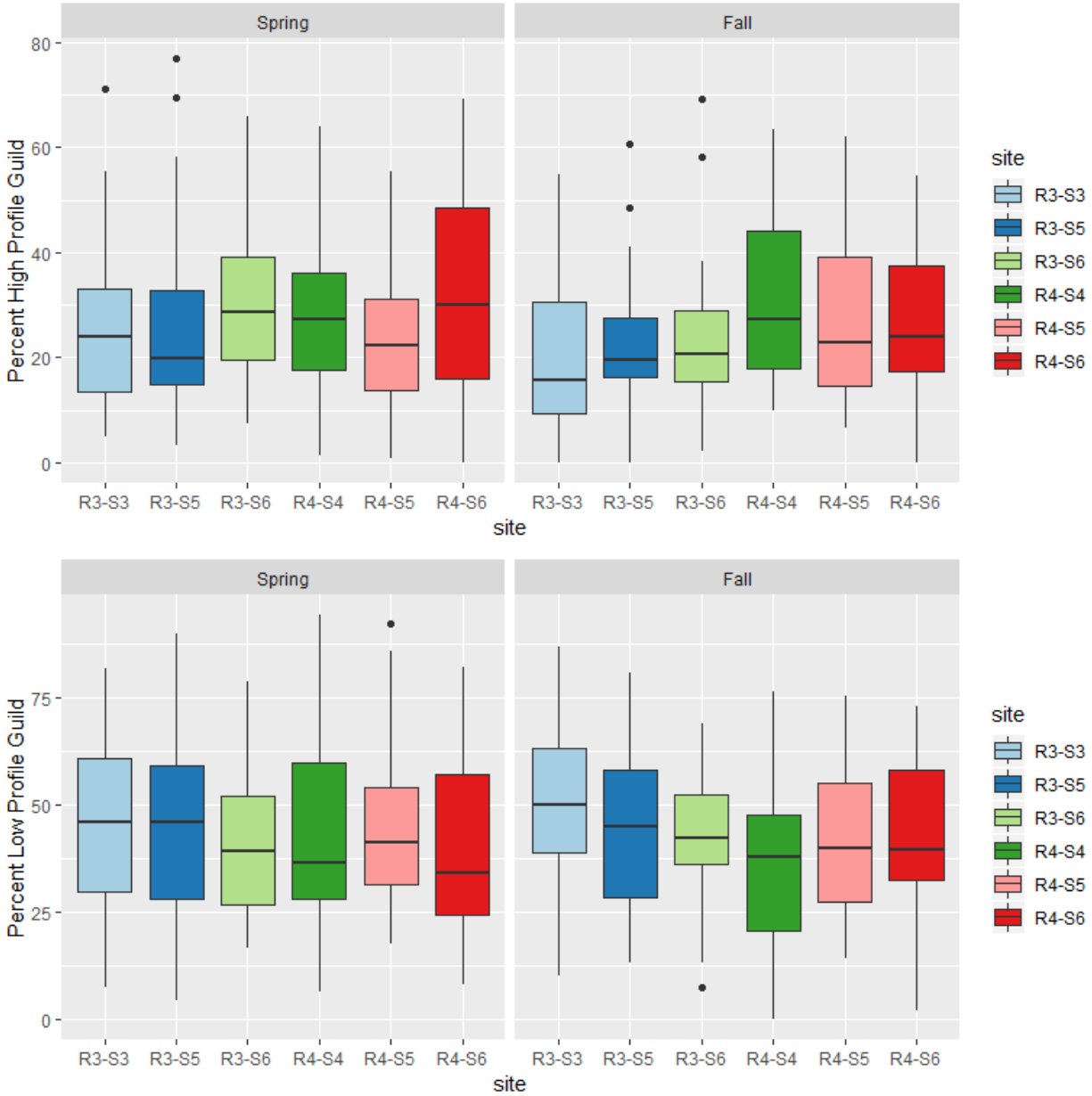

Figure A8 Periphyton percent high profile and low profile for abundance by site and season for 2010-2018.

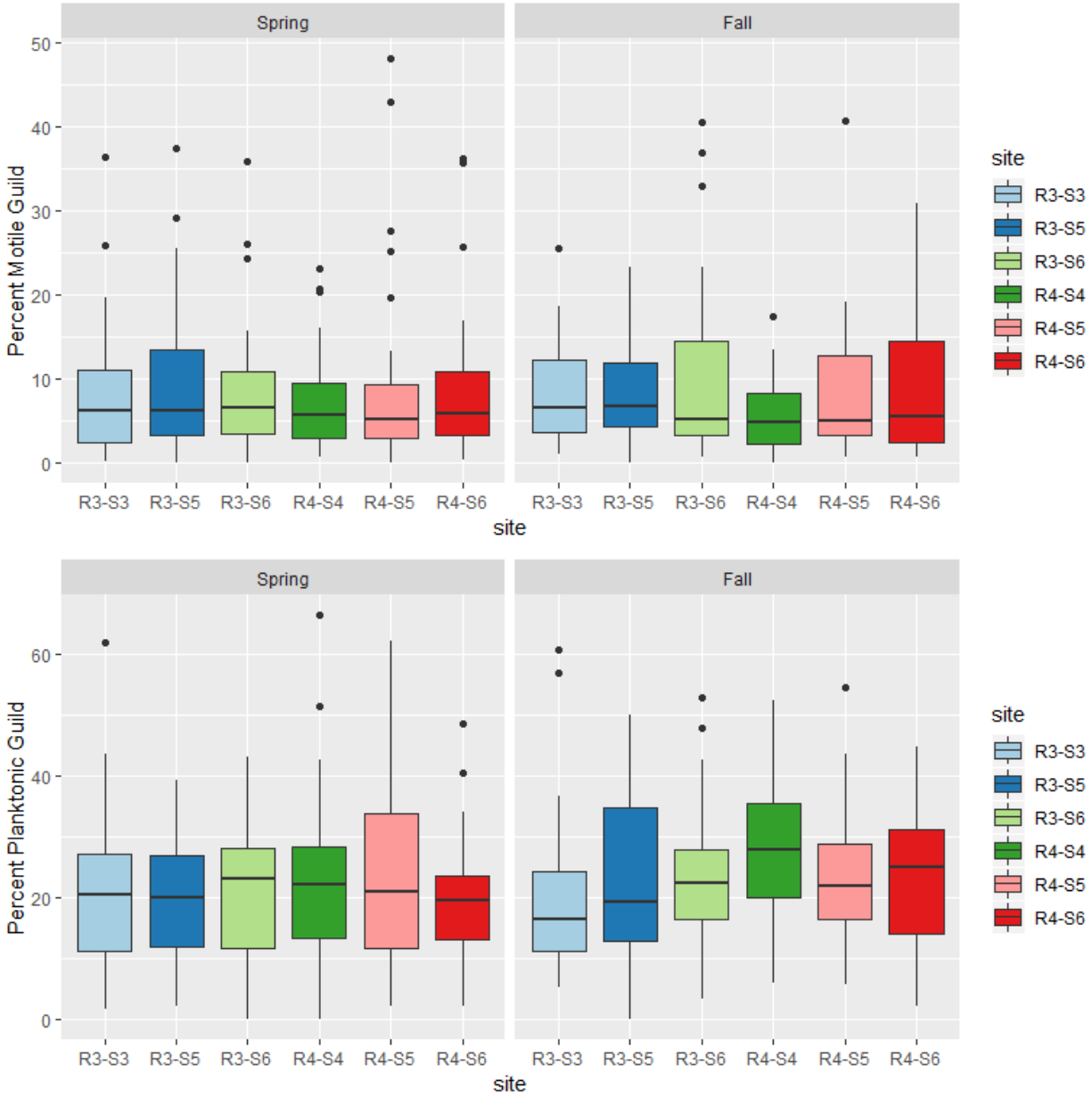

Figure A9 Periphyton percent motile and planktonic guild for abundance by site and season for 2010-2018.

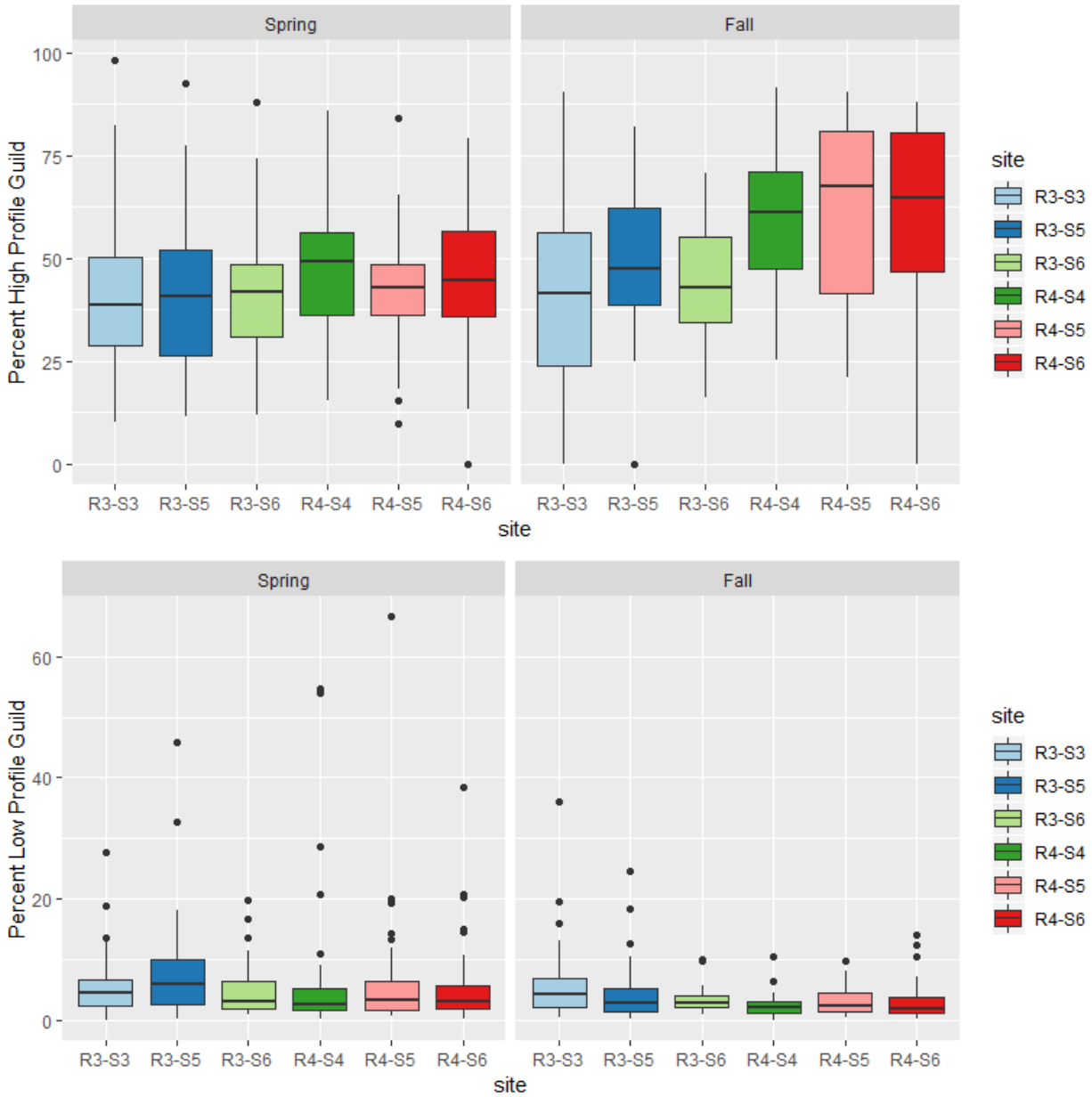

Figure A10 Periphyton percent high profile and low profile for biovolume by site and season for 2010-2018.

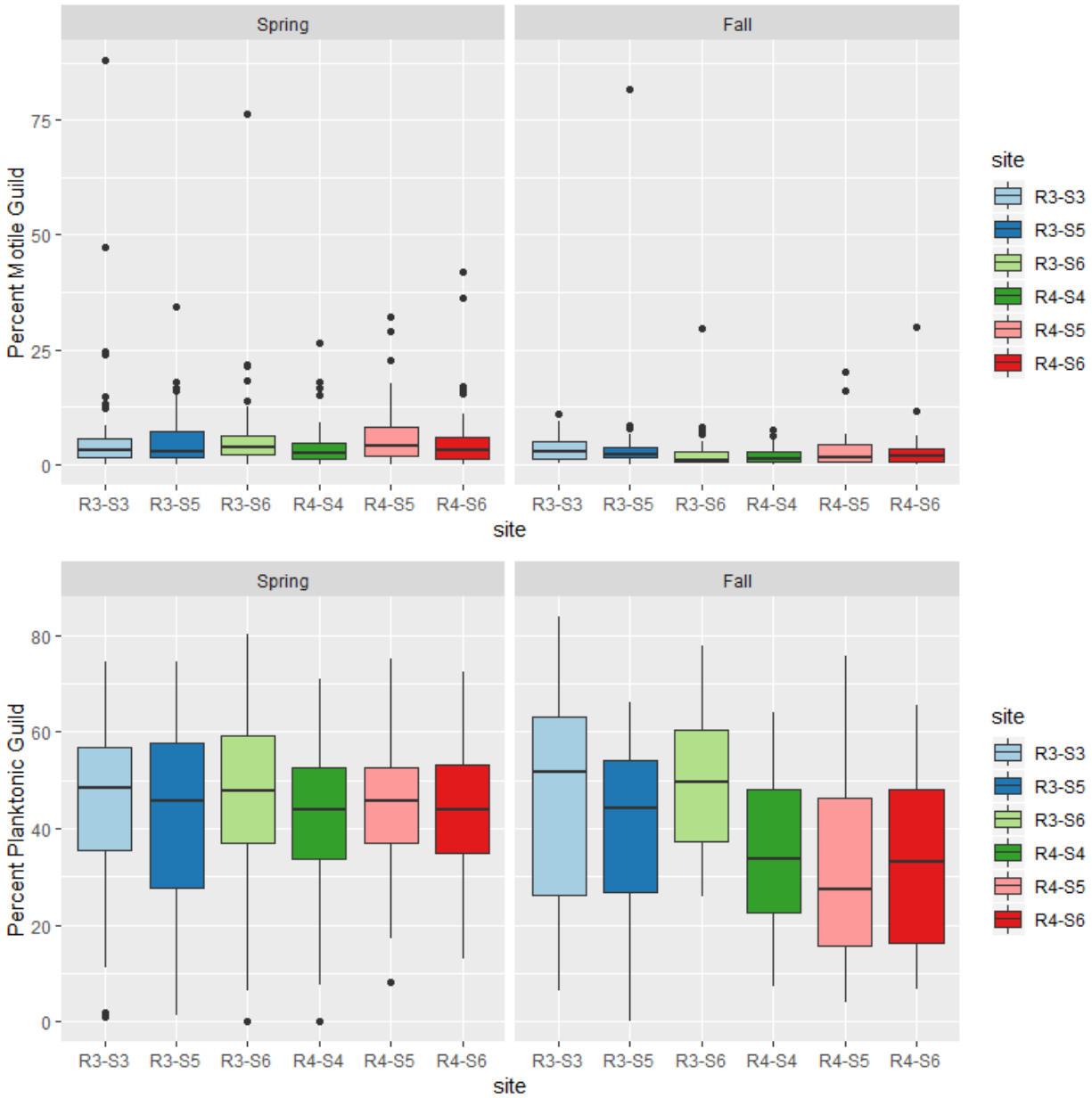

Figure A11 Periphyton percent motile and planktonic guild for biovolume by site and season for 2010-2018.

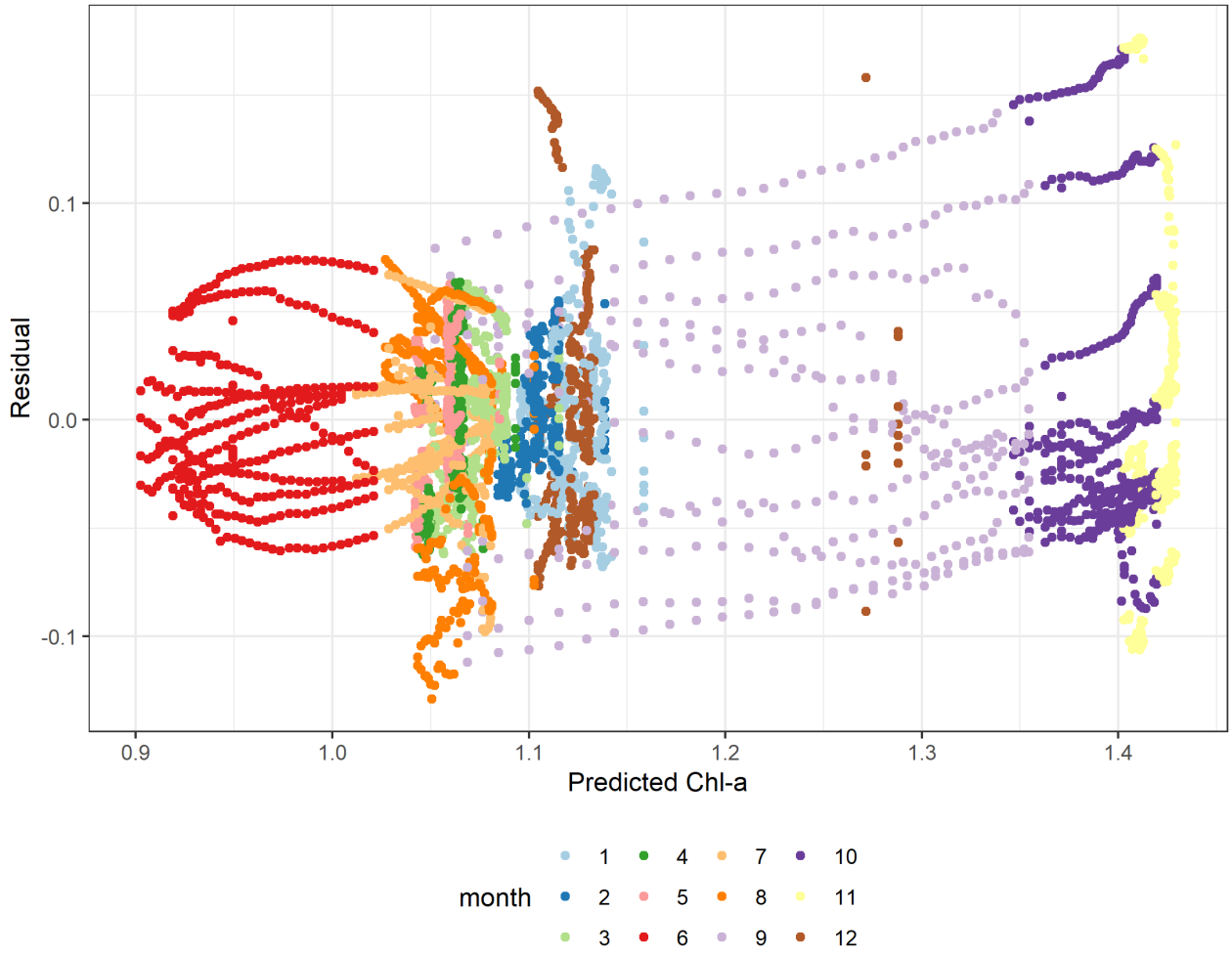

Figure A12 Residual plot for R3 periphyton chl-a model without interaction term.

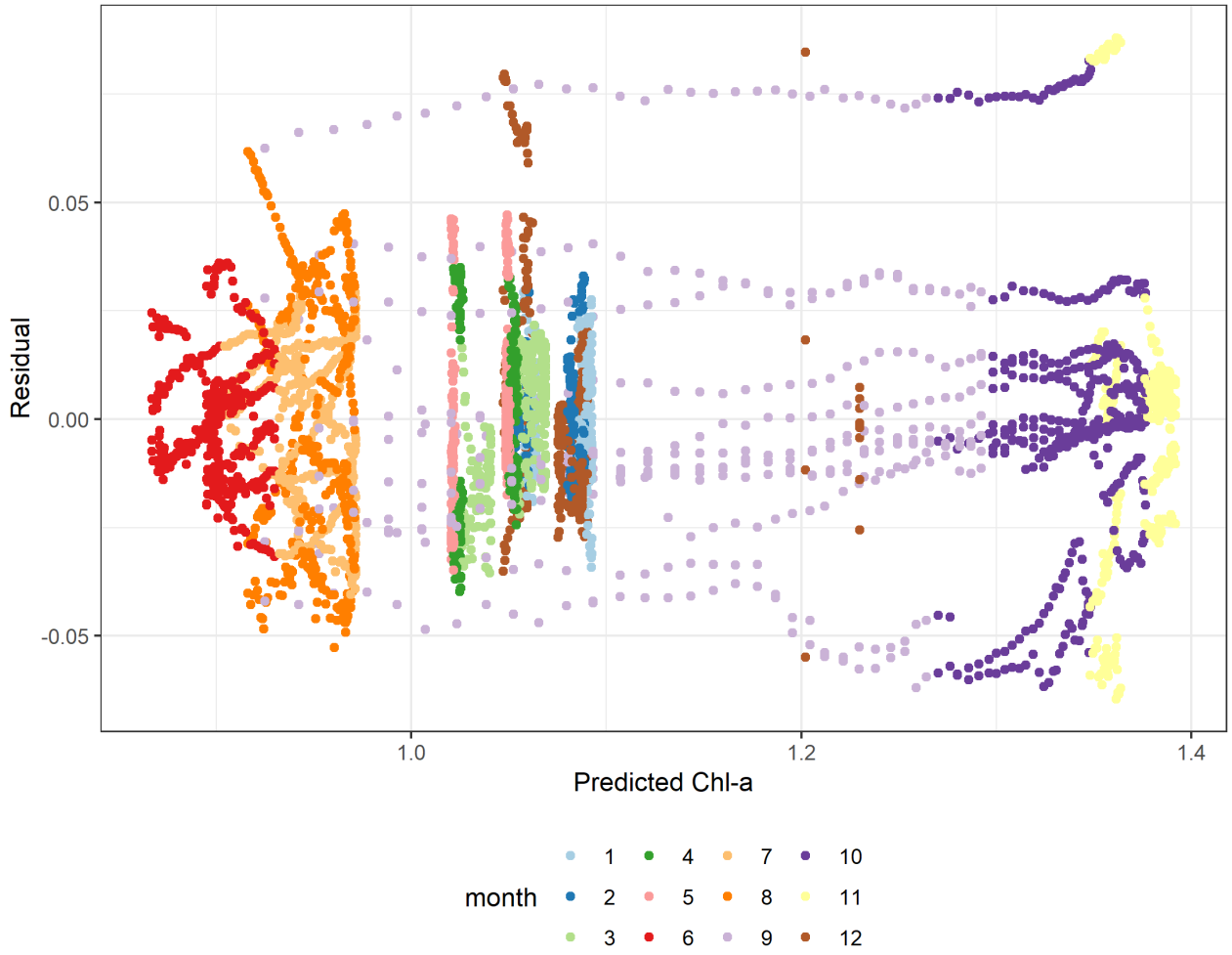

Figure A13 Residual plot for R4 periphyton chl-a model without interaction term.

APPENDIX D VELOCITY AND FLOW RESULTS

Table A2 Summary of model for hourly velocity and flow for 2018.Spring.R3.S3.T1

term	estimate	std.error	statistic	p.value	adjr2
(Intercept)	1.97e-01	2.54e-02	7.76e+00	2.10e-14	6.17e-01
log(mean)	1.69e-01	4.16e-03	4.07e+01	8.55e-217	6.17e-01

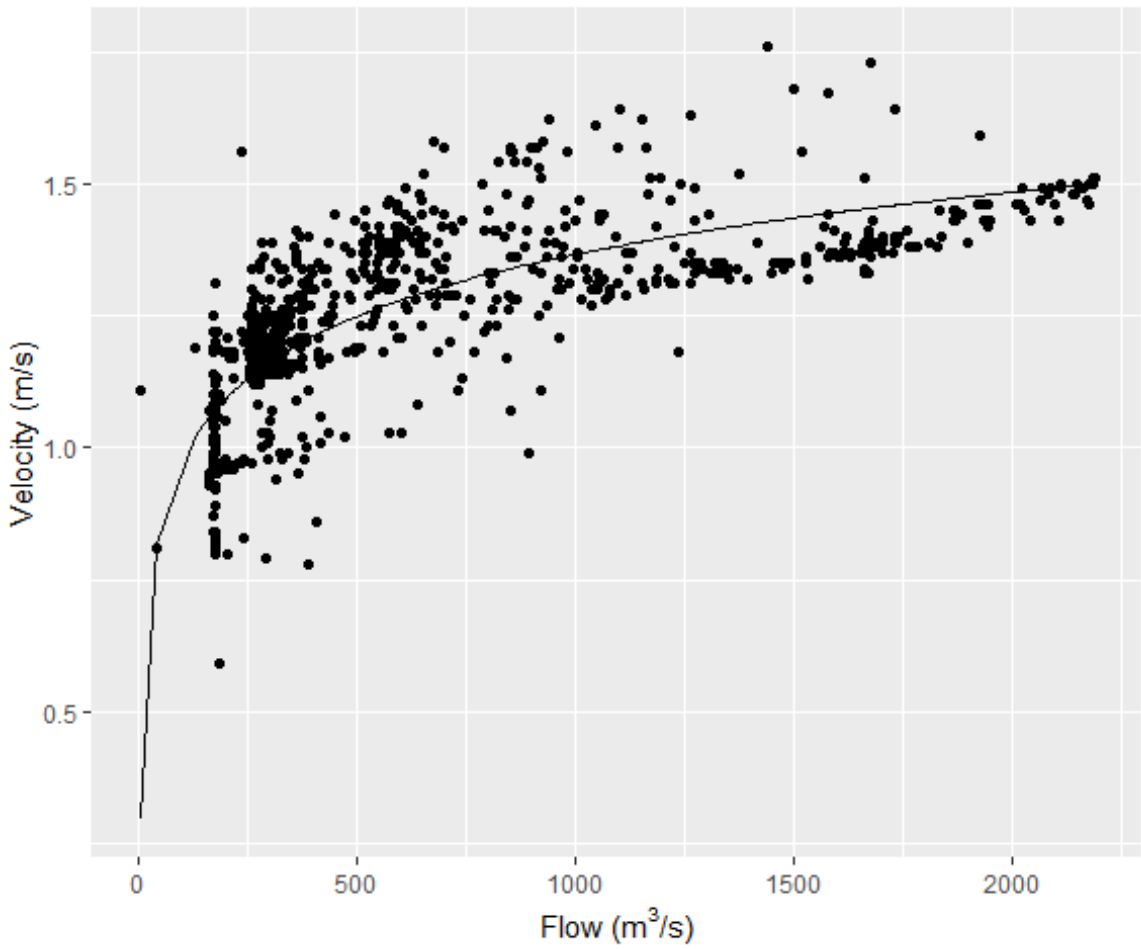

Figure A14 Hourly velocity and flow for spring 2018 deployment for 2018.Spring.R3.S3.T1

Table A3 Summary of model for hourly velocity and flow for 2018.Spring.R3.S3.T2

term	estimate	std.error	statistic	p.value	adjr2
(Intercept)	9.79e-01	9.62e-03	1.02e+02	0.00e+00	6.23e-01
poly(mean, 2, raw = TRUE)1	8.30e-04	2.98e-05	2.79e+01	1.08e-127	6.23e-01

term	estimate	std.error	statistic	p.value	adjr2
poly(mean, 2, raw = TRUE)2	-2.93e-07	1.50e-08	-1.96e+01	7.70e-73	6.23e-01

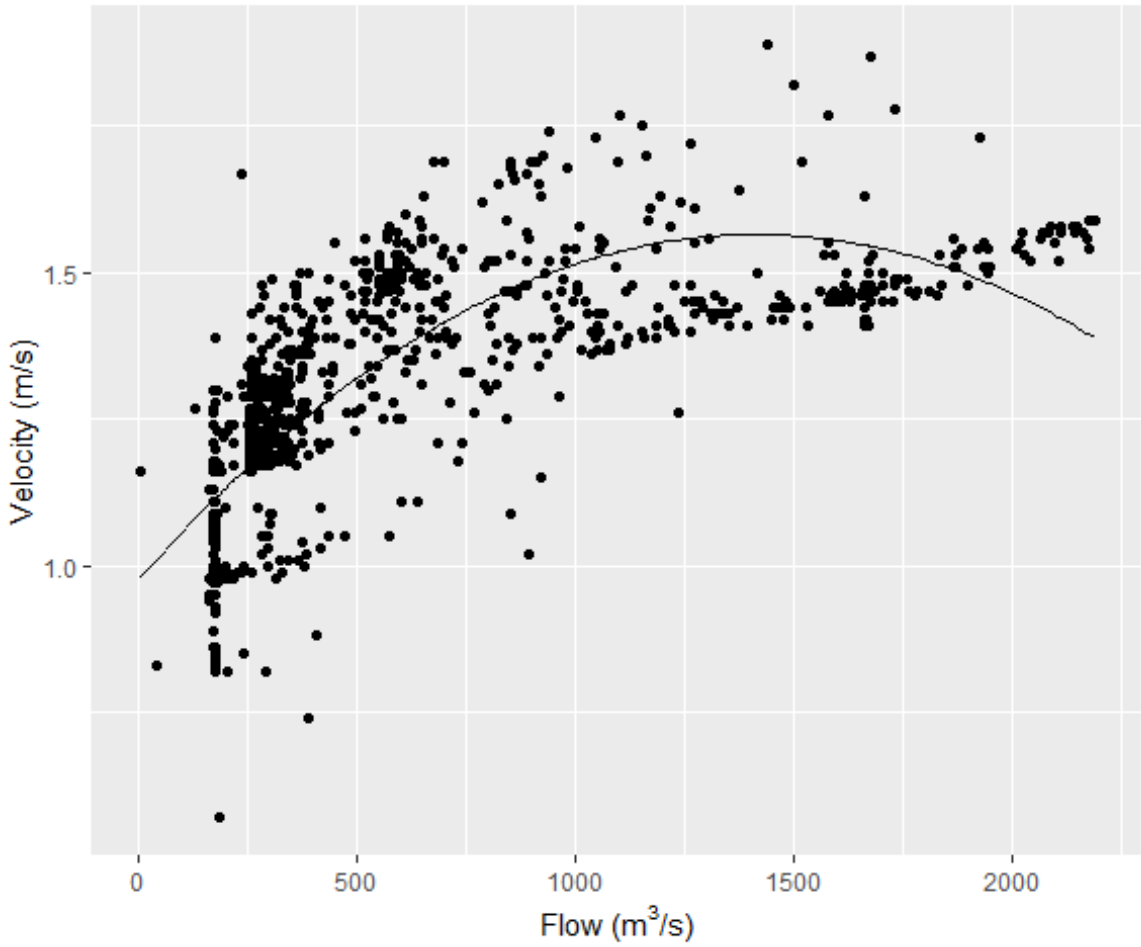

Figure A15 Hourly velocity and flow for spring 2018 deployment for 2018.Spring.R3.S3.T2

Table A4 Summary of model for hourly velocity and flow for 2018.Spring.R3.S3.T3

term	estimate	std.error	statistic	p.value	adjr2
(Intercept)	4.97e-01	1.32e-02	3.76e+01	1.83e-195	7.59e-01
poly(mean, 2, raw = TRUE)1	1.38e-03	4.09e-05	3.38e+01	8.52e-169	7.59e-01
poly(mean, 2, raw = TRUE)2	-4.44e-07	2.06e-08	-2.16e+01	1.17e-85	7.59e-01

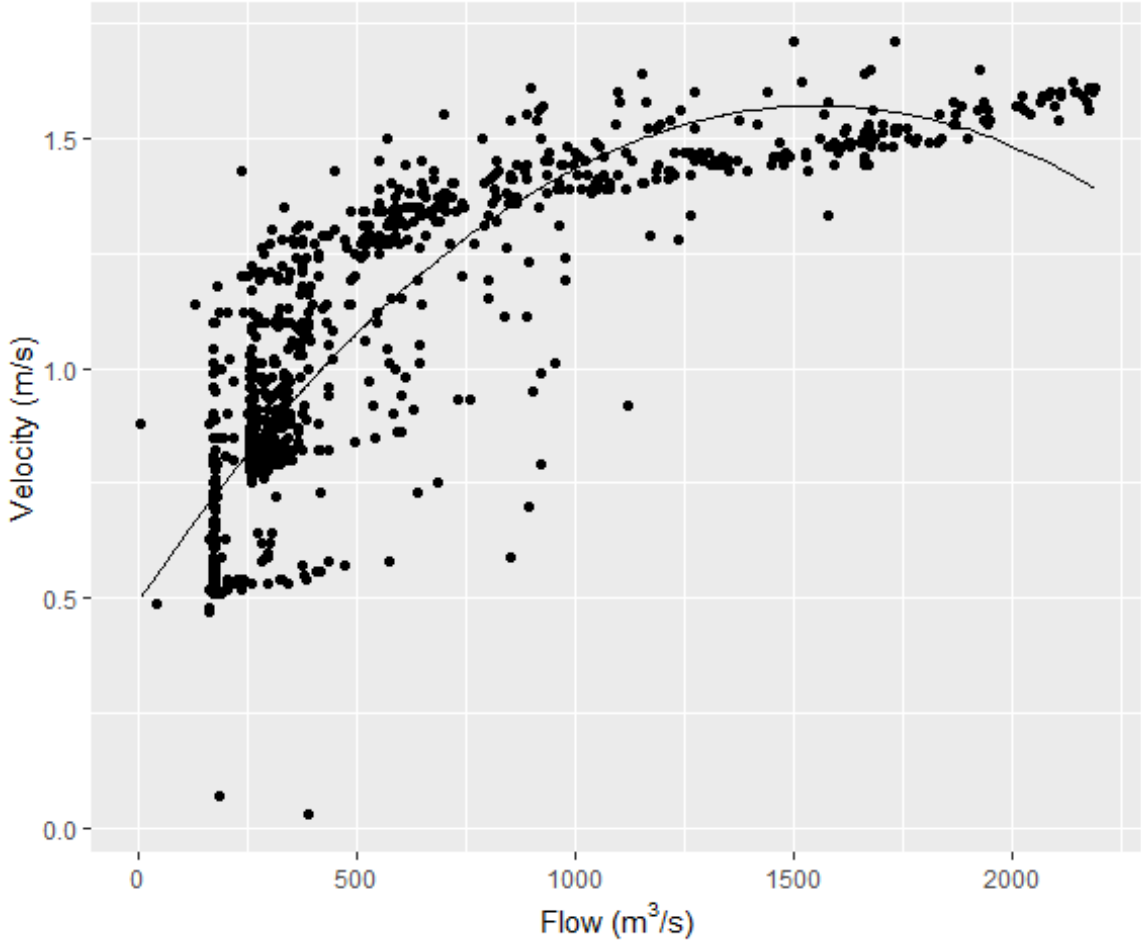

Figure A16 Hourly velocity and flow for spring 2018 deployment for 2018.Spring.R3.S3.T3

Table A5 Summary of model for hourly velocity and flow for 2018.Spring.R3.S3.T4

term	estimate	std.error	statistic	p.value	adjr2
(Intercept)	2.80e-01	1.42e-02	1.97e+01	3.54e-73	8.02e-01
poly(mean, 2, raw = TRUE)1	1.54e-03	4.41e-05	3.48e+01	1.21e-175	8.02e-01
poly(mean, 2, raw = TRUE)2	-4.58e-07	2.21e-08	-2.07e+01	1.30e-79	8.02e-01

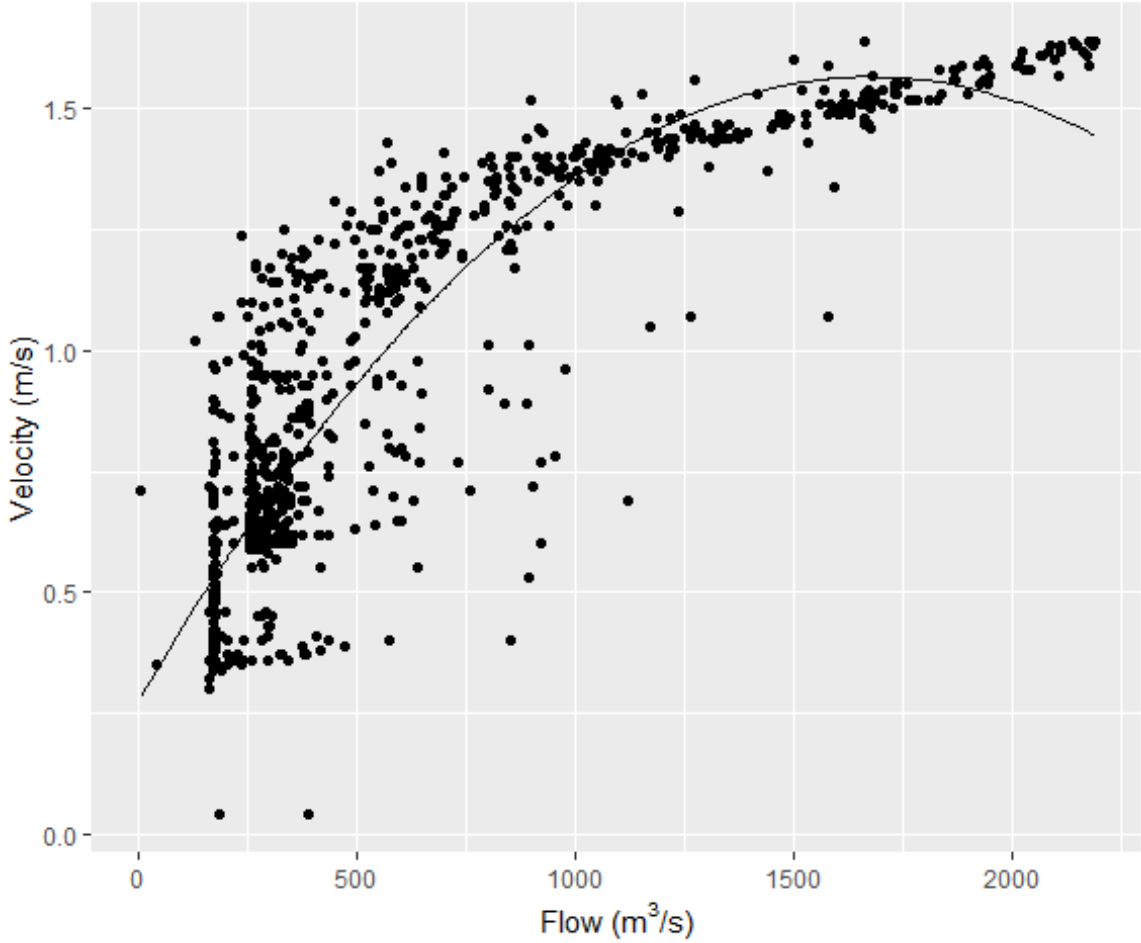

Figure A17 Hourly velocity and flow for spring 2018 deployment for 2018.Spring.R3.S3.T4

Table A6 Summary of model for hourly velocity and flow for 2018.Spring.R3.S3.T5

term	estimate	std.error	statistic	p.value	adjr2
(Intercept)	1.25e-01	4.24e-02	2.95e+00	3.32e-03	7.57e-01
poly(mean, 2, raw = TRUE)1	1.07e-03	8.91e-05	1.20e+01	8.86e-29	7.57e-01
poly(mean, 2, raw = TRUE)2	-1.65e-07	3.89e-08	-4.24e+00	2.82e-05	7.57e-01

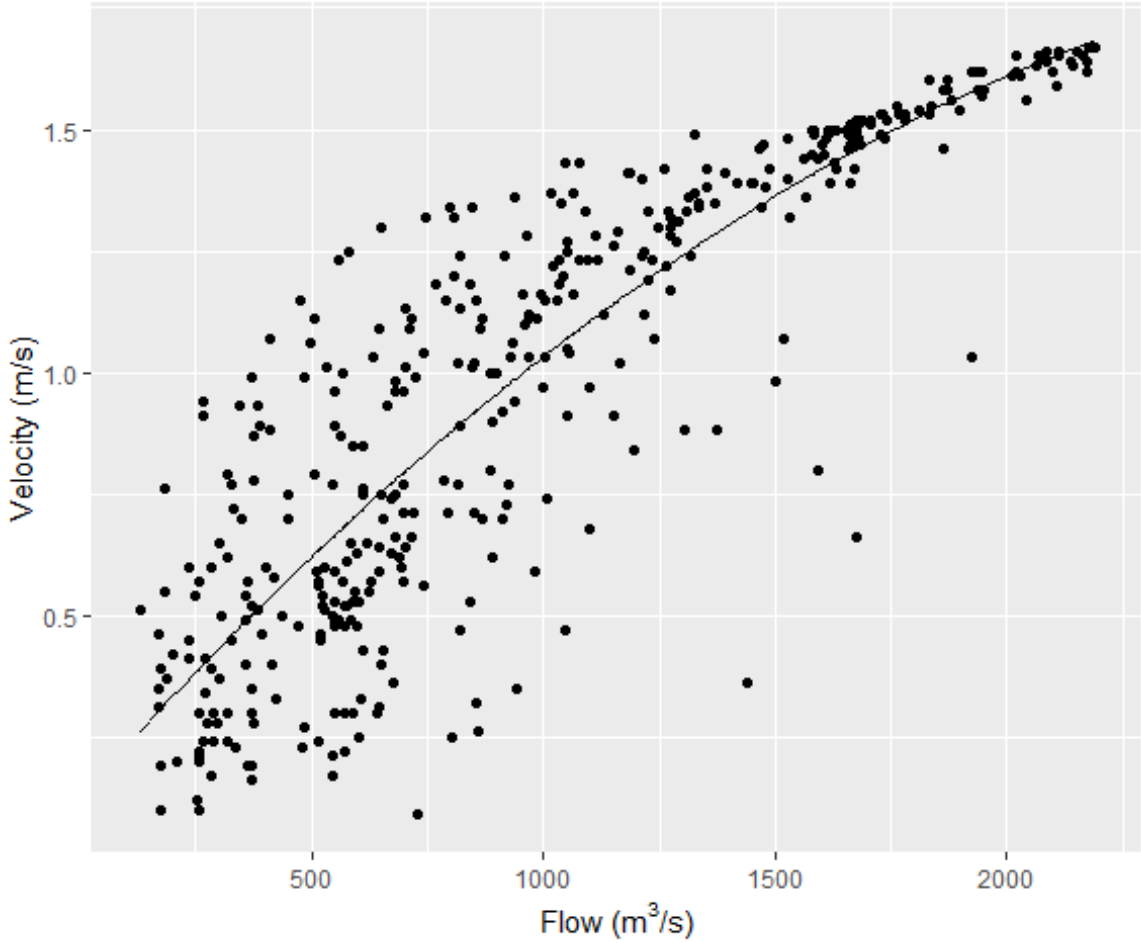

Figure A18 Hourly velocity and flow for spring 2018 deployment for 2018.Spring.R3.S3.T5

Table A7 Summary of model for hourly velocity and flow for 2018.Spring.R3.S3.T6

term	estimate	std.error	statistic	p.value	adjr2
(Intercept)	2.27e-01	3.53e-02	6.44e+00	5.97e-10	6.99e-01
mean	6.27e-04	2.55e-05	2.45e+01	1.89e-69	6.99e-01

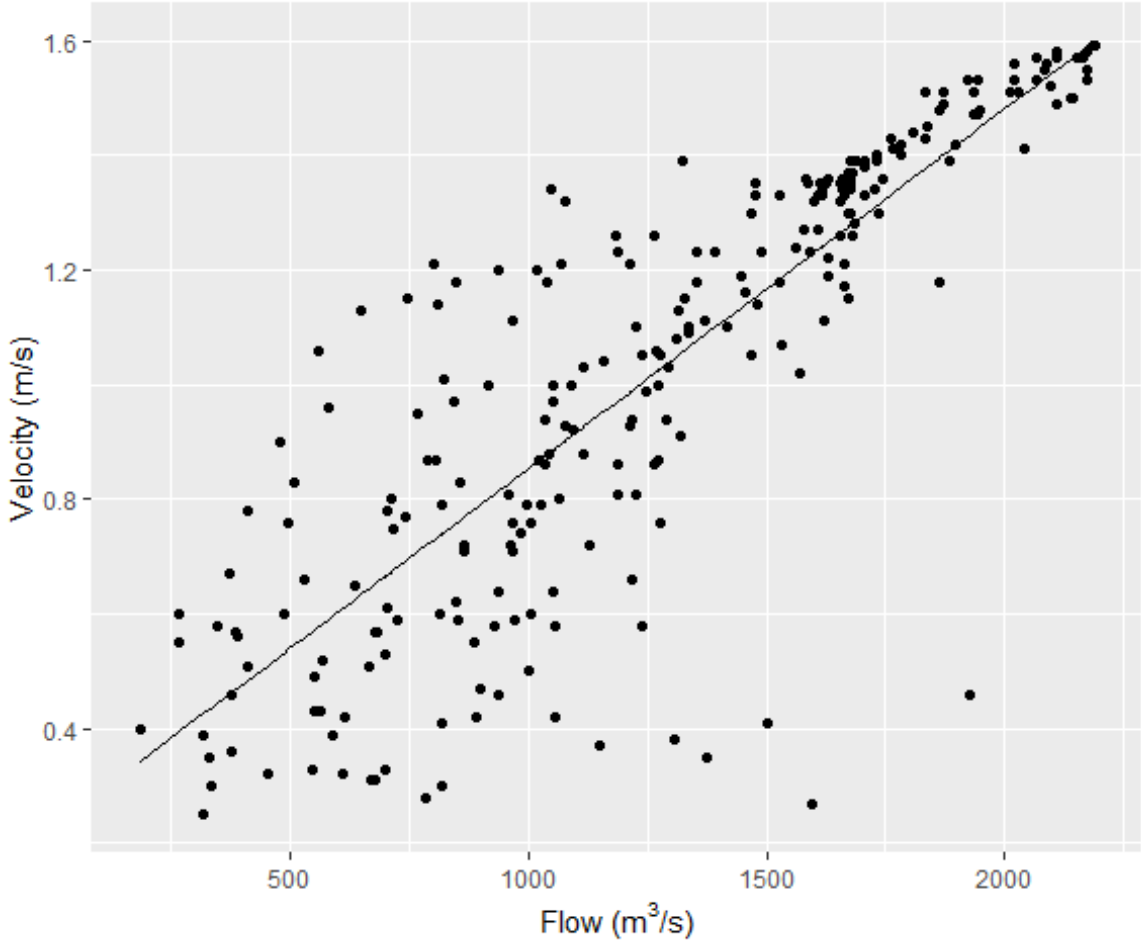

Figure A19 Hourly velocity and flow for spring 2018 deployment for 2018.Spring.R3.S3.T6

Table A8 Summary of model for hourly velocity and flow for 2018.Spring.R3.S5.T3

term	estimate	std.error	statistic	p.value	adjr2
(Intercept)	-1.92e-01	1.61e-02	-1.19e+01	9.99e-31	9.01e-01
poly(mean, 2, raw = TRUE)1	1.52e-03	4.98e-05	3.04e+01	2.26e-145	9.01e-01
poly(mean, 2, raw = TRUE)2	-1.77e-07	2.51e-08	-7.06e+00	3.14e-12	9.01e-01

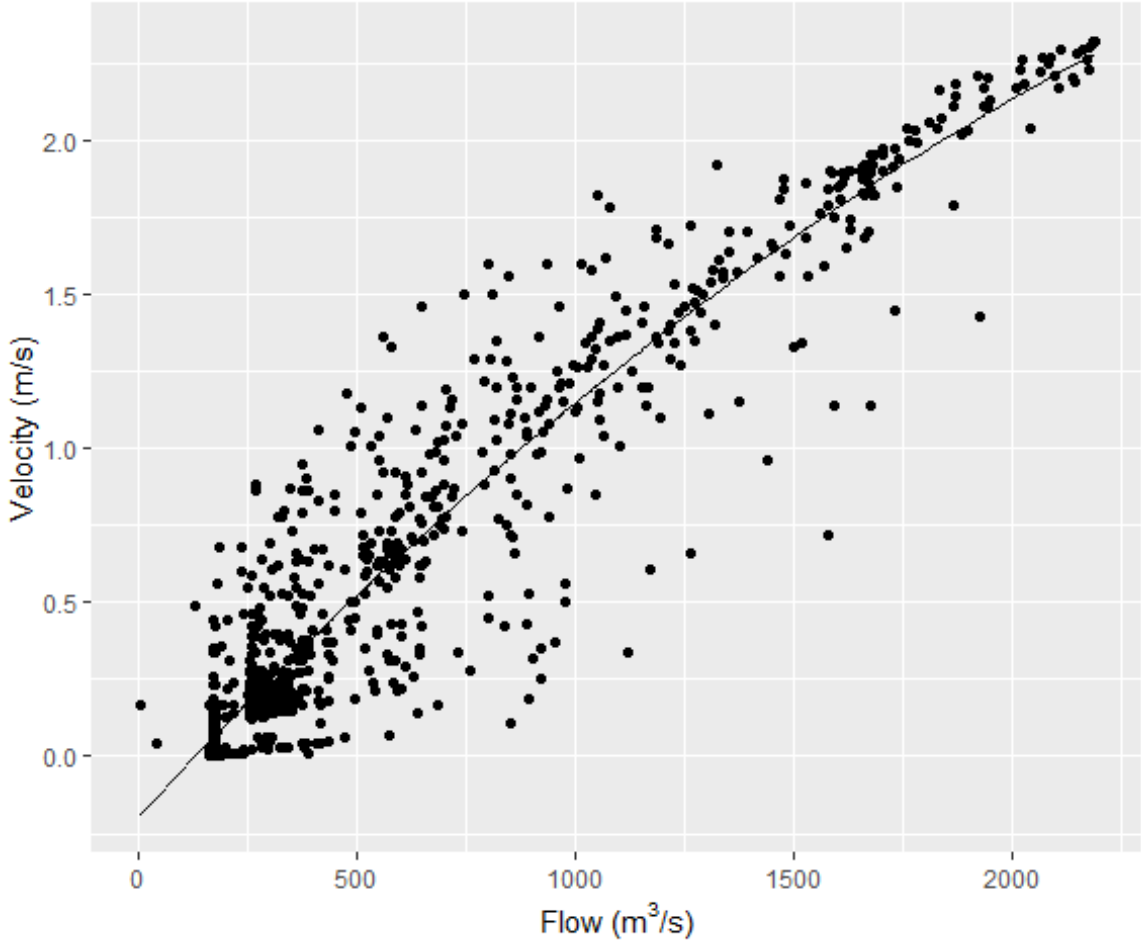

Figure A20 Hourly velocity and flow for spring 2018 deployment for 2018.Spring.R3.S5.T3

Table A9 Summary of model for hourly velocity and flow for 2018.Spring.R3.S5.T5

term	estimate	std.error	statistic	p.value	adjr2
(Intercept)	-1.57e-01	1.42e-02	-1.10e+01	9.66e-26	8.99e-01
mean	1.00e-03	1.42e-05	7.08e+01	3.65e-281	8.99e-01

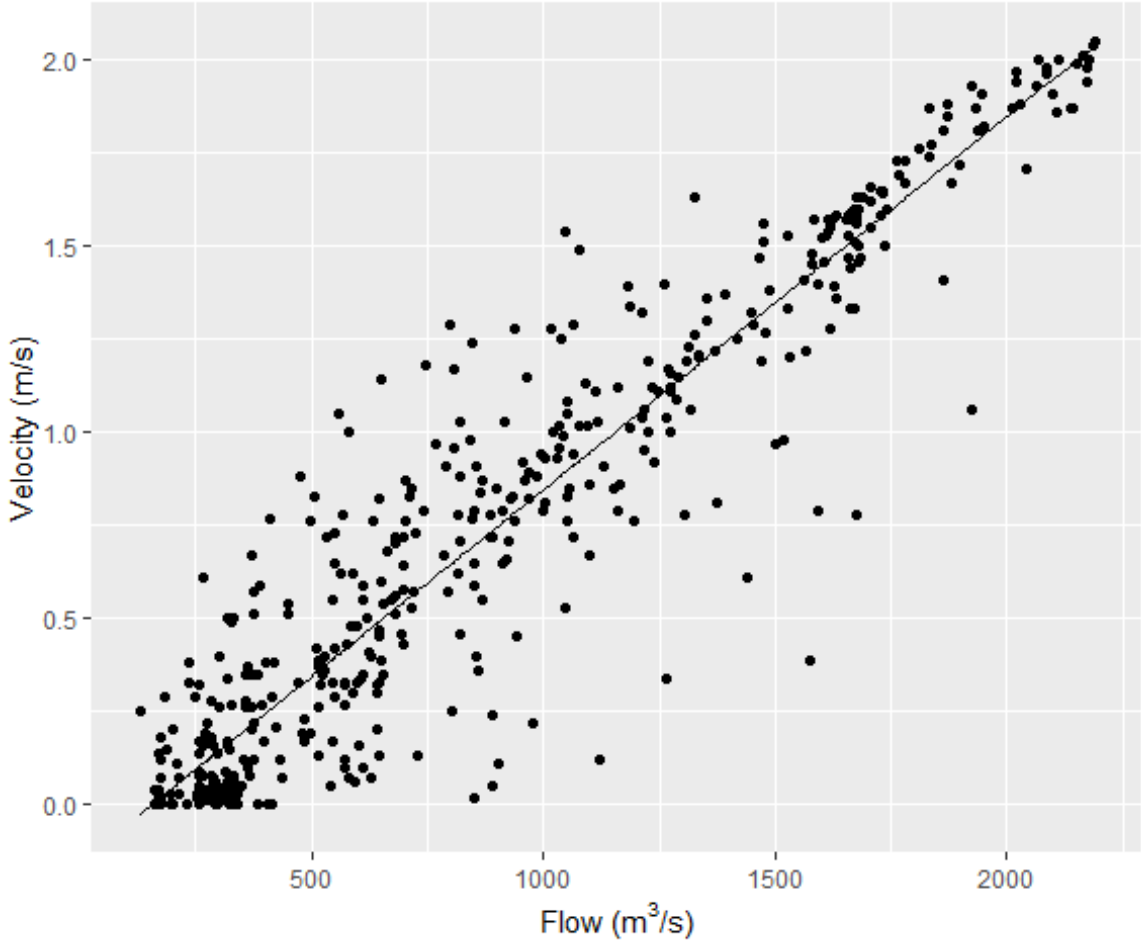

Figure A21 Hourly velocity and flow for spring 2018 deployment for 2018.Spring.R3.S5.T5

Table A10 Summary of model for hourly velocity and flow for 2018.Spring.R3.S5.T6

term	estimate	std.error	statistic	p.value	adjr2
(Intercept)	-1.62e-01	2.09e-02	-7.76e+00	4.72e-14	9.06e-01
poly(mean, 2, raw = TRUE)1	7.55e-04	5.46e-05	1.38e+01	5.13e-37	9.06e-01
poly(mean, 2, raw = TRUE)2	7.58e-08	2.62e-08	2.89e+00	4.01e-03	9.06e-01

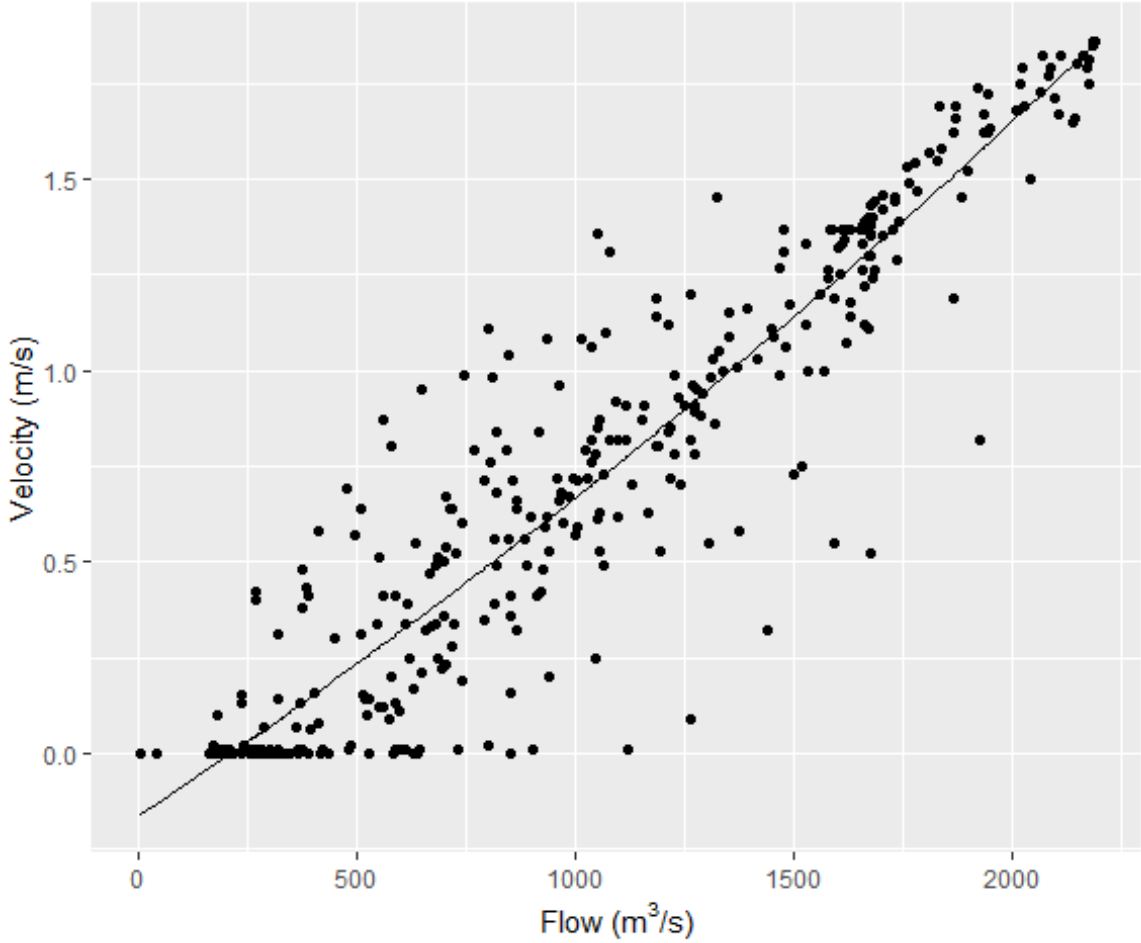

Figure A22 Hourly velocity and flow for spring 2018 deployment for 2018.Spring.R3.S5.T6

Table A11 Summary of model for hourly velocity and flow for 2018.Spring.R3.S6.T1

term	estimate	std.error	statistic	p.value	adjr2
(Intercept)	1.27e+00	6.46e-03	1.97e+02	0.000000e+00	8.1e-01
poly(mean, 2, raw = TRUE)1	1.13e-03	2.00e-05	5.67e+01	7.259998e-319	8.1e-01
poly(mean, 2, raw = TRUE)2	-4.69e-07	1.00e-08	-4.67e+01	1.650000e-256	8.1e-01

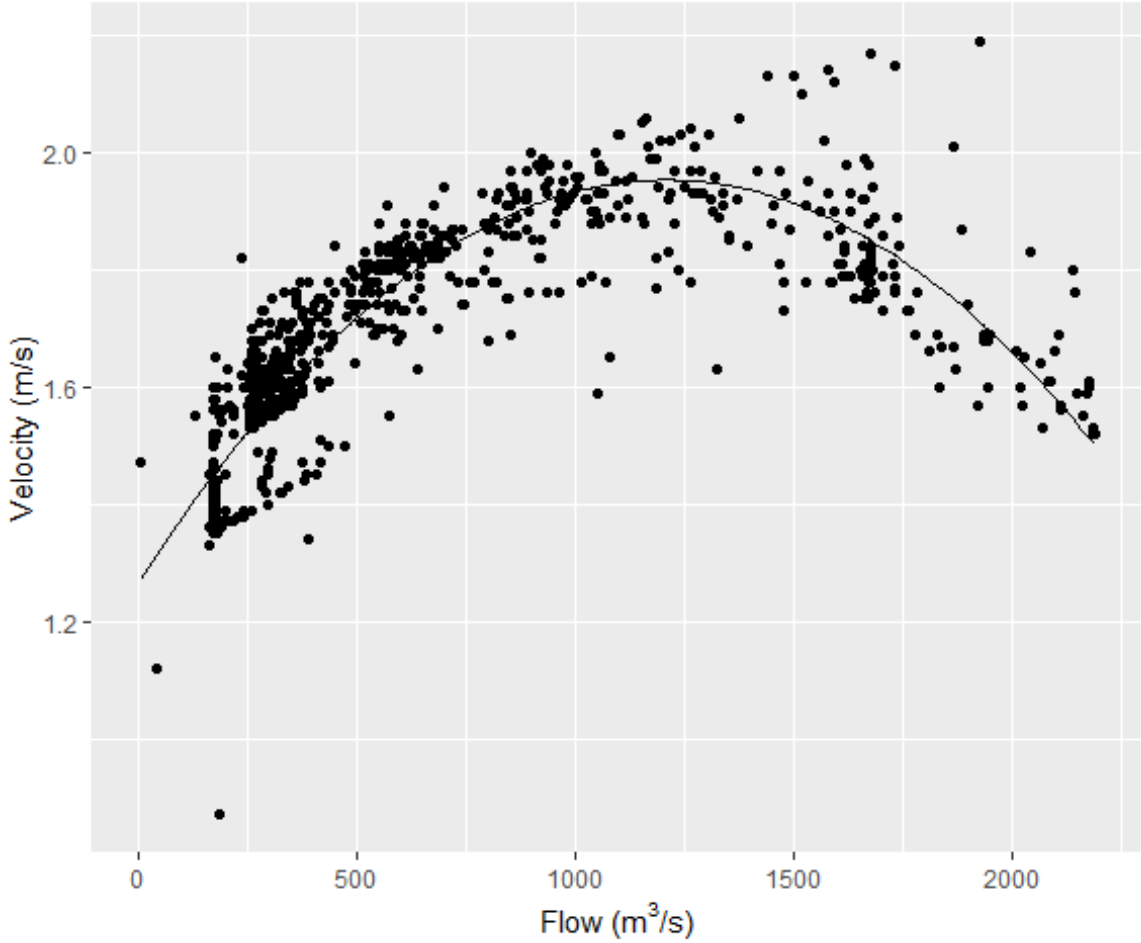

Figure A23 Hourly velocity and flow for spring 2018 deployment for 2018.Spring.R3.S6.T1

Table A12 Summary of model for hourly velocity and flow for 2018.Spring.R3.S6.T2

term	estimate	std.error	statistic	p.value	adjr2
(Intercept)	1.19e+00	6.92e-03	1.73e+02	0.000000e+00	8.27e-01
poly(mean, 2, raw = TRUE)1	1.23e-03	2.14e-05	5.73e+01	2.865581e-322	8.27e-01
poly(mean, 2, raw = TRUE)2	-4.92e-07	1.08e-08	-4.57e+01	3.950000e-250	8.27e-01

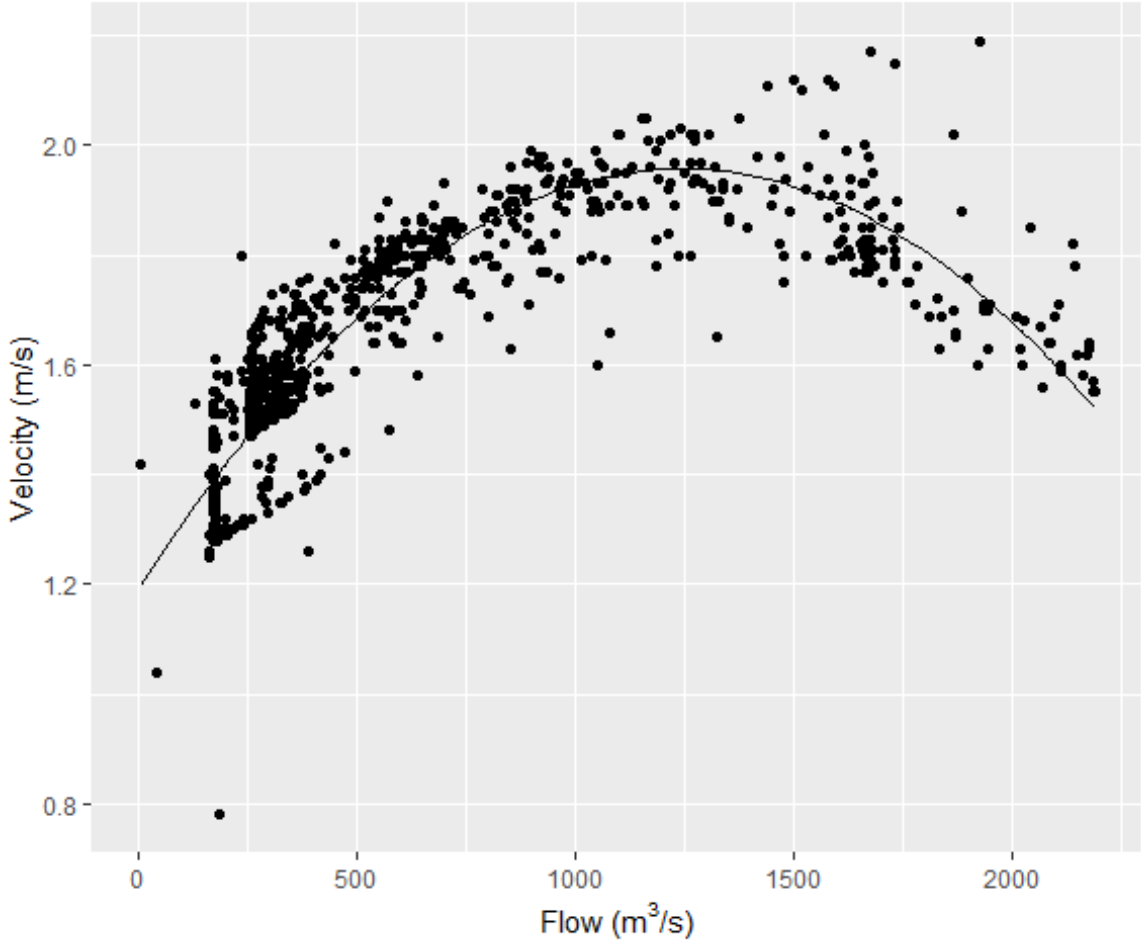

Figure A24 Hourly velocity and flow for spring 2018 deployment for 2018.Spring.R3.S6.T2

Table A13 Summary of model for hourly velocity and flow for 2018.Spring.R3.S6.T3

term	estimate	std.error	statistic	p.value	adjr2
(Intercept)	8.31e-01	1.02e-02	8.15e+01	0.00e+00	8.61e-01
poly(mean, 2, raw = TRUE)1	1.72e-03	3.15e-05	5.46e+01	3.64e-306	8.61e-01
poly(mean, 2, raw = TRUE)2	-6.16e-07	1.58e-08	-3.89e+01	4.85e-204	8.61e-01

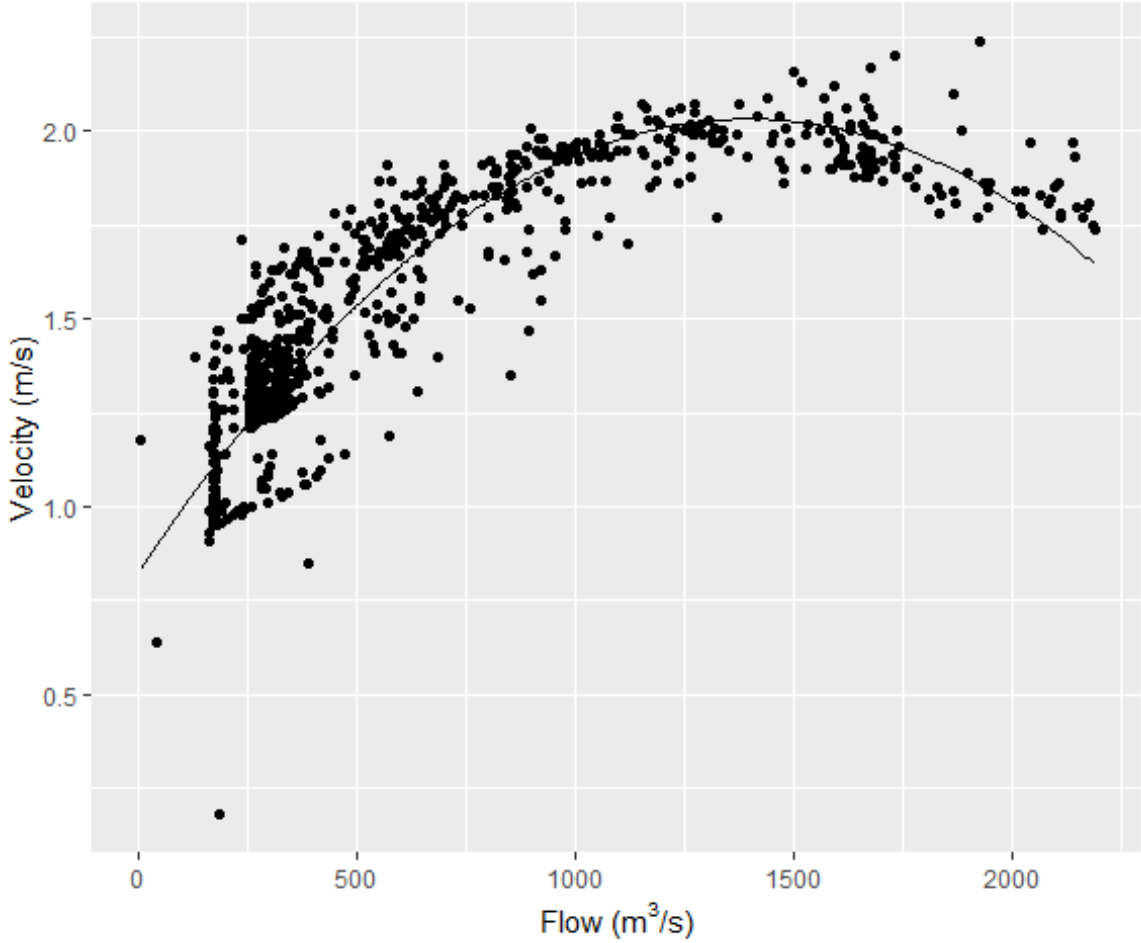

Figure A25 Hourly velocity and flow for spring 2018 deployment for 2018.Spring.R3.S6.T3

Table A14 Summary of model for hourly velocity and flow for 2018.Spring.R3.S6.T4

term	estimate	std.error	statistic	p.value	adjr2
(Intercept)	-2.56e-01	2.21e-02	-1.16e+01	5.82e-29	8.73e-01
poly(mean, 2, raw = TRUE)1	2.54e-03	6.31e-05	4.03e+01	2.26e-200	8.73e-01
poly(mean, 2, raw = TRUE)2	-7.35e-07	3.09e-08	-2.38e+01	8.97e-97	8.73e-01

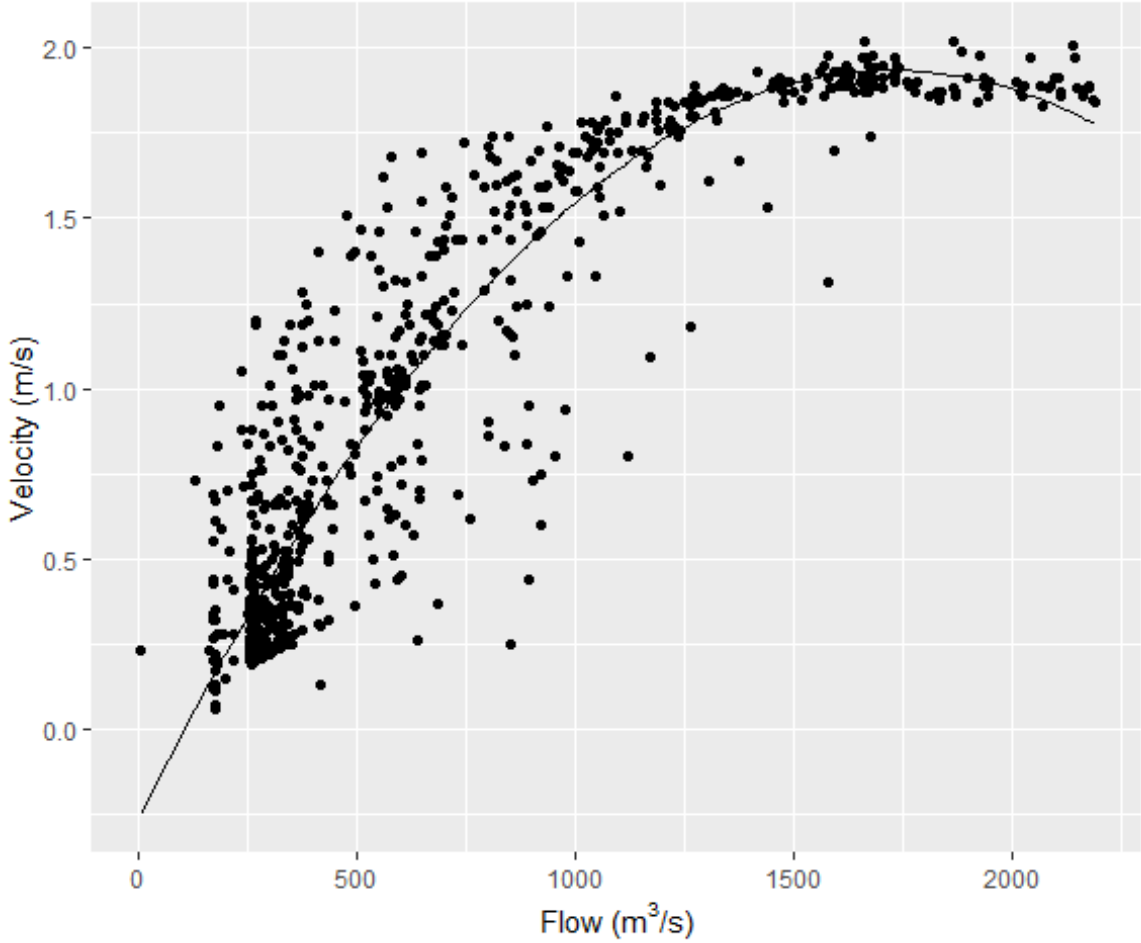

Figure A26 Hourly velocity and flow for spring 2018 deployment for 2018.Spring.R3.S6.T4

Table A15 Summary of model for hourly velocity and flow for 2018.Spring.R3.S6.T5

term	estimate	std.error	statistic	p.value	adjr2
(Intercept)	-1.21e-01	7.26e-02	-1.66e+00	9.85e-02	8.37e-01
poly(mean, 2, raw = TRUE)1	1.56e-03	1.80e-04	8.64e+00	2.54e-15	8.37e-01
poly(mean, 2, raw = TRUE)2	-2.02e-07	9.27e-08	-2.18e+00	3.06e-02	8.37e-01

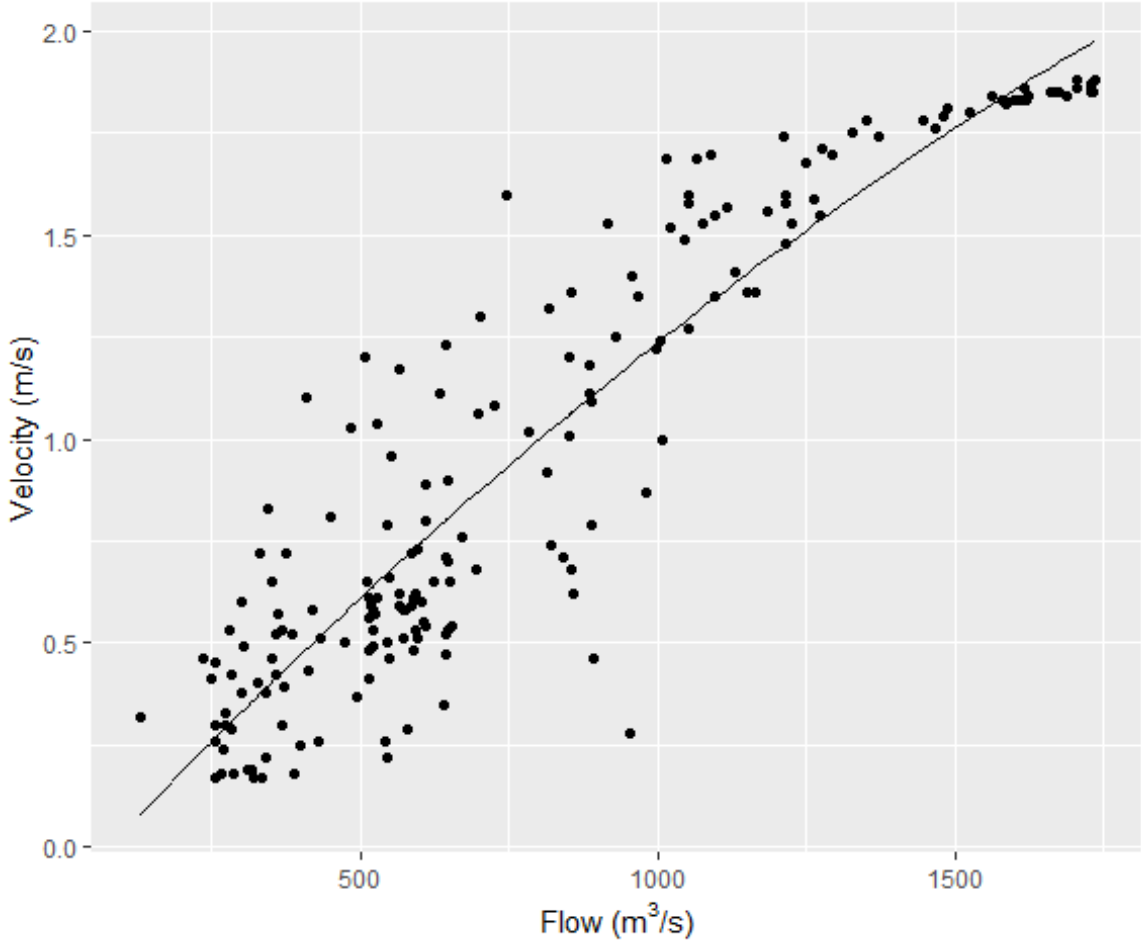

Figure A27 Hourly velocity and flow for spring 2018 deployment for 2018.Spring.R3.S6.T5

Table A16 Summary of model for hourly velocity and flow for 2018.Spring.R3.S6.T6

term	estimate	std.error	statistic	p.value	adjr2
(Intercept)	-4.01e-01	1.40e-01	-2.87e+00	4.51e-03	7.1e-01
poly(mean, 2, raw = TRUE)1	1.68e-03	2.17e-04	7.75e+00	2.66e-13	7.1e-01
poly(mean, 2, raw = TRUE)2	-2.86e-07	7.94e-08	-3.60e+00	3.90e-04	7.1e-01

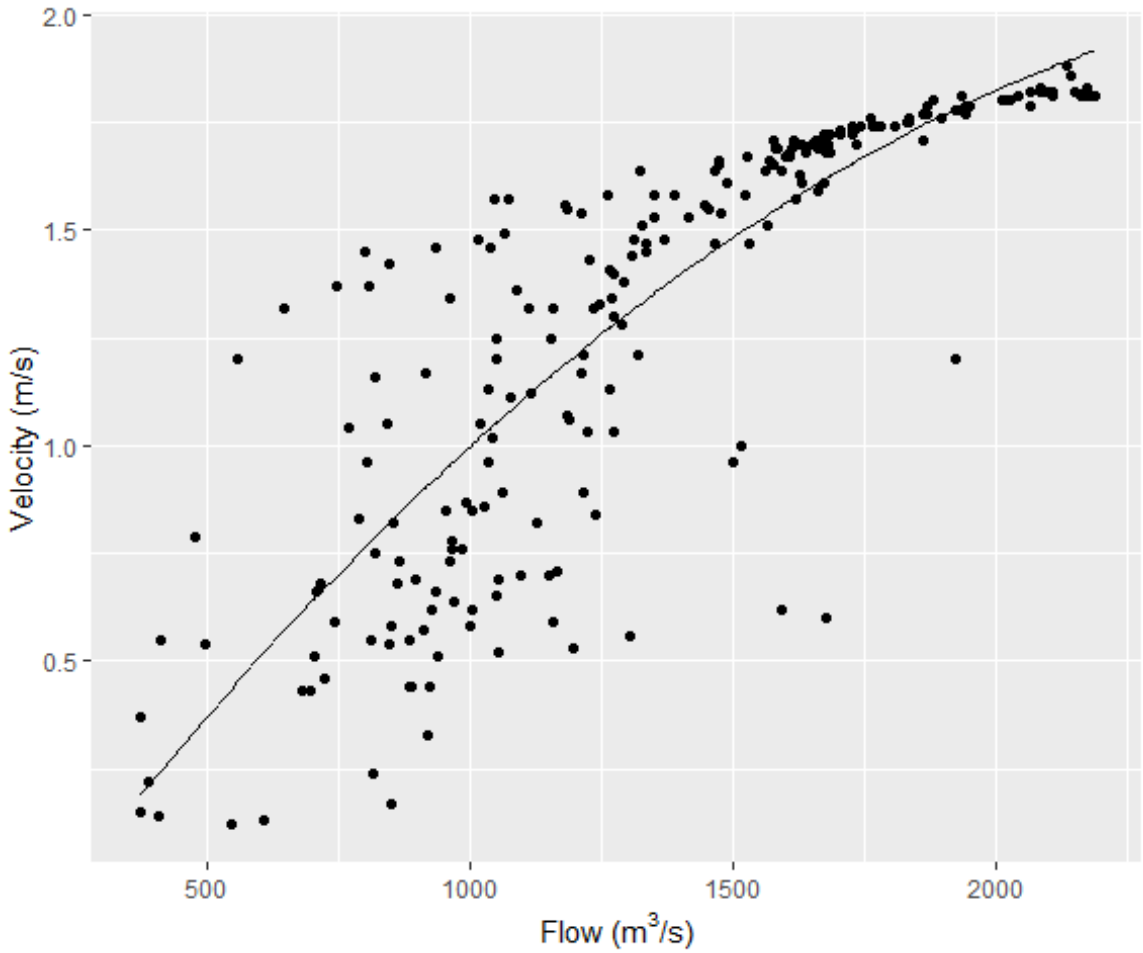

Figure A28 Hourly velocity and flow for spring 2018 deployment for 2018.Spring.R3.S6.T6

Table A17 Summary of model for hourly velocity and flow for 2018.Spring.R4.S4.T1

term	estimate	std.error	statistic	p.value	adjr2
(Intercept)	3.37e-01	3.47e-03	9.73e+01	0.00e+00	9.94e-01
poly(mean, 2, raw = TRUE)1	1.49e-03	1.08e-05	1.38e+02	0.00e+00	9.94e-01
poly(mean, 2, raw = TRUE)2	-2.48e-07	5.41e-09	-4.58e+01	2.92e-250	9.94e-01

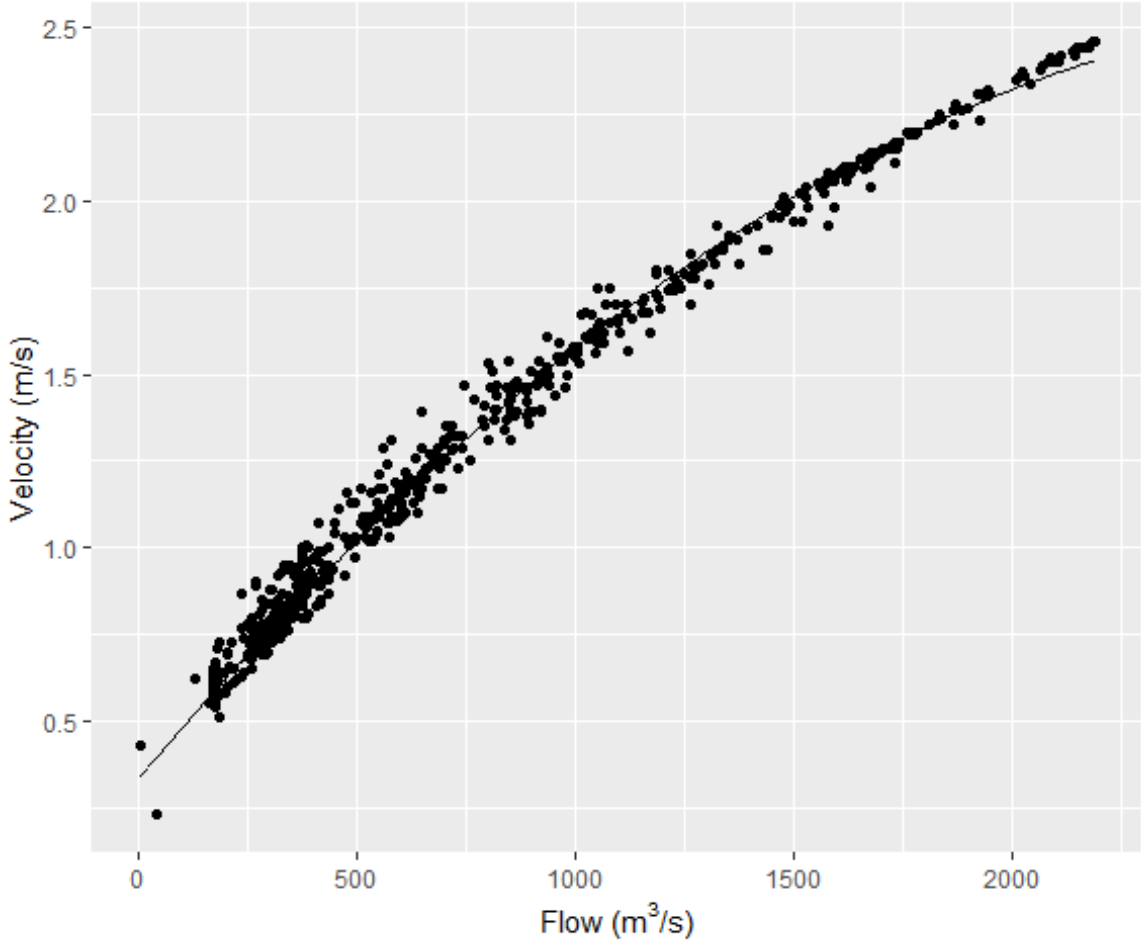

Figure A29 Hourly velocity and flow for spring 2018 deployment for 2018.Spring.R4.S4.T1

Table A18 Summary of model for hourly velocity and flow for 2018.Spring.R4.S4.T2

term	estimate	std.error	statistic	p.value	adjr2
(Intercept)	7.08e-02	4.53e-03	1.56e+01	1.39e-49	9.9e-01
poly(mean, 2, raw = TRUE)1	1.50e-03	1.40e-05	1.06e+02	0.00e+00	9.9e-01
poly(mean, 2, raw = TRUE)2	-2.30e-07	7.07e-09	-3.26e+01	1.57e-160	9.9e-01

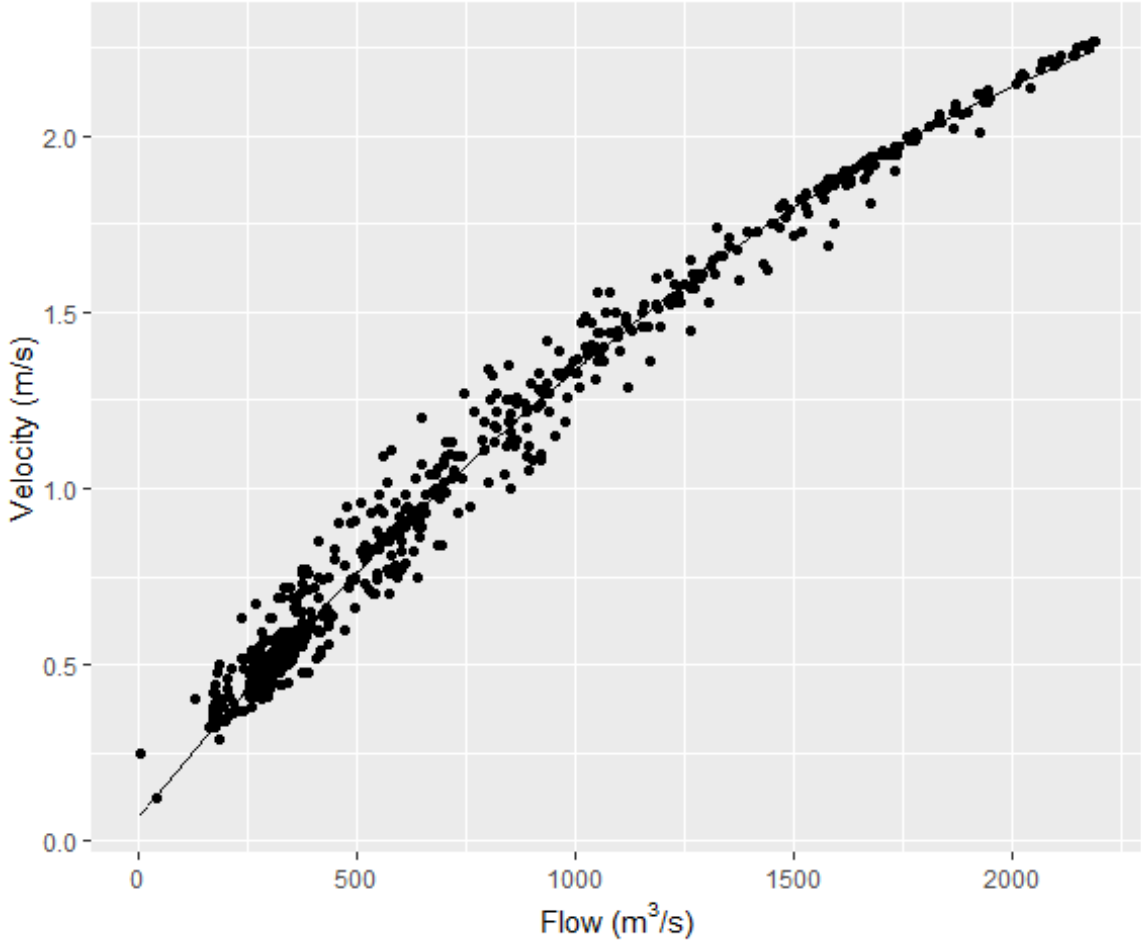

Figure A30 Hourly velocity and flow for spring 2018 deployment for 2018.Spring.R4.S4.T2

Table A19 Summary of model for hourly velocity and flow for 2018.Spring.R4.S4.T3

term	estimate	std.error	statistic	p.value	adjr2
(Intercept)	3.81e-02	4.90e-03	7.78e+00	1.80e-14	9.89e-01
poly(mean, 2, raw = TRUE)1	1.56e-03	1.52e-05	1.03e+02	0.00e+00	9.89e-01
poly(mean, 2, raw = TRUE)2	-2.55e-07	7.64e-09	-3.34e+01	4.47e-166	9.89e-01

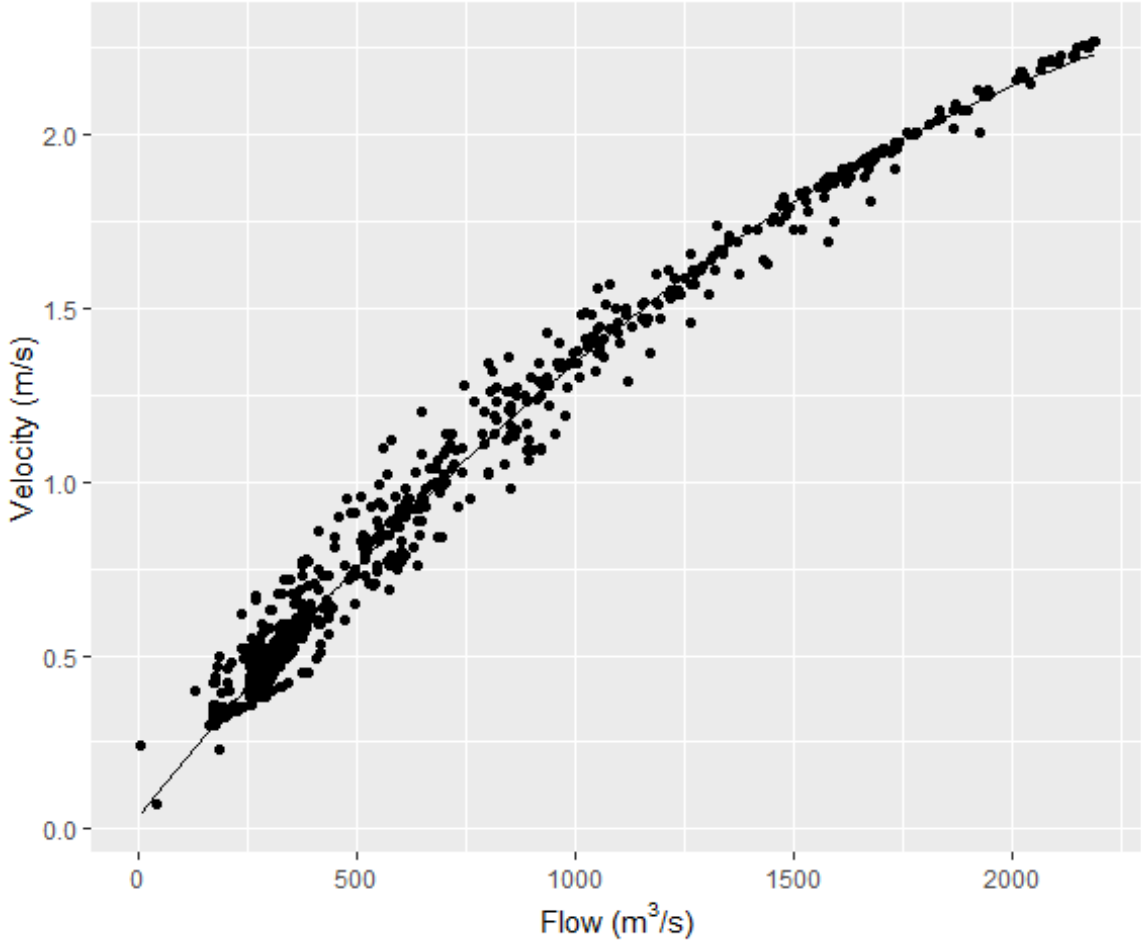

Figure A31 Hourly velocity and flow for spring 2018 deployment for 2018.Spring.R4.S4.T3

Table A20 Summary of model for hourly velocity and flow for 2018.Spring.R4.S4.T5

term	estimate	std.error	statistic	p.value	adjr2
(Intercept)	-3.84e-01	2.73e-02	-1.41e+01	4.17e-37	9.57e-01
poly(mean, 2, raw = TRUE)1	1.53e-03	5.33e-05	2.87e+01	1.89e-101	9.57e-01
poly(mean, 2, raw = TRUE)2	-2.13e-07	2.23e-08	-9.56e+00	9.53e-20	9.57e-01

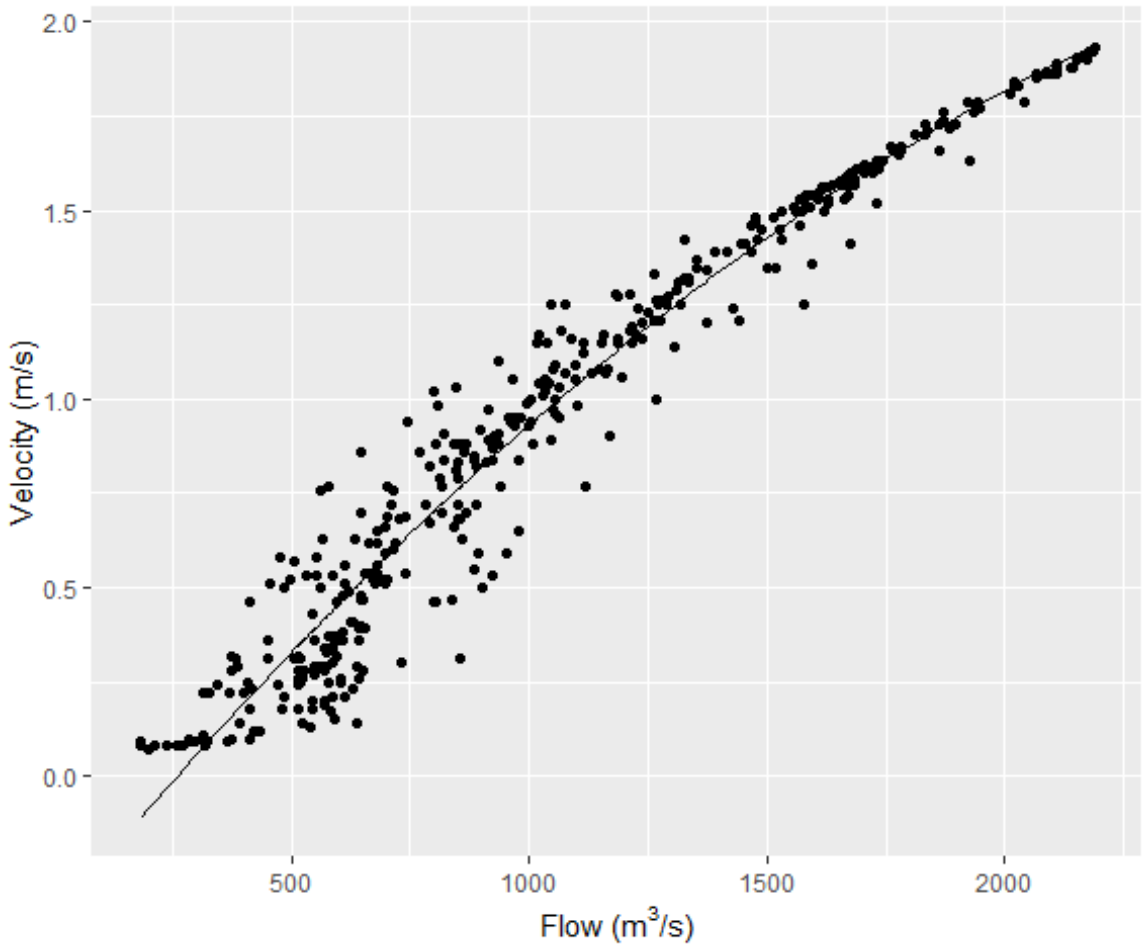

Figure A32 Hourly velocity and flow for spring 2018 deployment for 2018.Spring.R4.S4.T5

Table A21 Summary of model for hourly velocity and flow for 2018.Spring.R4.S4.T6

term	estimate	std.error	statistic	p.value	adjr2
(Intercept)	-7.60e-01	7.73e-02	-9.83e+00	1.10e-19	9.25e-01
poly(mean, 2, raw = TRUE)1	1.44e-03	1.17e-04	1.23e+01	6.41e-28	9.25e-01
poly(mean, 2, raw = TRUE)2	-1.71e-07	4.14e-08	-4.14e+00	4.61e-05	9.25e-01

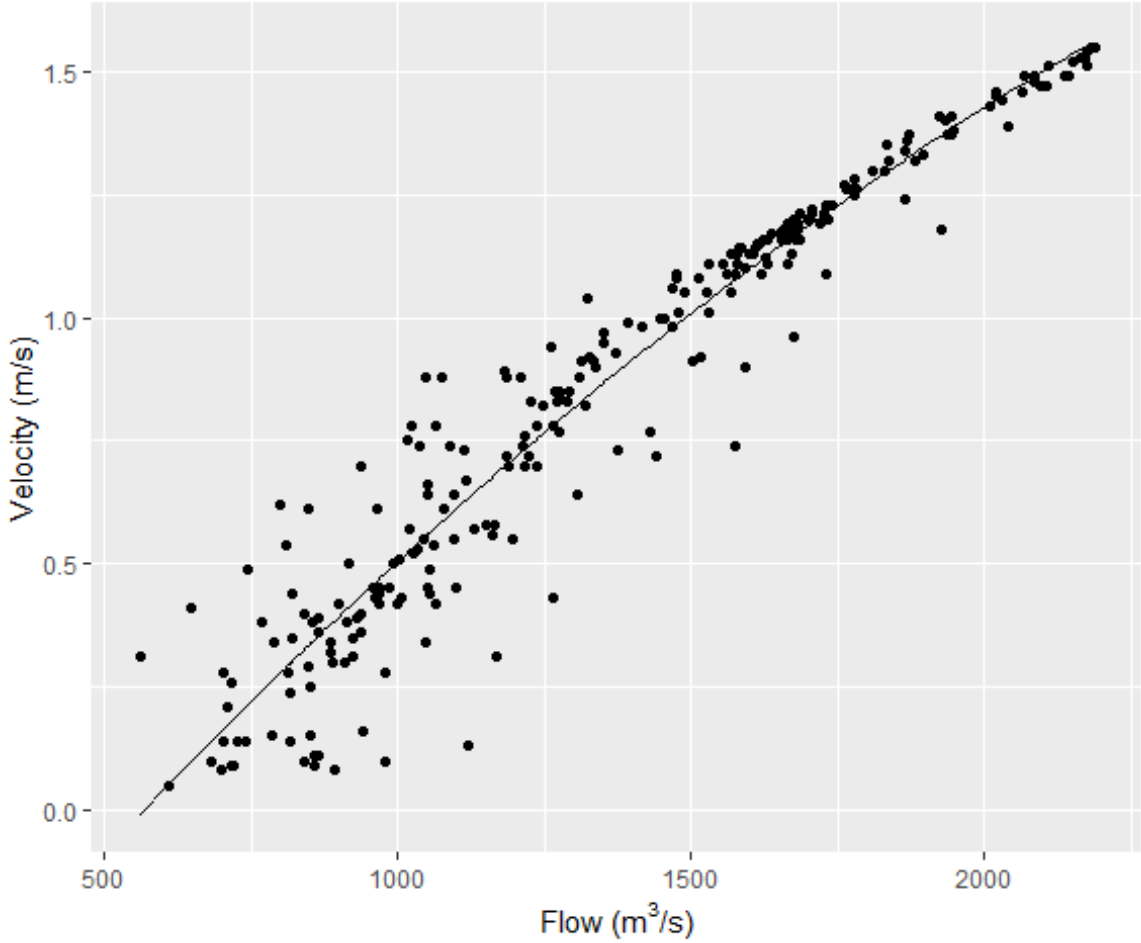

Figure A33 Hourly velocity and flow for spring 2018 deployment for 2018.Spring.R4.S4.T6

Table A22 Summary of model for hourly velocity and flow for 2018.Spring.R4.S5.T1

term	estimate	std.error	statistic	p.value	adjr2
(Intercept)	3.00e-02	5.99e-03	5.01e+00	6.40e-07	9.86e-01
poly(mean, 2, raw = TRUE)1	1.10e-03	1.86e-05	5.92e+01	0.00e+00	9.86e-01
poly(mean, 2, raw = TRUE)2	4.24e-08	9.35e-09	4.53e+00	6.62e-06	9.86e-01

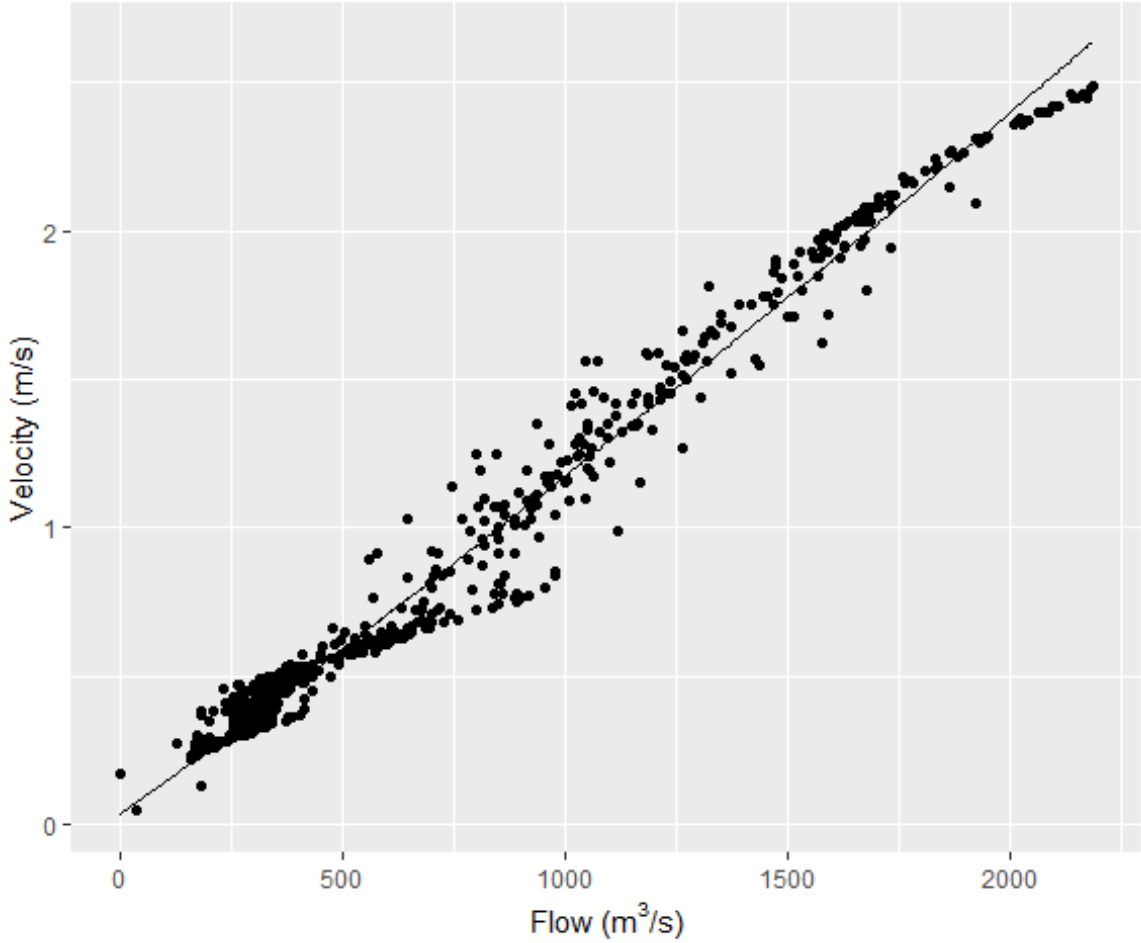

Figure A34 Hourly velocity and flow for spring 2018 deployment for 2018.Spring.R4.S5.T1

Table A23 Summary of model for hourly velocity and flow for 2018.Spring.R4.S5.T2

term	estimate	std.error	statistic	p.value	adjr2
(Intercept)	8.20e-02	5.38e-03	1.52e+01	2.32e-47	9.89e-01
poly(mean, 2, raw = TRUE)1	1.28e-03	1.67e-05	7.67e+01	0.00e+00	9.89e-01
poly(mean, 2, raw = TRUE)2	-3.57e-08	8.41e-09	-4.24e+00	2.39e-05	9.89e-01

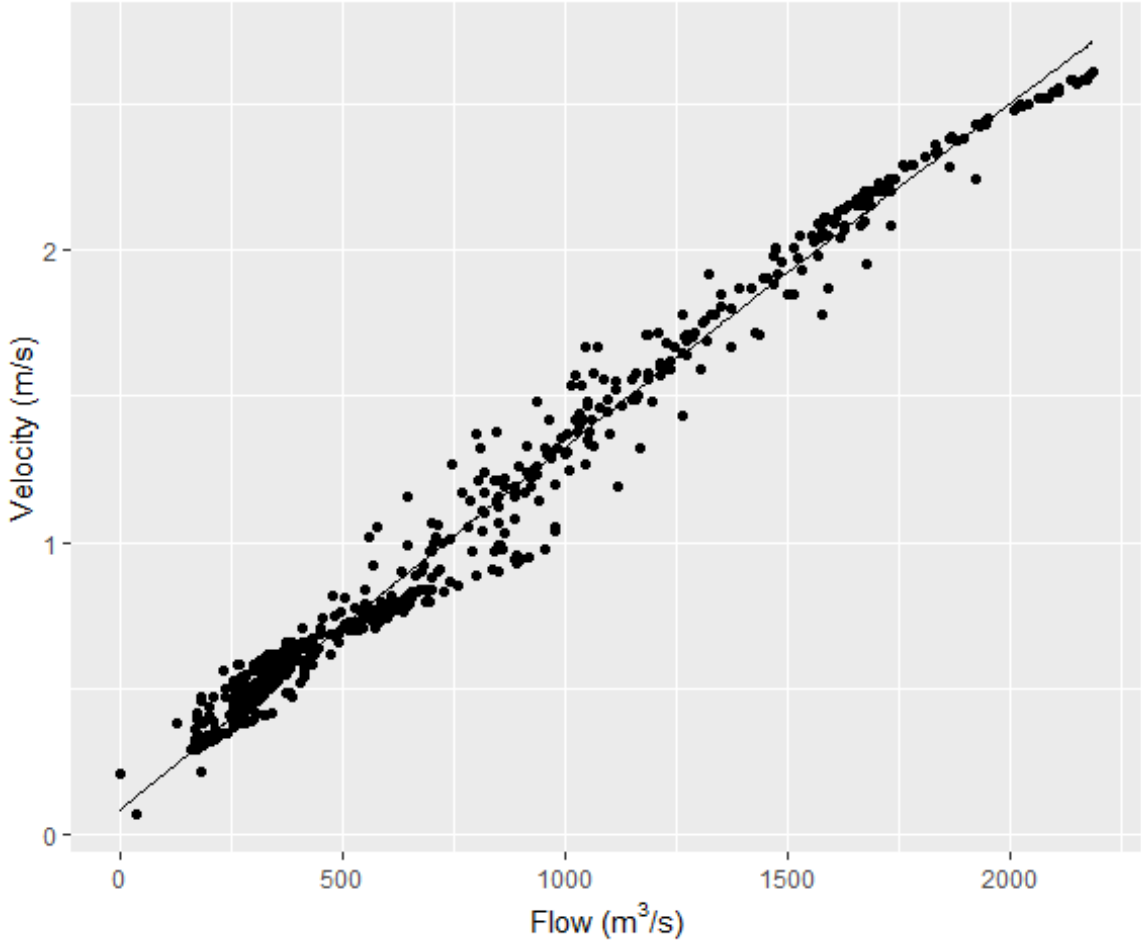

Figure A35 Hourly velocity and flow for spring 2018 deployment for 2018.Spring.R4.S5.T2

Table A24 Summary of model for hourly velocity and flow for 2018.Spring.R4.S5.T3

term	estimate	std.error	statistic	p.value	adjr2
(Intercept)	2.38e-02	5.35e-03	4.44e+00	1.00000e-05	9.86e-01
poly(mean, 2, raw = TRUE)1	9.55e-04	1.66e-05	5.75e+01	7.90505e-323	9.86e-01
poly(mean, 2, raw = TRUE)2	5.18e-08	8.36e-09	6.19e+00	8.59000e-10	9.86e-01

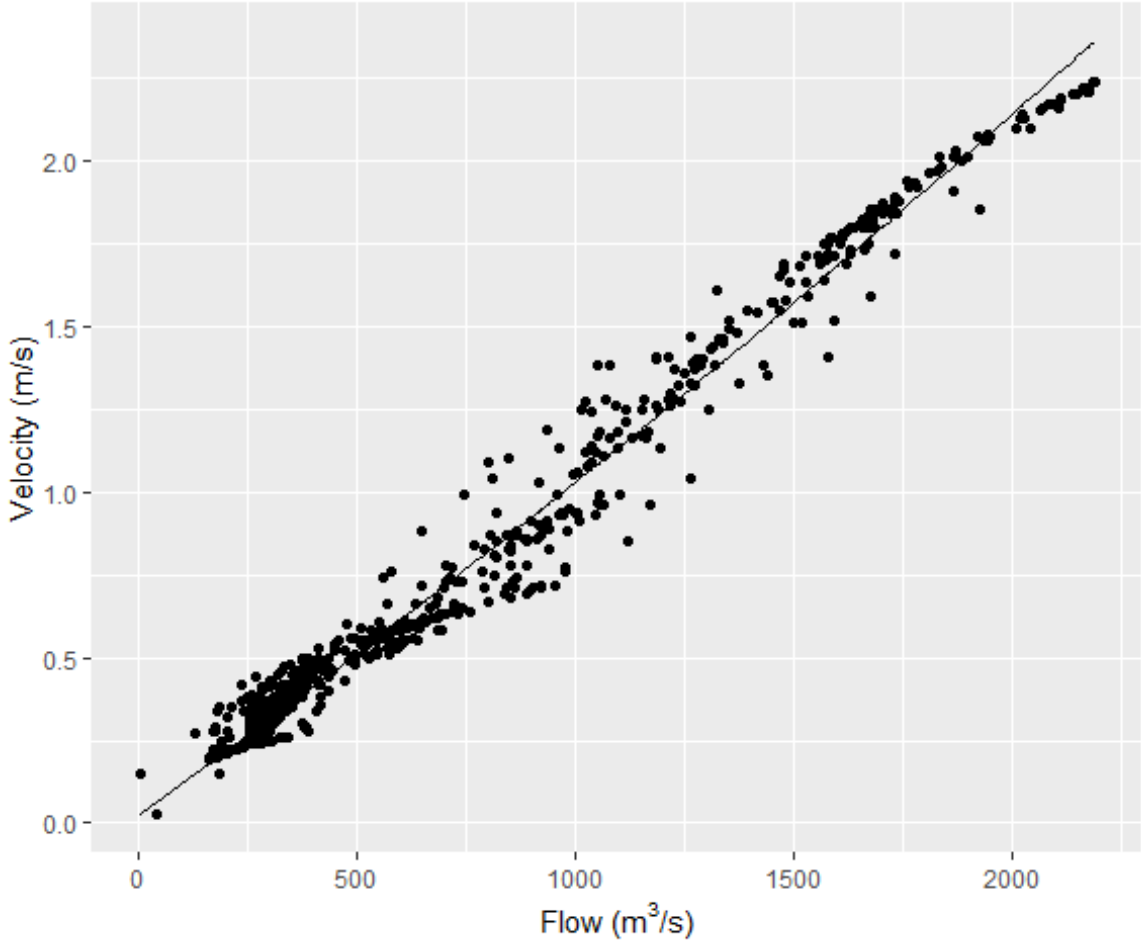

Figure A36 Hourly velocity and flow for spring 2018 deployment for 2018.Spring.R4.S5.T3

Table A25 Summary of model for hourly velocity and flow for 2018.Spring.R4.S5.T4

term	estimate	std.error	statistic	p.value	adjr2
(Intercept)	-8.11e-02	5.37e-03	-1.51e+01	1.25e-46	9.85e-01
poly(mean, 2, raw = TRUE)1	8.64e-04	1.65e-05	5.23e+01	4.05e-288	9.85e-01
poly(mean, 2, raw = TRUE)2	7.43e-08	8.29e-09	8.96e+00	1.55e-18	9.85e-01

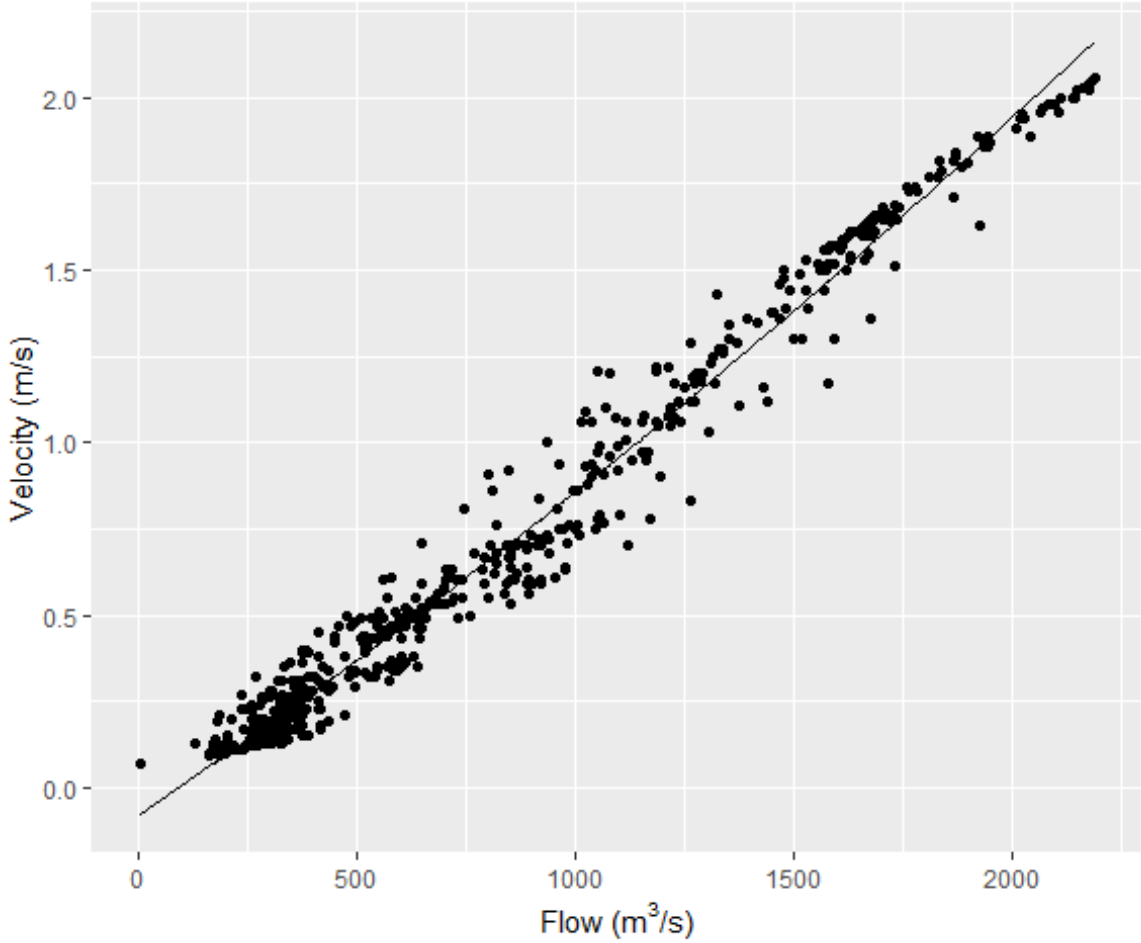

Figure A37 Hourly velocity and flow for spring 2018 deployment for 2018.Spring.R4.S5.T4

Table A26 Summary of model for hourly velocity and flow for 2018.Spring.R4.S5.T5

term	estimate	std.error	statistic	p.value	adjr2
(Intercept)	-9.89e-01	1.04e-01	-9.55e+00	1.15e-18	9.34e-01
poly(mean, 2, raw = TRUE)1	1.56e-03	1.54e-04	1.01e+01	1.74e-20	9.34e-01
poly(mean, 2, raw = TRUE)2	-9.01e-08	5.42e-08	-1.66e+00	9.77e-02	9.34e-01

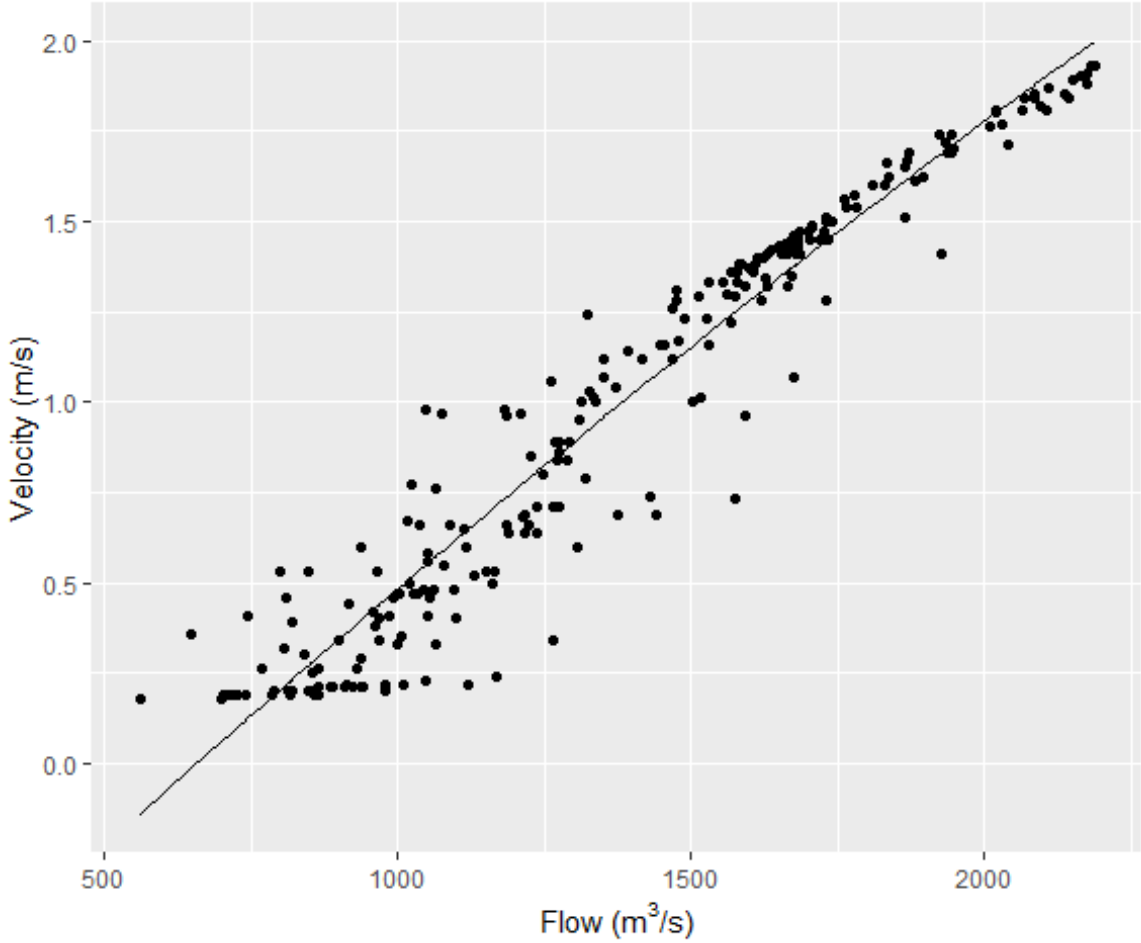

Figure A38 Hourly velocity and flow for spring 2018 deployment for 2018.Spring.R4.S5.T5

Table A27 Summary of model for hourly velocity and flow for 2018.Spring.R4.S5.T6

term	estimate	std.error	statistic	p.value	adjr2
(Intercept)	-1.58e-01	8.88e-02	-1.78e+00	7.71e-02	9.31e-01
poly(mean, 2, raw = TRUE)1	1.99e-05	1.29e-04	1.55e-01	8.77e-01	9.31e-01
poly(mean, 2, raw = TRUE)2	3.78e-07	4.46e-08	8.48e+00	2.86e-15	9.31e-01

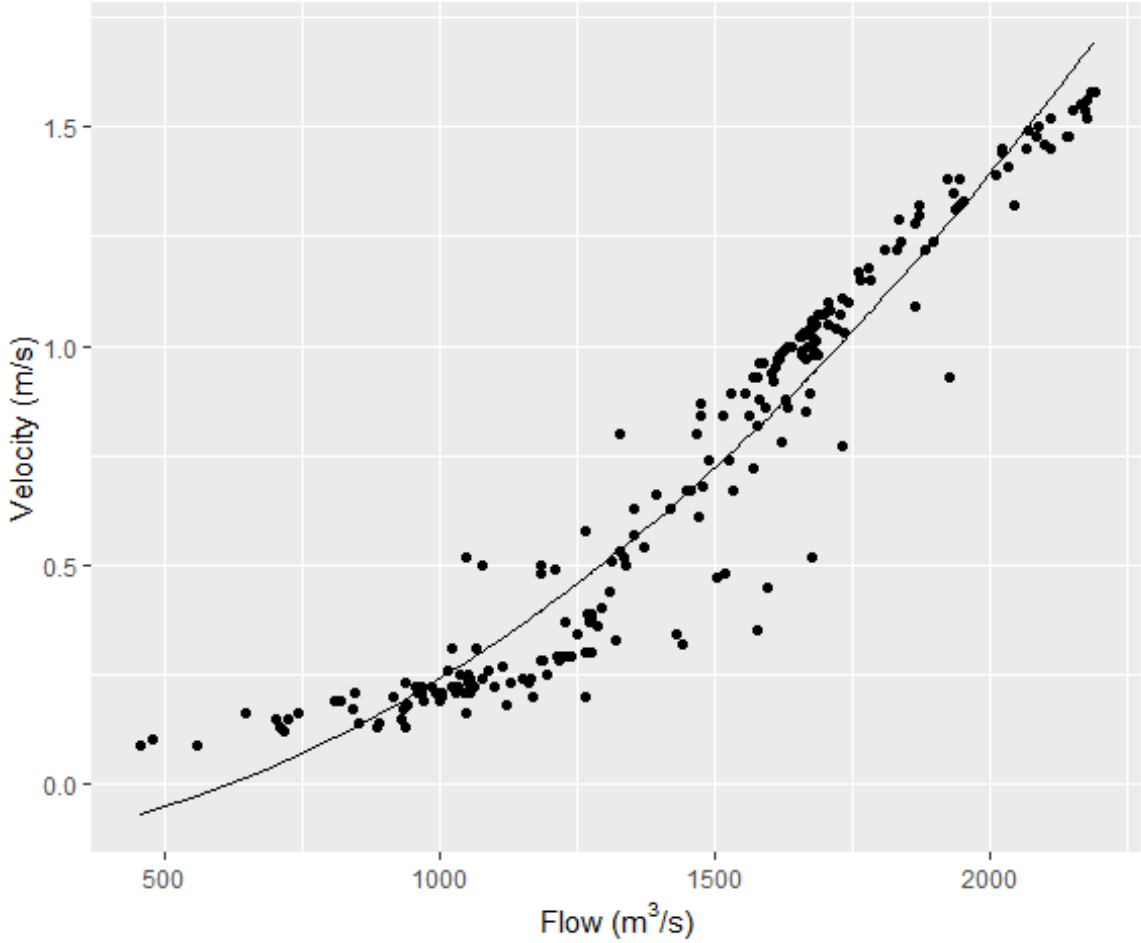

Figure A39 Hourly velocity and flow for spring 2018 deployment for 2018.Spring.R4.S5.T6

Table A28 Summary of model for hourly velocity and flow for 2018.Spring.R4.S6.T1

term	estimate	std.error	statistic	p.value	adjr2
(Intercept)	-1.02e-01	4.56e-03	-2.23e+01	3.16e-90	9.92e-01
poly(mean, 2, raw = TRUE)1	1.81e-03	1.41e-05	1.28e+02	0.00e+00	9.92e-01
poly(mean, 2, raw = TRUE)2	-3.08e-07	7.12e-09	-4.33e+01	8.88e-234	9.92e-01

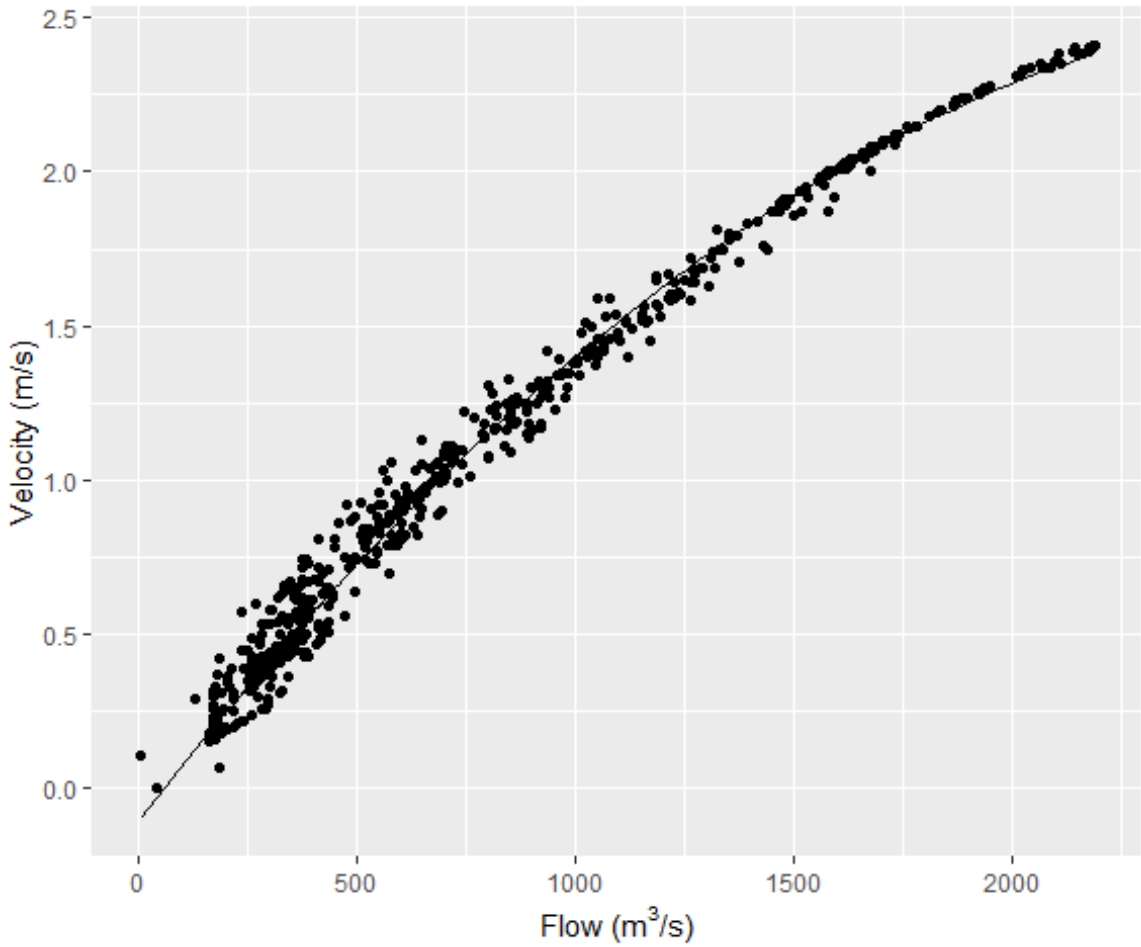

Figure A40 Hourly velocity and flow for spring 2018 deployment for 2018.Spring.R4.S6.T1

Table A29 Summary of model for hourly velocity and flow for 2018.Spring.R4.S6.T2

term	estimate	std.error	statistic	p.value	adjr2
(Intercept)	-1.77e-01	4.86e-03	-3.65e+01	1.54e-187	9.91e-01
poly(mean, 2, raw = TRUE)1	1.48e-03	1.51e-05	9.85e+01	0.00e+00	9.91e-01
poly(mean, 2, raw = TRUE)2	-1.61e-07	7.58e-09	-2.12e+01	6.46e-83	9.91e-01

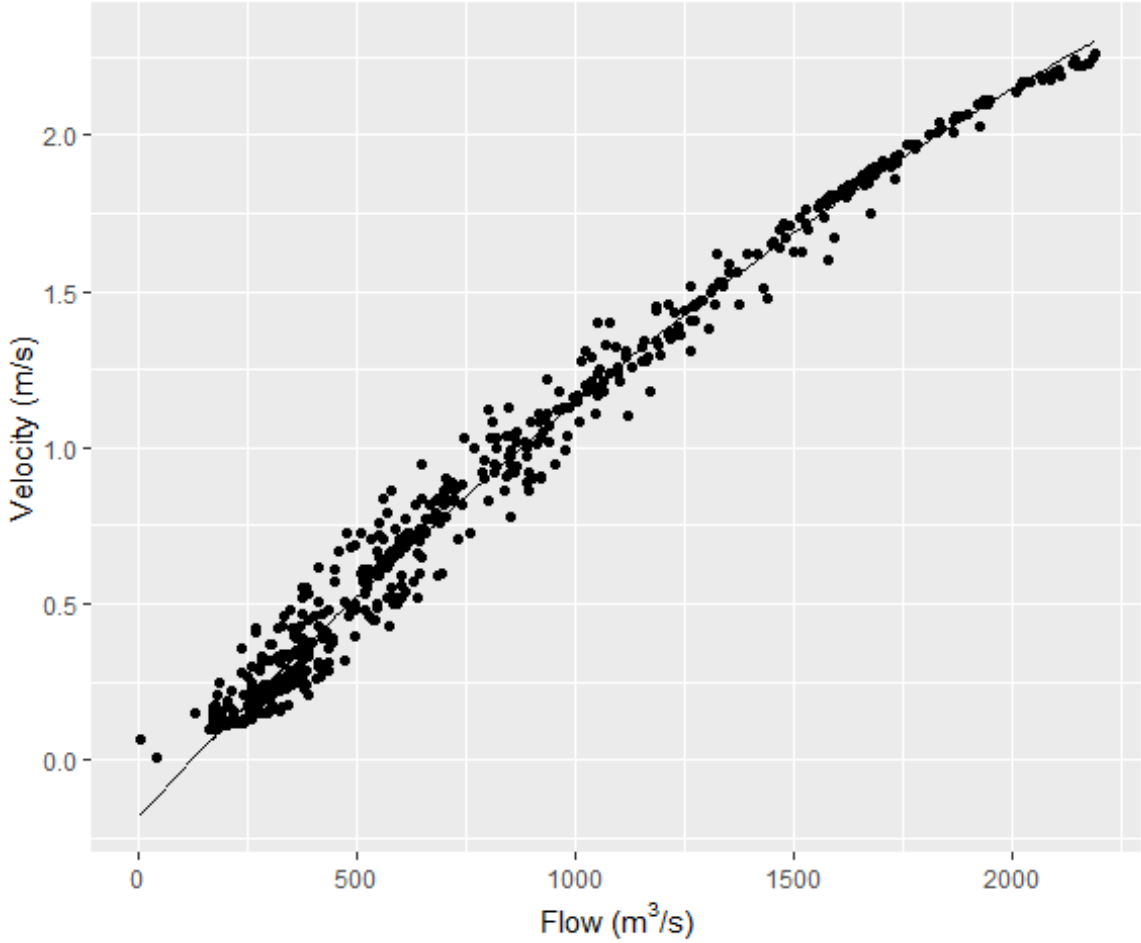

Figure A41 Hourly velocity and flow for spring 2018 deployment for 2018.Spring.R4.S6.T2

Table A30 Summary of model for hourly velocity and flow for 2018.Spring.R4.S6.T3

term	estimate	std.error	statistic	p.value	adjr2
(Intercept)	-1.46e-01	4.94e-03	-2.96e+01	2.04e-139	9.9e-01
poly(mean, 2, raw = TRUE)1	1.27e-03	1.53e-05	8.33e+01	0.00e+00	9.9e-01
poly(mean, 2, raw = TRUE)2	-6.20e-08	7.69e-09	-8.07e+00	1.98e-15	9.9e-01

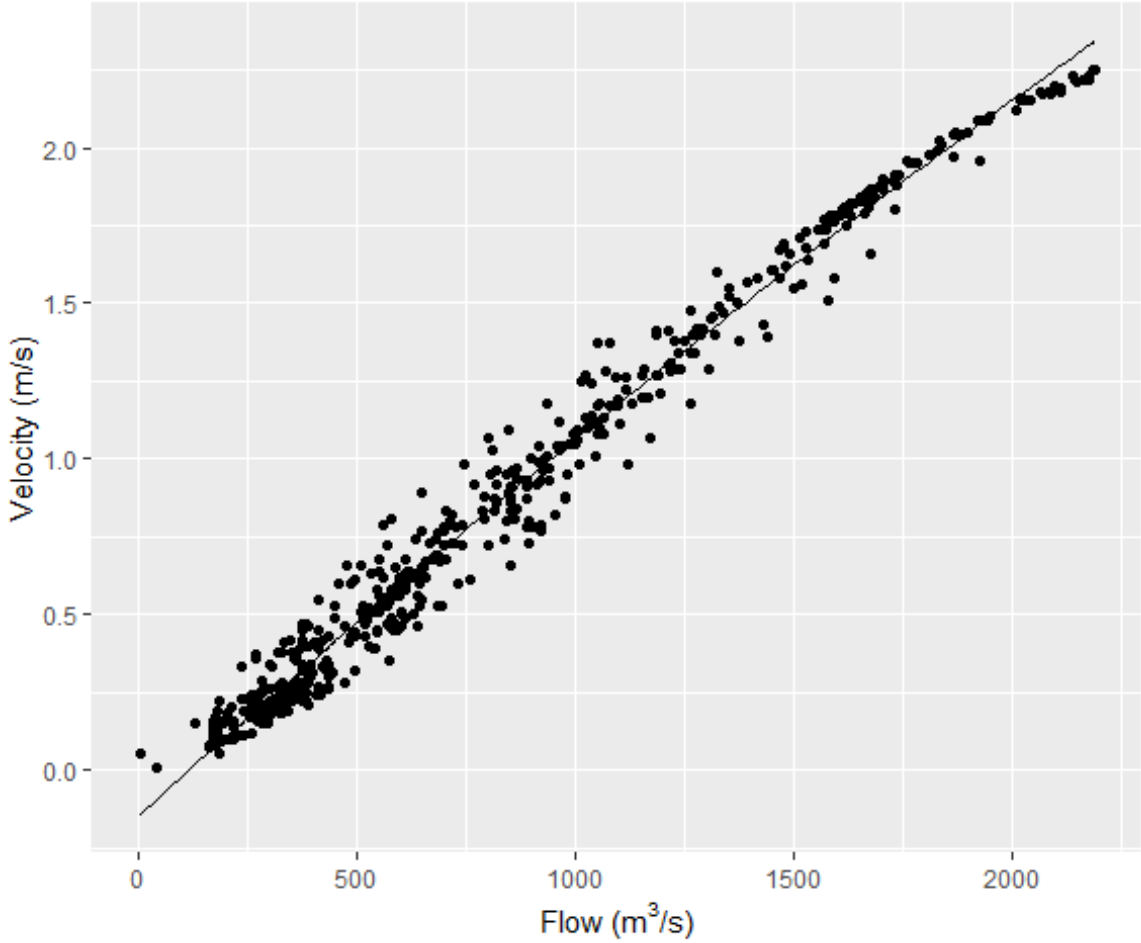

Figure A42 Hourly velocity and flow for spring 2018 deployment for 2018.Spring.R4.S6.T3

Table A31 Summary of model for hourly velocity and flow for 2018.Spring.R4.S6.T4

term	estimate	std.error	statistic	p.value	adjr2
(Intercept)	-1.53e-01	6.34e-03	-2.42e+01	3.49e-102	9.84e-01
poly(mean, 2, raw = TRUE)1	1.02e-03	1.95e-05	5.25e+01	1.72e-289	9.84e-01
poly(mean, 2, raw = TRUE)2	7.05e-08	9.79e-09	7.20e+00	1.19e-12	9.84e-01

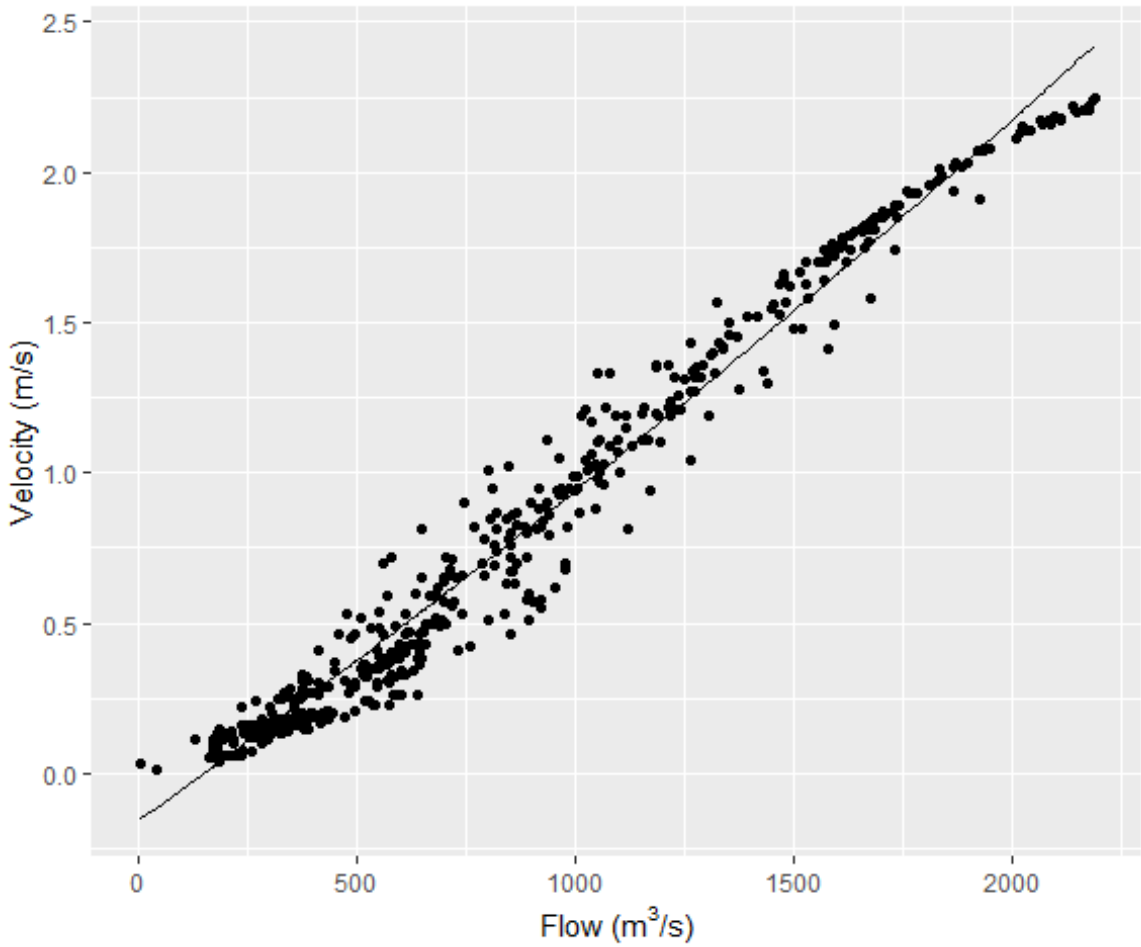

Figure A43 Hourly velocity and flow for spring 2018 deployment for 2018.Spring.R4.S6.T4

Table A32 Summary of model for hourly velocity and flow for 2018.Spring.R4.S6.T5

term	estimate	std.error	statistic	p.value	adjr2
(Intercept)	-2.91e-01	3.46e-02	-8.43e+00	5.56e-16	9.52e-01
poly(mean, 2, raw = TRUE)1	5.27e-04	6.66e-05	7.91e+00	2.20e-14	9.52e-01
poly(mean, 2, raw = TRUE)2	2.64e-07	2.76e-08	9.58e+00	8.54e-20	9.52e-01

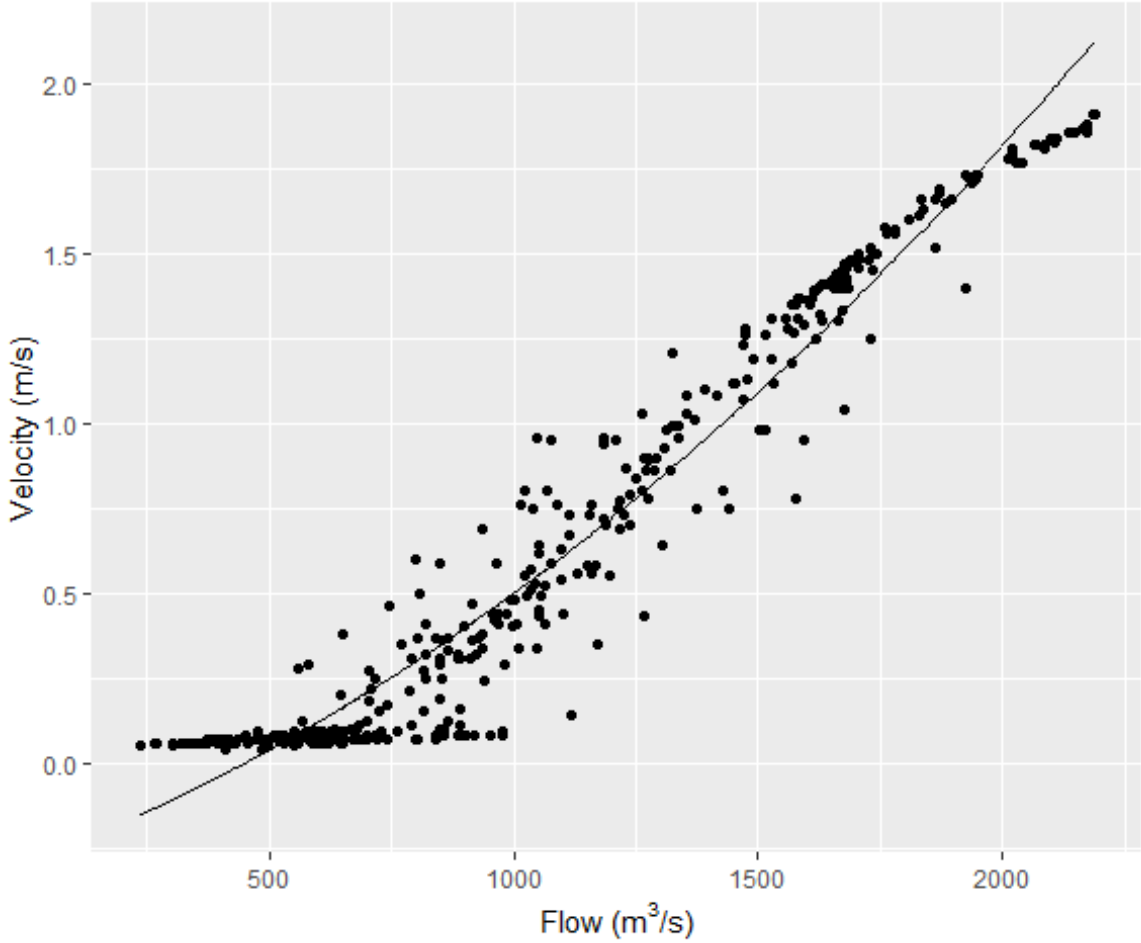

Figure A44 Hourly velocity and flow for spring 2018 deployment for 2018.Spring.R4.S6.T5

Table A33 Summary of model for hourly velocity and flow for 2018.Spring.R4.S6.T6

term	estimate	std.error	statistic	p.value	adjr2
(Intercept)	-8.34e-01	9.38e-02	-8.88e+00	1.10e-16	9.37e-01
poly(mean, 2, raw = TRUE)1	1.47e-03	1.40e-04	1.05e+01	1.02e-21	9.37e-01
poly(mean, 2, raw = TRUE)2	-7.68e-08	4.95e-08	-1.55e+00	1.22e-01	9.37e-01

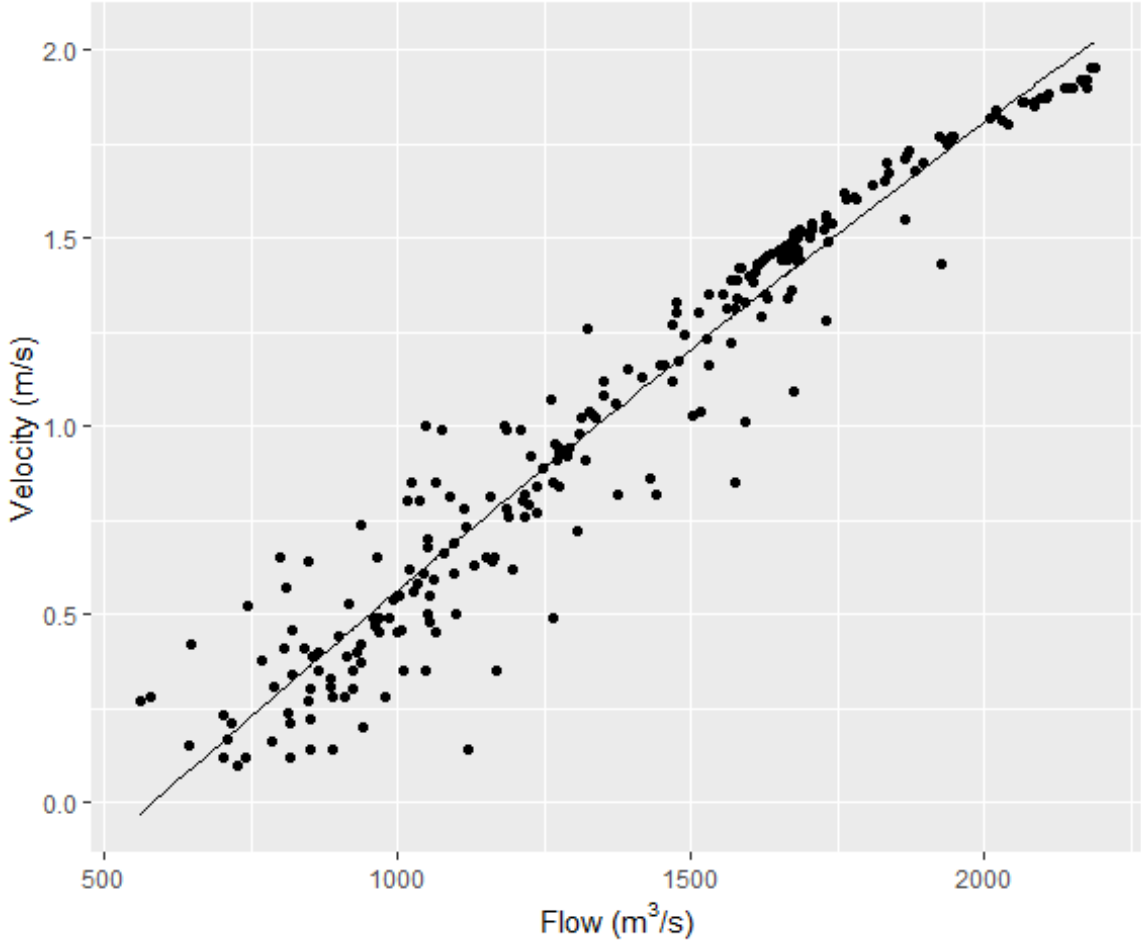

Figure A45 Hourly velocity and flow for spring 2018 deployment for 2018.Spring.R4.S6.T6

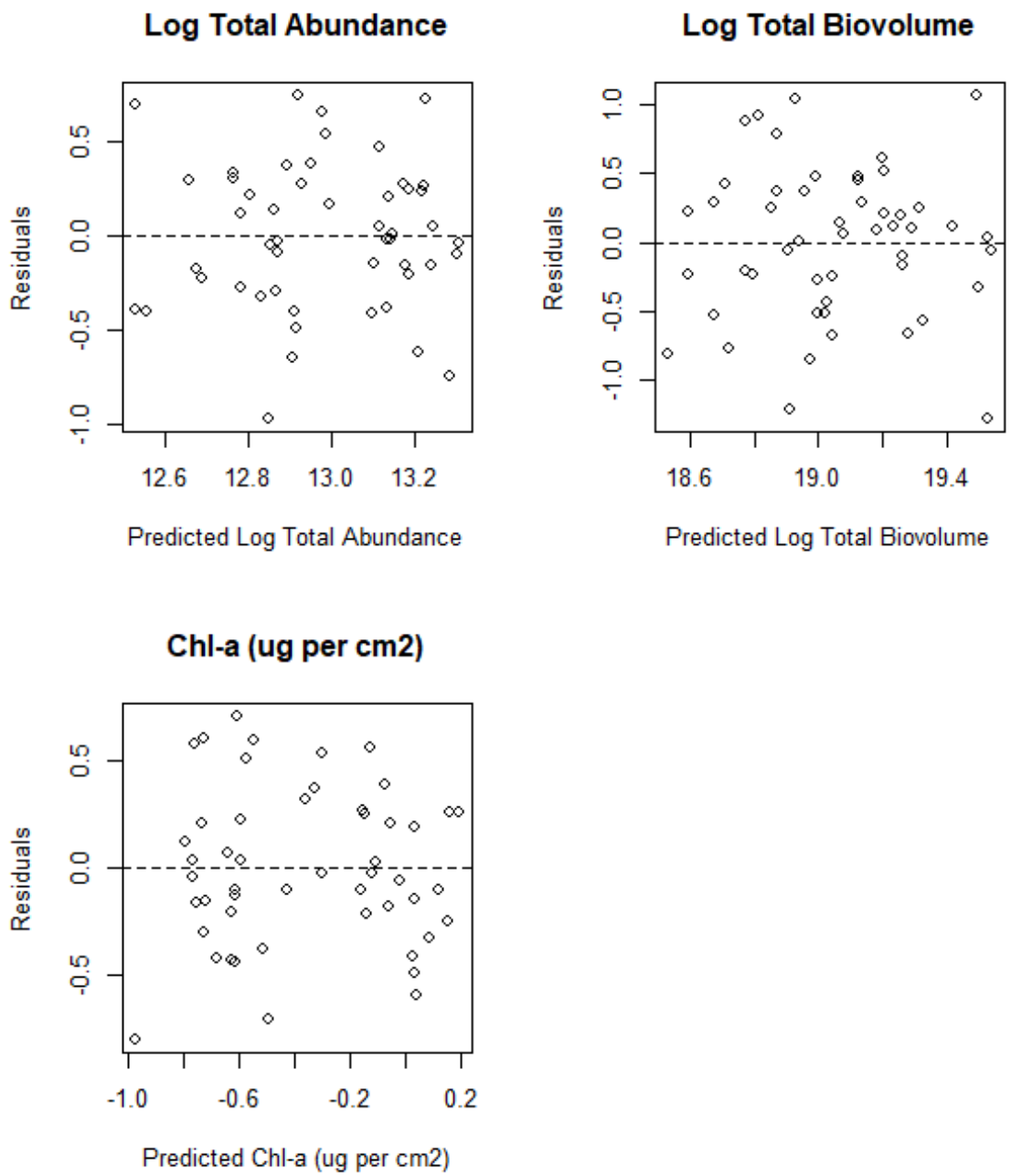

Figure A46 Residual Plots for spring R3 Periphyton Models

Table A34 Summary of plausible models identified using model averaging (those with a delta AIC <3) with pseudo-R2 values and coefficients for mostly submerged R3 riverine samples for spring.

Response	X.Intercept.	Average Temperature in Water	Maximum Velocity (m/s)	Median Velocity (m/s)	Hours over 10 photons/ m2/sec	R.2	df	AICc	delta	weight
Chl-a (ug per cm2)	-0.361	0.614		-0.187		0.443	4.000	48.900	0.000	0.309
Chl-a (ug per cm2)	-0.361	0.622				0.406	3.000	49.700	0.808	0.207
Chl-a (ug per cm2)	-0.361	0.616		-0.204	0.117	0.456	5.000	50.100	1.210	0.169
Chl-a (ug per cm2)	-0.361	0.623	-0.018	-0.187		0.443	5.000	51.300	2.450	0.091
Chl-a (ug per cm2)	-0.361	0.625			0.086	0.414	4.000	51.400	2.510	0.088
Log Total Abundance	13.000	0.316				0.185	4.000	58.200	0.000	0.190
Log Total Abundance	13.000	0.340			0.184	0.224	5.000	58.300	0.032	0.187
Log Total Abundance	12.900					0.118	3.000	59.800	1.560	0.087
Log Total Abundance	13.000	0.280	0.117		0.197	0.233	6.000	60.200	1.990	0.070
Log Total Abundance	13.000	0.307		-0.104		0.188	5.000	60.500	2.250	0.061
Log Total Abundance	13.000		0.198			0.146	4.000	60.600	2.340	0.059
Log Total Abundance	13.000	0.281	0.064			0.187	5.000	60.600	2.360	0.058
Log Total Abundance	13.000	0.335		-0.101	0.182	0.227	6.000	60.600	2.400	0.057
Log Total Abundance	13.000		0.250		0.189	0.185	5.000	60.700	2.430	0.056
Log Total Abundance	13.000				0.137	0.138	4.000	61.000	2.770	0.047
Log Total Biovolume	19.000				0.274	0.166	4.000	90.500	0.000	0.160
Log Total Biovolume	19.000					0.123	3.000	90.600	0.134	0.150

Response	X.Intercept.	Average Temperature in Water	Maximum Velocity (m/s)	Median Velocity (m/s)	Hours over 10 photons/ m2/sec	R.2	df	AICc	delta	weight
Log Total Biovolume	19.100	0.289			0.312	0.200	5.000	90.900	0.351	0.135
Log Total Biovolume	19.000	0.236				0.143	4.000	91.900	1.340	0.082
Log Total Biovolume	19.000	0.434	-0.295		0.273	0.221	6.000	92.100	1.610	0.072
Log Total Biovolume	19.000	0.425	-0.371			0.176	5.000	92.400	1.860	0.063
Log Total Biovolume	19.000		-0.176			0.131	4.000	92.600	2.060	0.057
Log Total Biovolume	19.000			-0.144		0.127	4.000	92.800	2.260	0.052
Log Total Biovolume	19.000			-0.134	0.267	0.169	5.000	92.800	2.280	0.051
Log Total Biovolume	19.000		-0.100		0.250	0.167	5.000	92.900	2.410	0.048

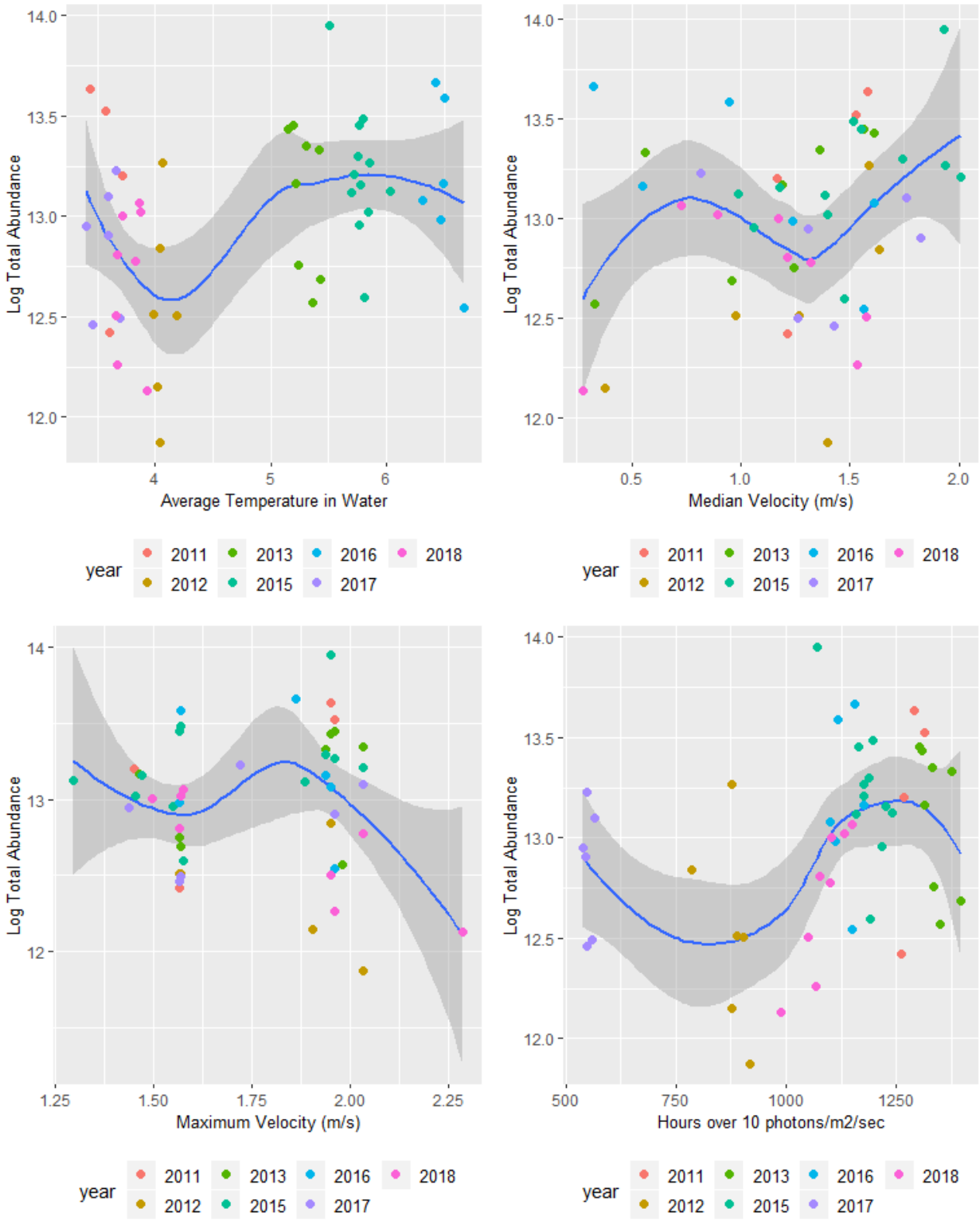

Figure A47 Log (total abundance) vs. environmental and operationalvariables by year, R3 riverine samplers. Grey ribbon is the standard deviation for LOWESS line.

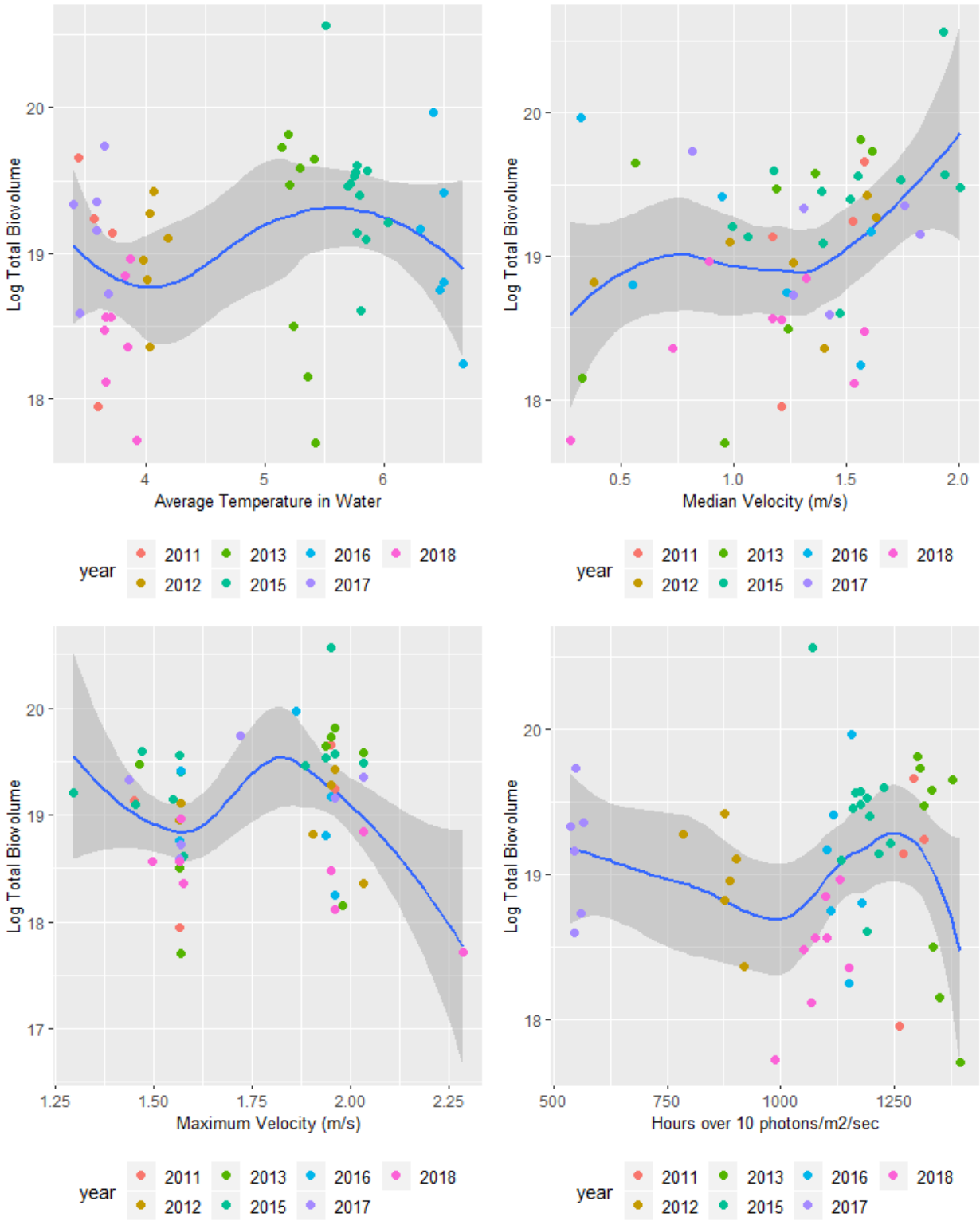

Figure A48 Log (total biovolume) vs. environmental and operationalvariables by year, R3 riverine samplers. Grey ribbon is the standard deviation for LOWESS line.

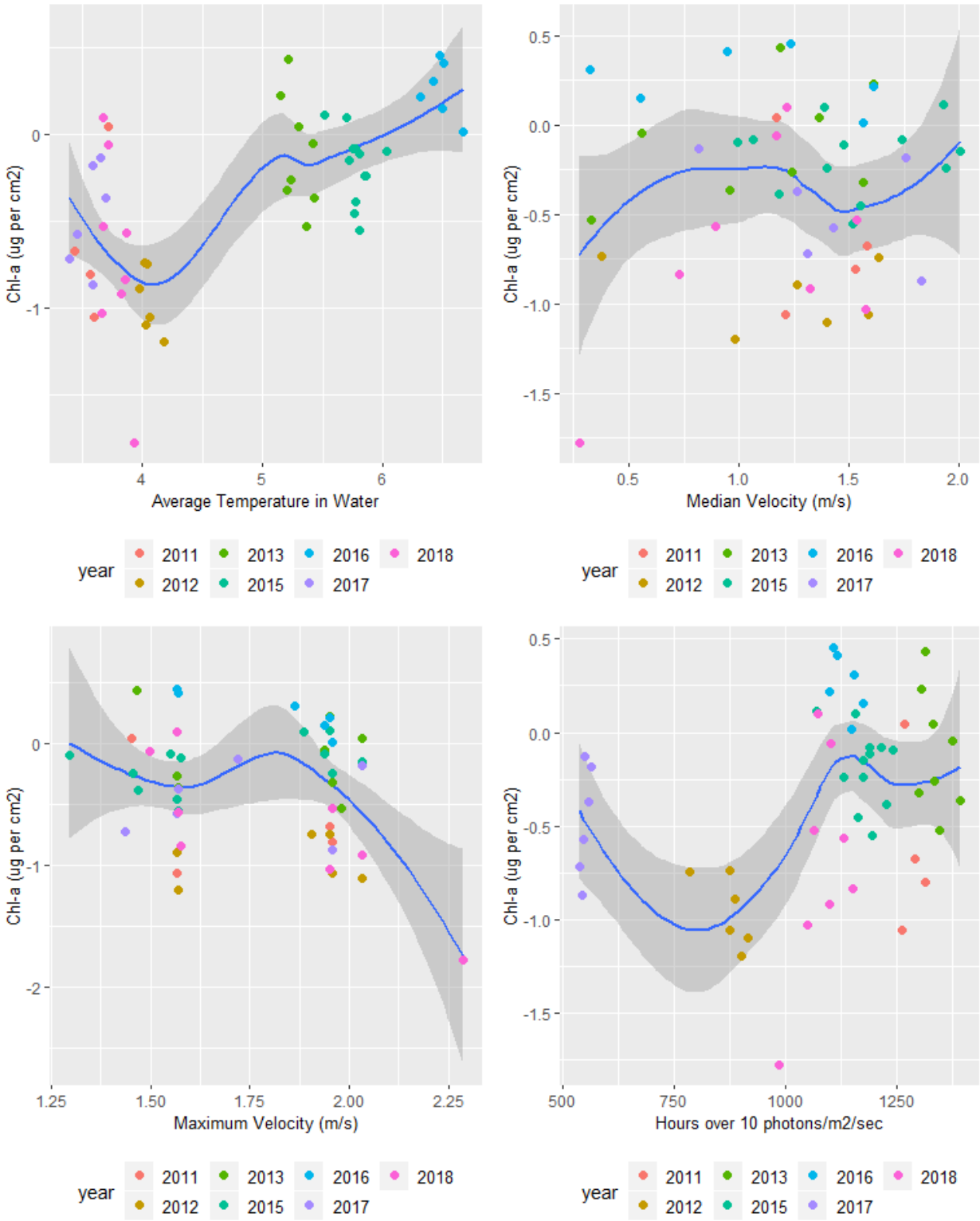

Figure A49 Log (chl-a) vs. environmental and operationalvariables by year, R3 riverine samplers. Grey ribbon is the standard deviation for LOWESS line.

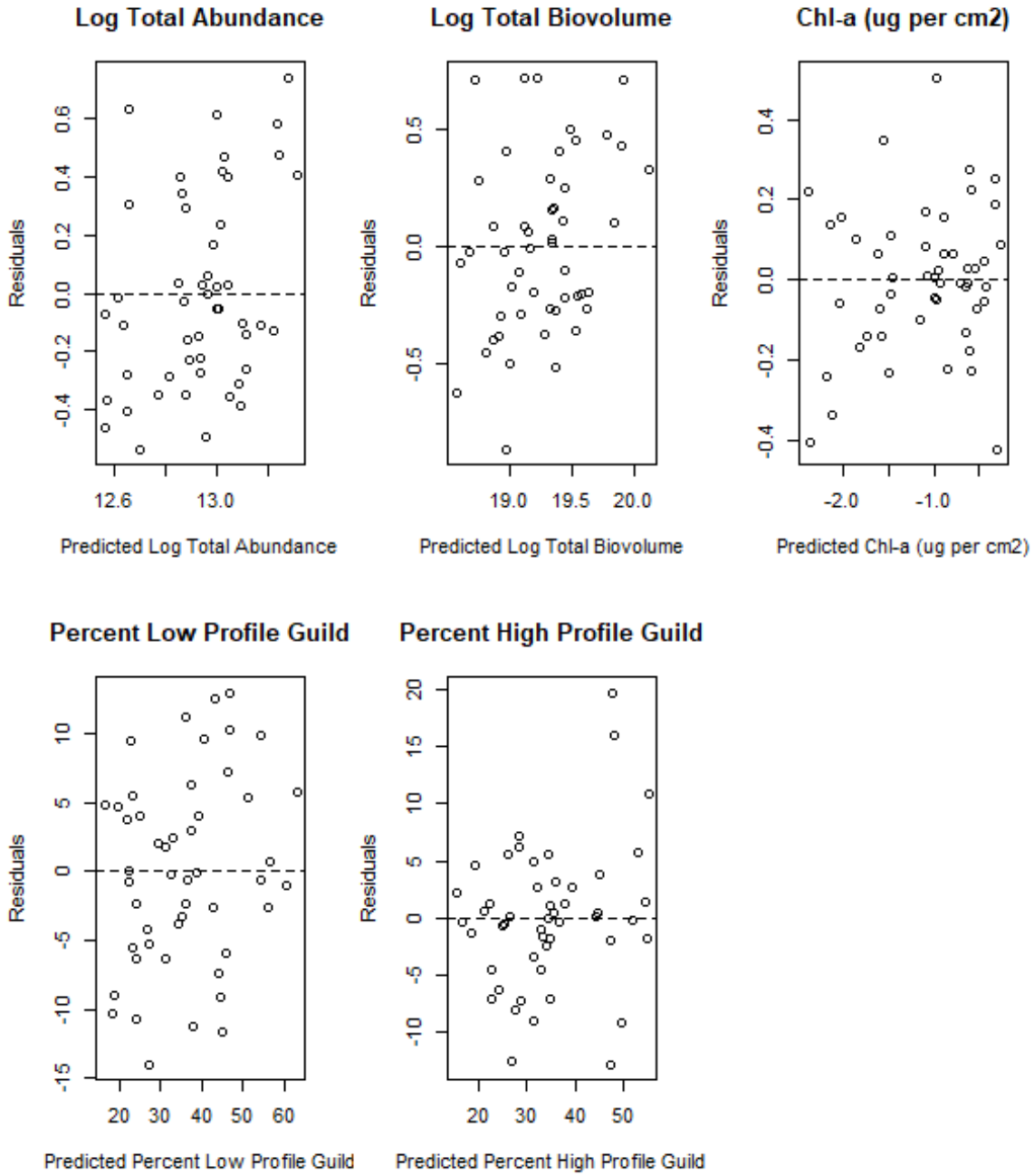

Figure A50 Residual Plots for spring R4 Periphyton Models

Table A35 Summary of plausible models identified using model averaging (those with a delta AIC <3) with pseudo-R2 values and coefficients for mostly submerged R4 riverine samples for spring.

Response	X.Intercept.	Average Temperature in Water	Maximum Velocity (m/s)	Median Velocity (m/s)	Hours over 10 photons/ m2/sec	R.2	df	AICc	delta	weight
Chl-a (ug per cm2)	-1.160	1.000	-0.263			0.723	5.000	46.500	0.000	0.265
Chl-a (ug per cm2)	-1.170	0.882				0.708	4.000	46.600	0.100	0.252
Chl-a (ug per cm2)	-1.160	0.869			0.115	0.712	5.000	48.400	1.910	0.102
Chl-a (ug per cm2)	-1.170	0.863		-0.090		0.712	5.000	48.400	1.920	0.102
Chl-a (ug per cm2)	-1.160	0.984	-0.262	-0.096		0.727	6.000	48.400	1.950	0.100
Chl-a (ug per cm2)	-1.160	0.995	-0.251		0.028	0.723	6.000	49.000	2.540	0.074
Chl-a (ug per cm2)	-1.150	0.816		-0.181	0.229	0.723	6.000	49.100	2.640	0.071
Log Total Abundance	12.900			-0.256		0.096	4.000	61.900	0.000	0.244
Log Total Abundance	12.900					0.028	3.000	63.000	1.160	0.137
Log Total Abundance	12.900			-0.241	0.120	0.109	5.000	63.600	1.730	0.103
Log Total Abundance	12.900				0.174	0.055	4.000	64.000	2.130	0.084
Log Total Abundance	12.900	0.075		-0.240		0.100	5.000	64.100	2.240	0.080
Log Total Abundance	12.900		-0.033	-0.252		0.095	5.000	64.400	2.500	0.070
Log Total Abundance	12.900	0.130				0.044	4.000	64.600	2.710	0.063
Log Total Biovolume	19.200			-0.476		0.215	4.000	83.500	0.000	0.395
Log Total Biovolume	19.200			-0.481	0.124	0.222	5.000	85.500	2.060	0.141
Log Total Biovolume	19.200	-0.115		-0.494		0.220	5.000	85.700	2.210	0.131
Log Total Biovolume	19.200		-0.061	-0.471		0.216	5.000	85.900	2.430	0.117

Response	X.Intercept.	Average Temperature in Water	Maximum Velocity (m/s)	Median Velocity (m/s)	Hours over 10 photons/ m2/sec	R.2	df	AICc	delta	weight
Percent High Profile Guild	33.700	-16.600				0.454	4.000	373.000	0.000	0.336
Percent High Profile Guild	34.000	-17.500			5.350	0.475	5.000	374.000	0.563	0.253
Percent High Profile Guild	33.700	-16.600		-0.236		0.454	5.000	376.000	2.460	0.098
Percent High Profile Guild	33.700	-16.200	-0.766			0.454	5.000	376.000	2.470	0.098
Percent High Profile Guild	34.100	-18.000		-1.950	6.030	0.479	6.000	376.000	2.790	0.083
Percent Low Profile Guild	36.100	21.400			-7.940	0.494	5.000	383.000	0.000	0.363
Percent Low Profile Guild	36.600	20.200				0.458	4.000	384.000	0.892	0.232
Percent Low Profile Guild	36.100	21.700		1.010	-8.300	0.495	6.000	385.000	2.510	0.103
Percent Low Profile Guild	36.000	22.400	-1.810		-8.650	0.494	6.000	386.000	2.570	0.100

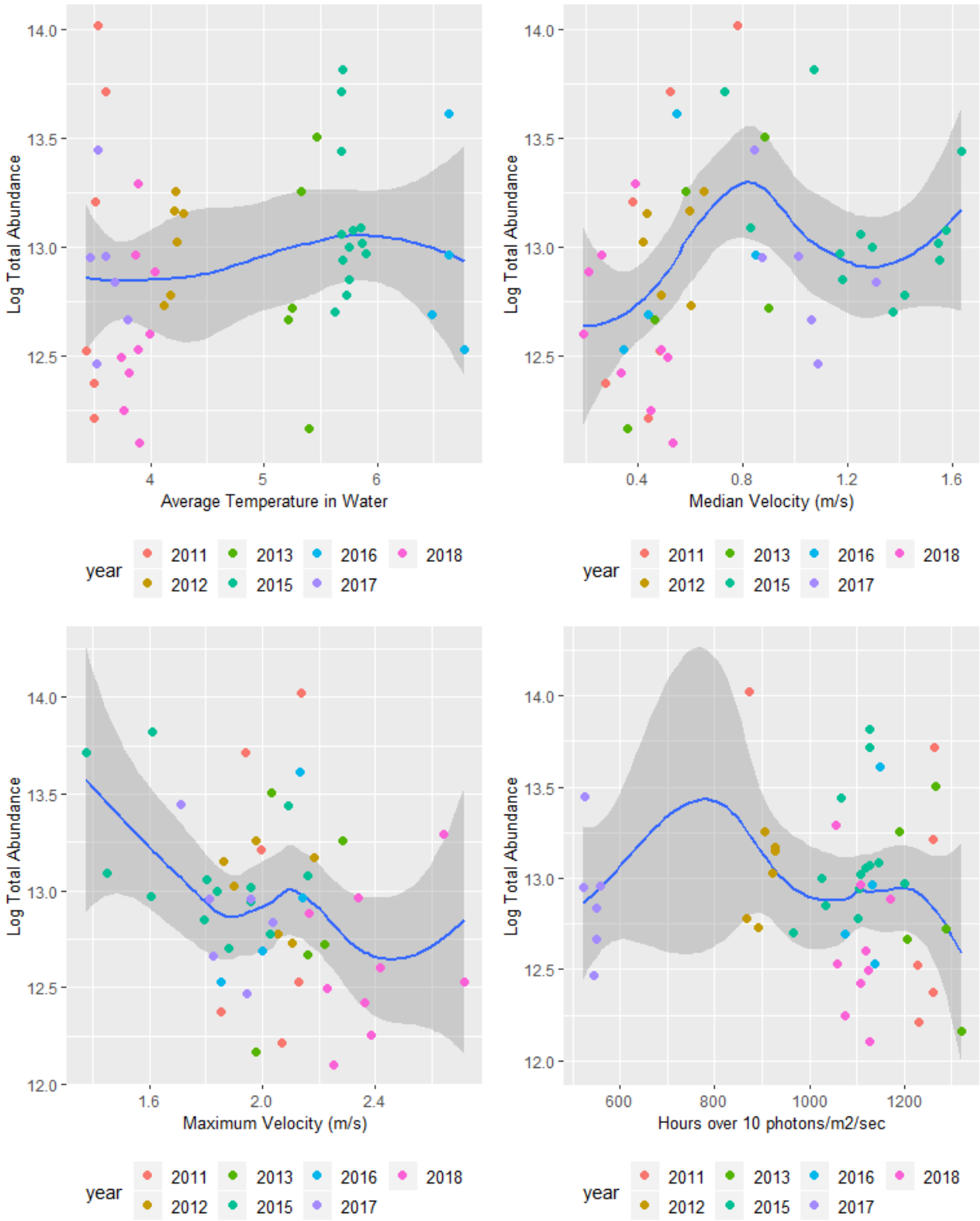

Figure A51 . Log (total abundance) vs. environmental and operationalvariables by year, R4 riverine samplers. Grey ribbon is the standard deviation for LOWESS line.

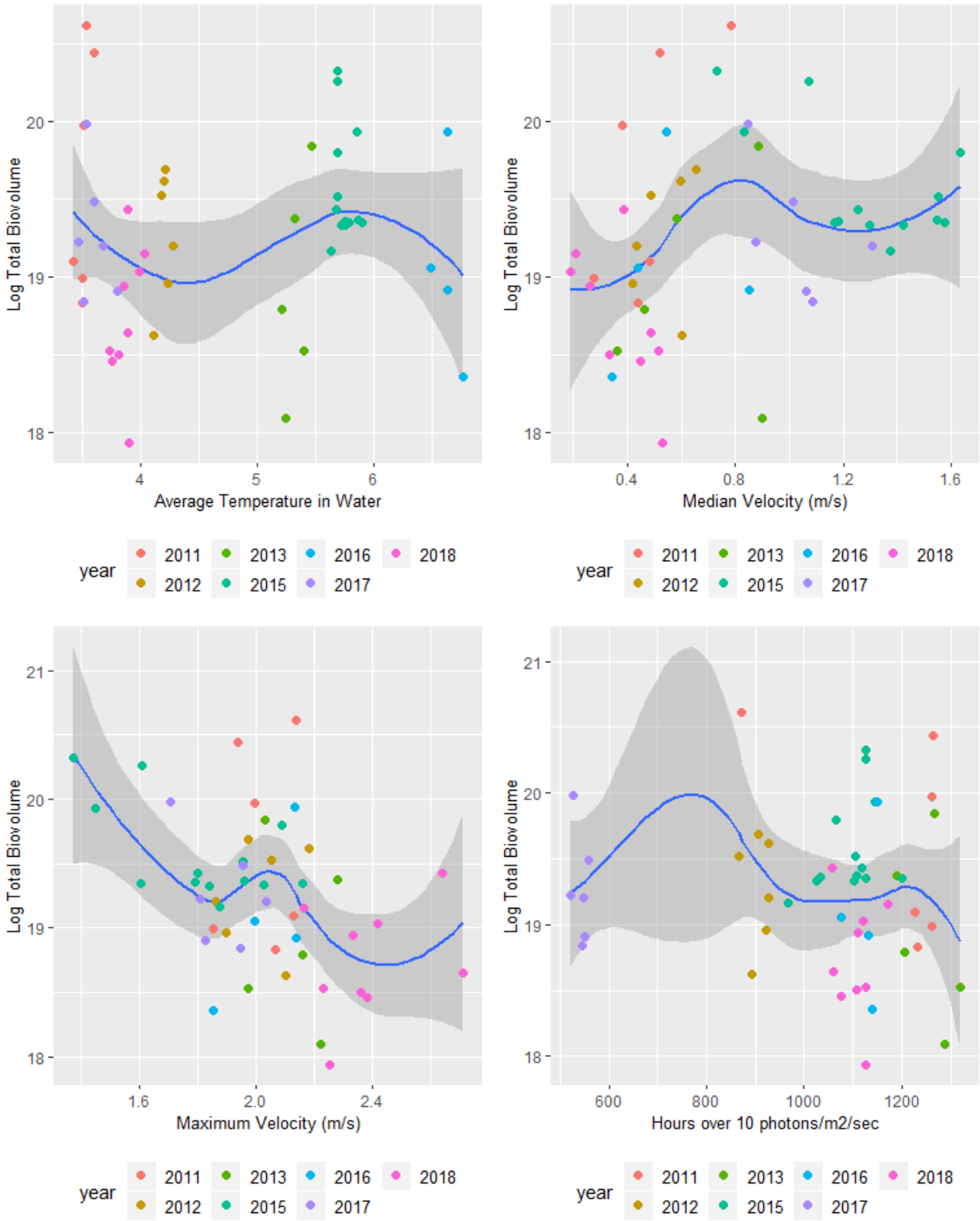

Figure A52 Log (total biovolume) vs. environmental and operationalvariables by year, R4 riverine samplers. Grey ribbon is the standard deviation for LOWESS line.

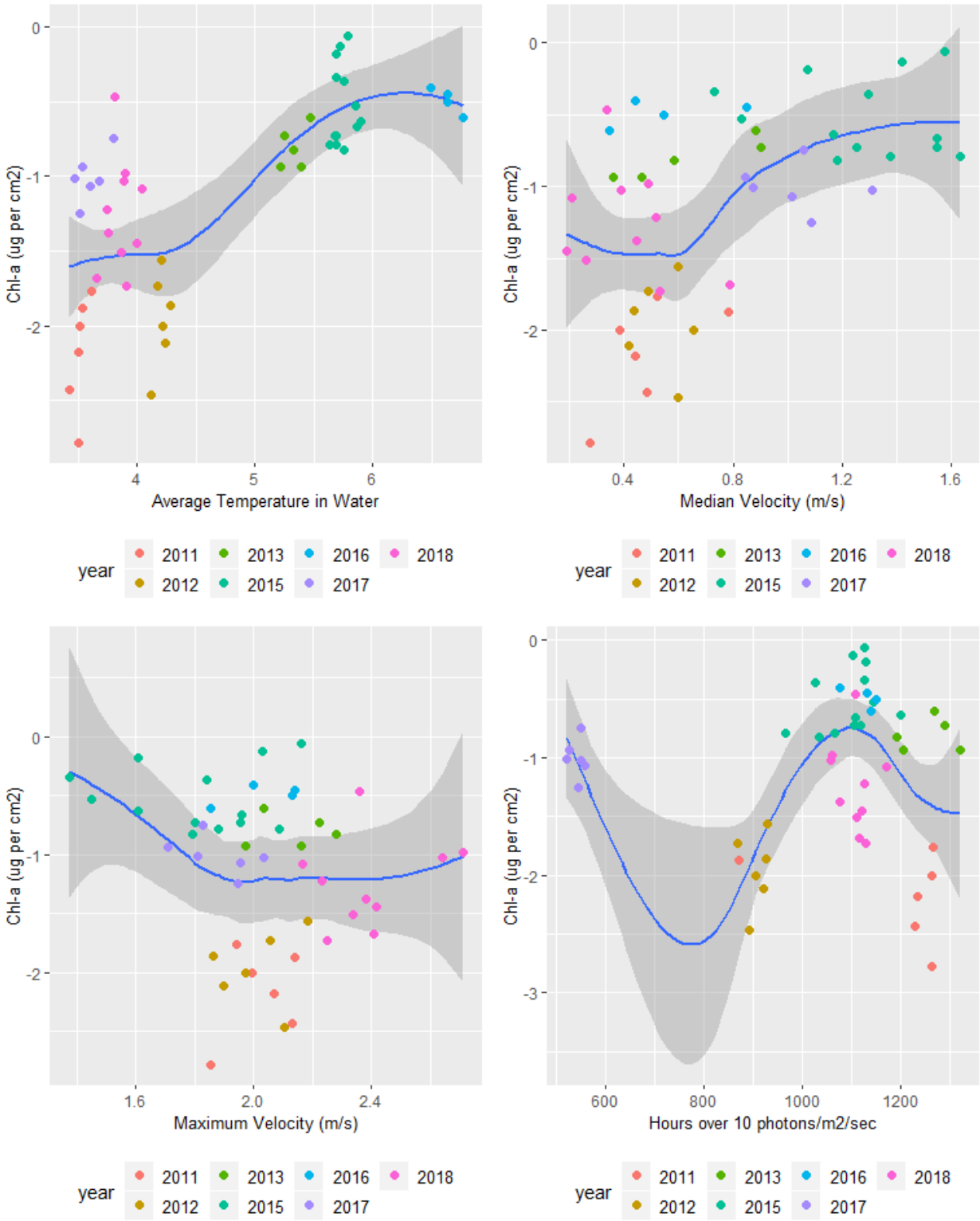

Figure A53 Log (chl-a) vs. environmental and operationalvariables by year, R4 riverine samplers. Grey ribbon is the standard deviation for LOWESS line.

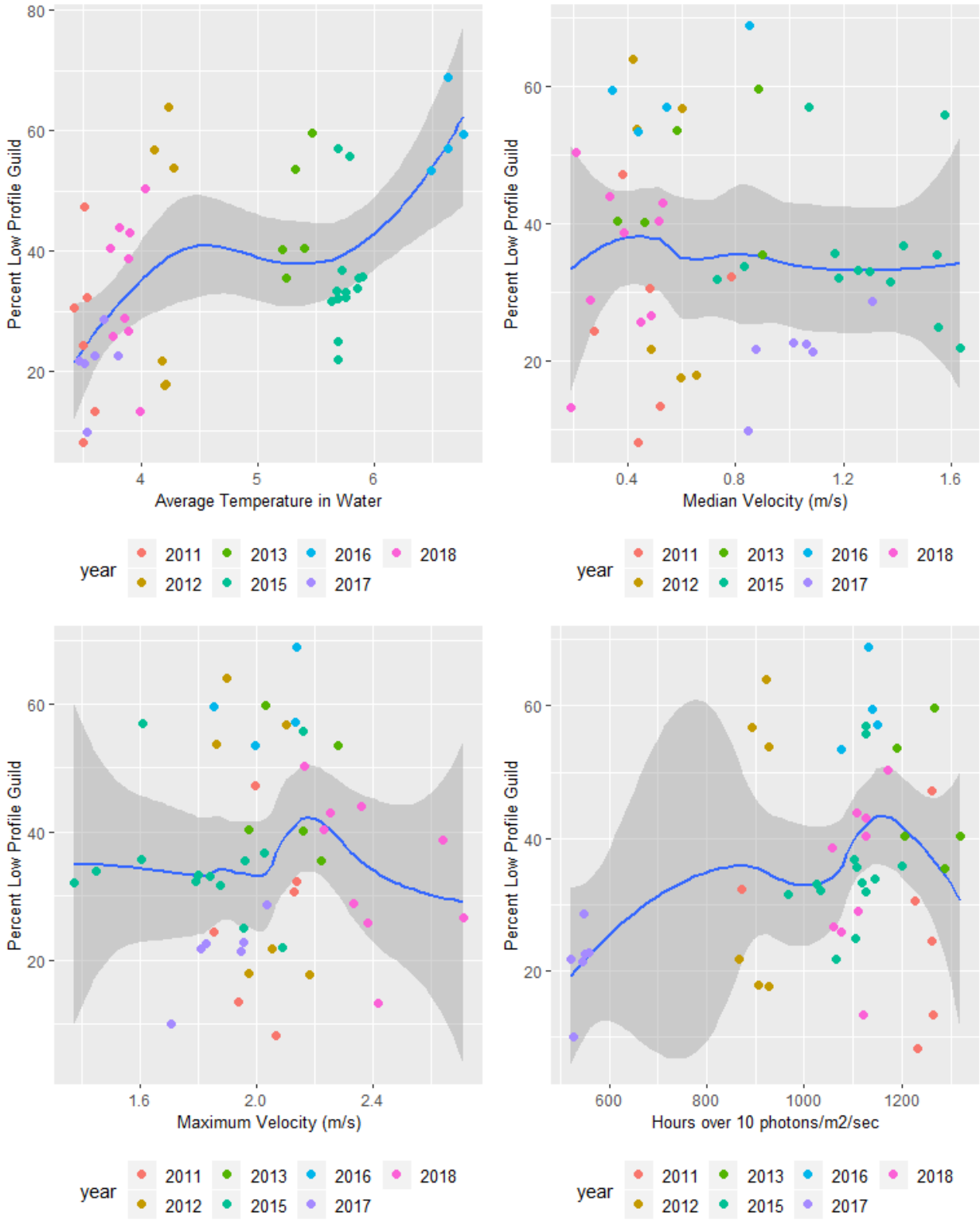

Figure A54 Percent Low Profile Guild vs. environmental and operationalvariables by year, R4 riverine samplers. Grey ribbon is the standard deviation for LOWESS line.

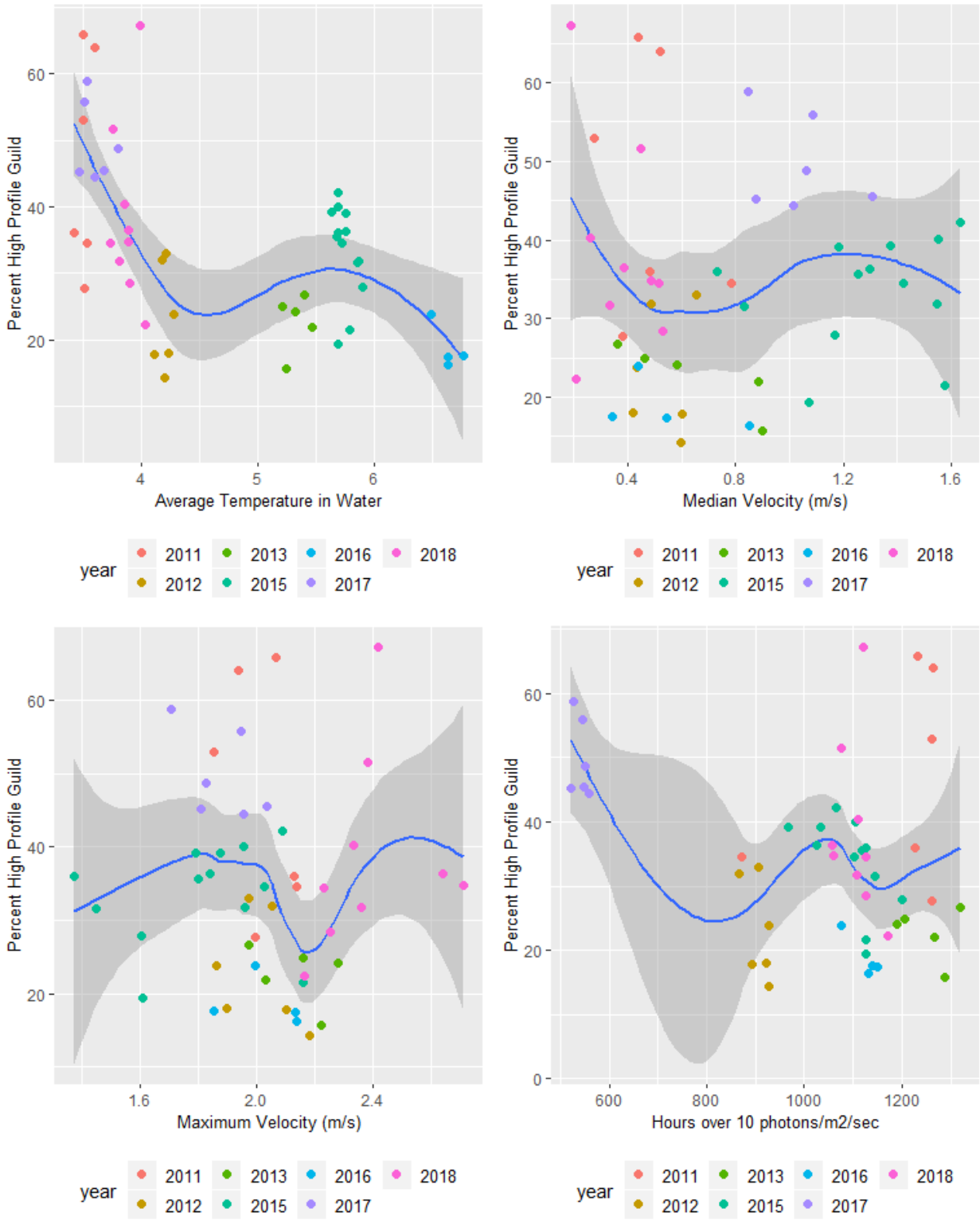

Figure A55 Percent High Profile Guild vs. environmental and operationalvariables by year, R4 riverine samplers. Grey ribbon is the standard deviation for LOWESS line.

APPENDIX F INVERTEBRATE STATISTICAL MODEL RESULTS

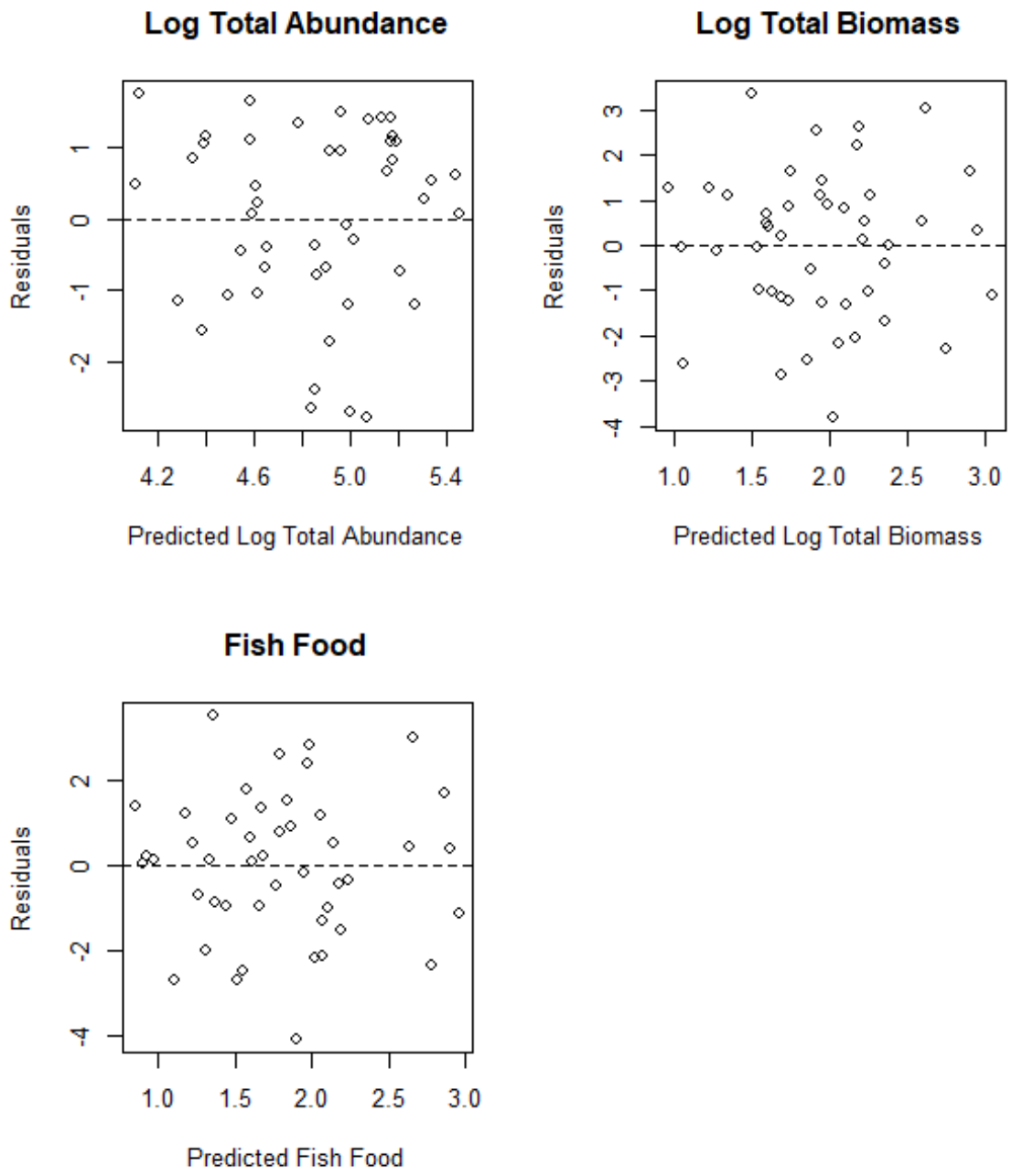

Figure A56 Residual Plots for spring R3 Benthic Invertebrate Models

Table A36 Summary of plausible models identified using model averaging (those with a delta AIC <3) with pseudo-R2 values and coefficients for mostly submerged R3 riverine samples for spring.

Response	X.Intercept.	Average Temperature in Water	Maximum Velocity (m/s)	Median Velocity (m/s)	R.2	df	AICc	delta	weight
Fish Food	1.790				0.000	2.000	186.000	0.000	0.391
Fish Food	1.790			0.364	0.011	3.000	188.000	1.800	0.159
Fish Food	1.790		-0.331		0.009	3.000	188.000	1.880	0.152
Fish Food	1.790	-0.038			0.000	3.000	188.000	2.290	0.125
Log Total Abundance	4.850				0.000	2.000	157.000	0.000	0.309
Log Total Abundance	4.850	0.493			0.037	3.000	158.000	0.573	0.232
Log Total Abundance	4.850		-0.284		0.012	3.000	159.000	1.730	0.130
Log Total Abundance	4.850			0.057	0.000	3.000	159.000	2.270	0.099
Log Total Abundance	4.850	0.490	-0.279		0.048	4.000	159.000	2.410	0.092
Log Total Abundance	4.850	0.493		0.059	0.037	4.000	160.000	2.950	0.071
Log Total Biomass	1.950				0.000	2.000	183.000	0.000	0.360
Log Total Biomass	1.950		-0.453		0.018	3.000	185.000	1.480	0.172
Log Total Biomass	1.950			0.392	0.013	3.000	185.000	1.690	0.155
Log Total Biomass	1.950	-0.067			0.000	3.000	186.000	2.270	0.116

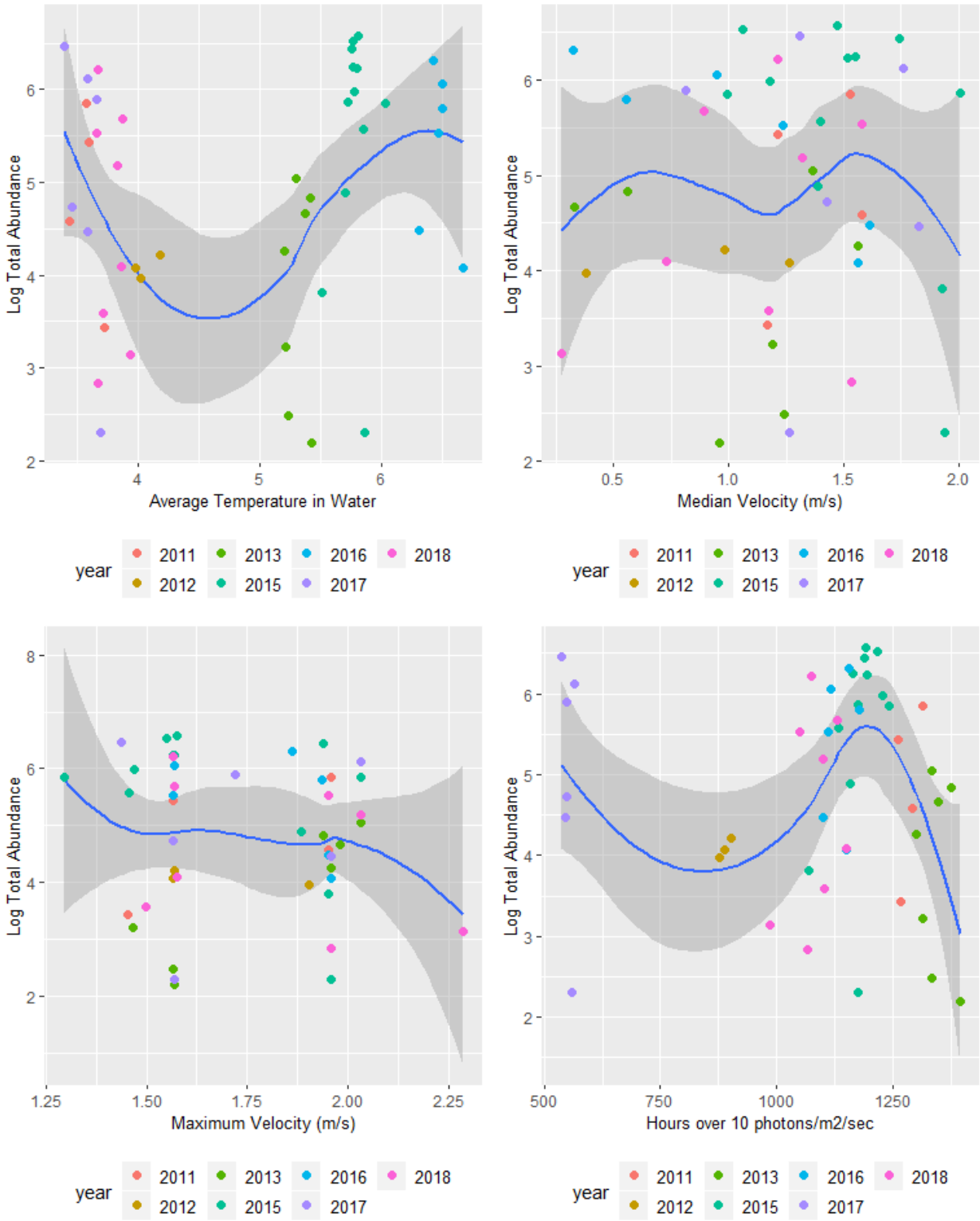

Figure A57 Log (abundance) vs. environmental and operationalvariables by year, R3 riverine samplers. Grey ribbon is the standard deviation for LOWESS line.

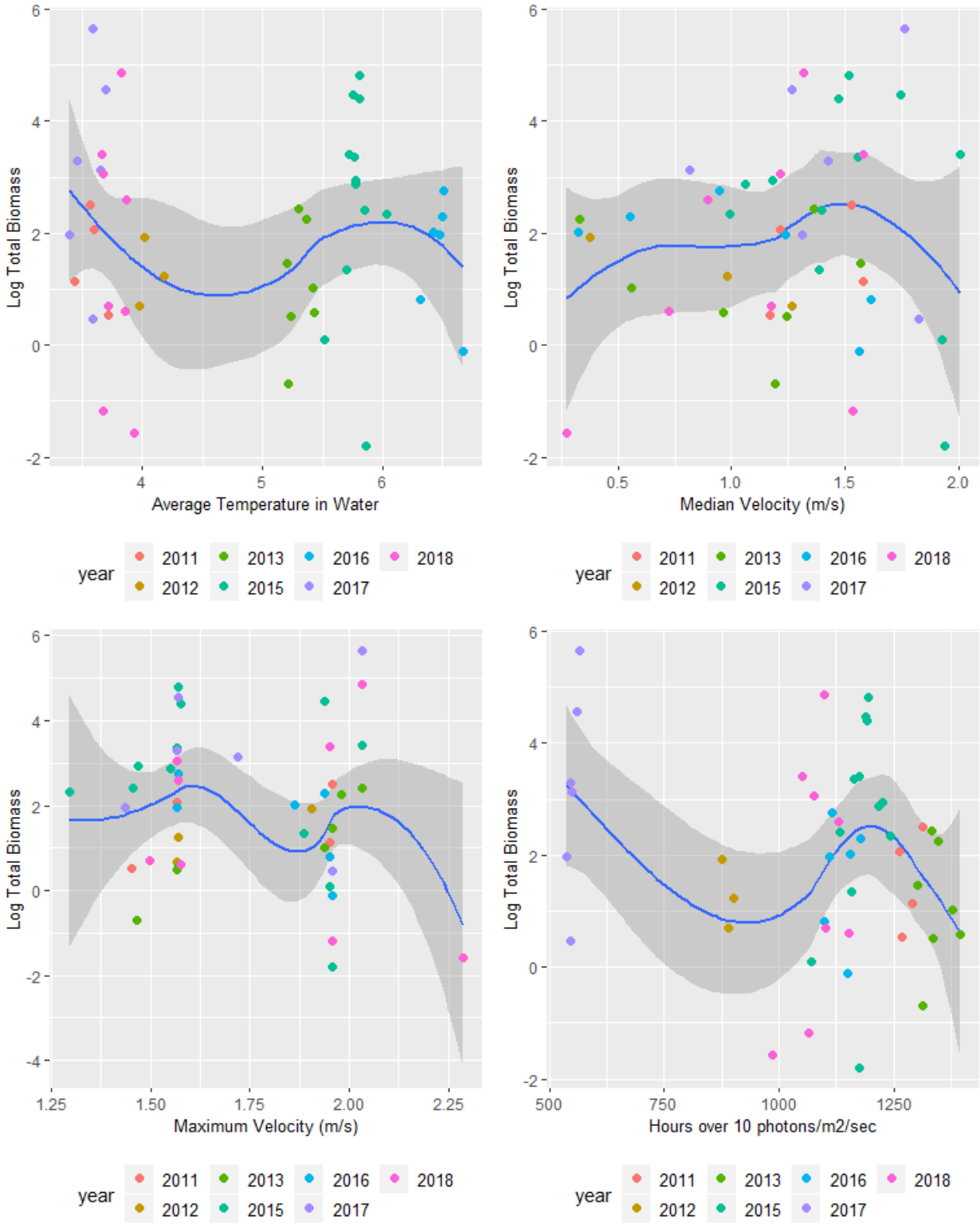

Figure A58 Log (biomass) vs. environmental and operationalvariables by year, R3 riverine samplers. Grey ribbon is the standard deviation for LOWESS line.

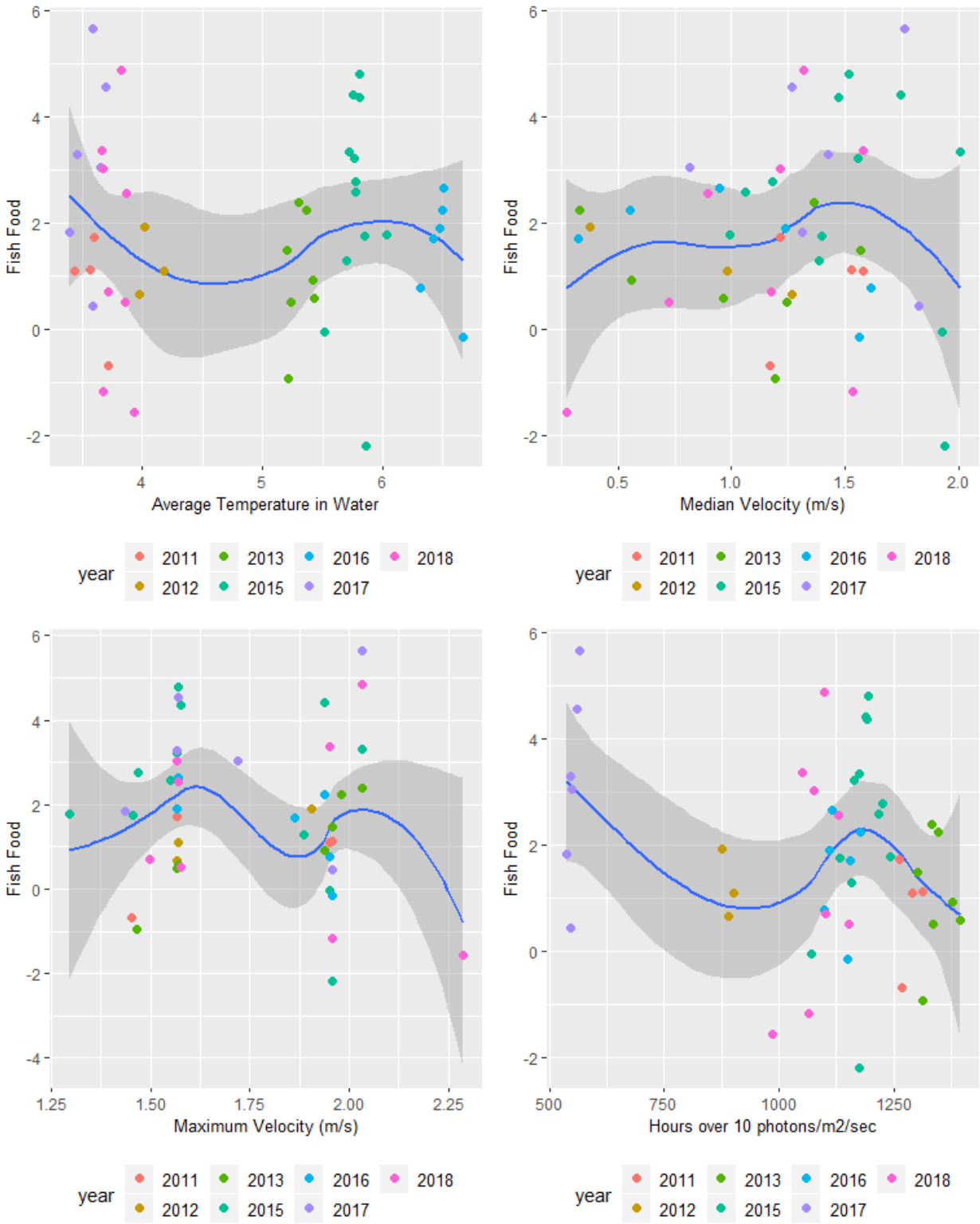

Figure A59 Log (fish food) vs. environmental and operationalvariables by year, R3 riverine samplers. Grey ribbon is the standard deviation for LOWESS line.

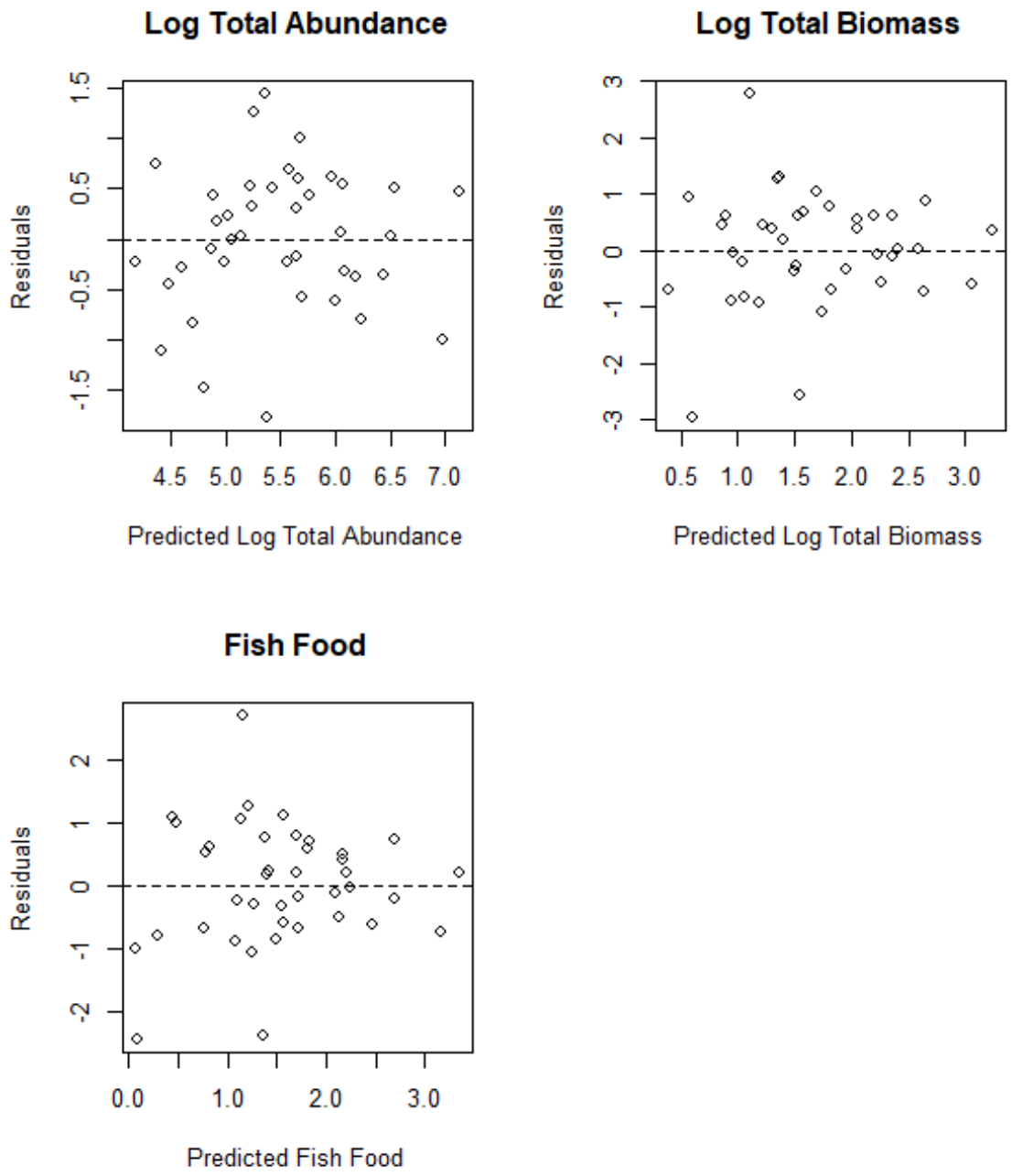

Figure A60 Residual Plots for spring R4 Benthic Invertebrate Models

Table A37 Summary of plausible models identified using model averaging (those with a delta AIC <3) with pseudo-R2 values and coefficients for mostly submerged R4 riverine samples for spring.

Response	X.Intercept.	Average Temperature in Water	Maximum Velocity (m/s)	Median Velocity (m/s)	R.2	df	AICc	delta	weight
Fish Food	1.460		-1.420		0.253	4.000	130.000	0.000	0.618
Fish Food	1.460	0.243	-1.410		0.252	5.000	133.000	2.680	0.162
Fish Food	1.440		-1.430	-0.106	0.249	5.000	133.000	2.810	0.152
Log Total Abundance	5.450		-1.280		0.388	4.000	104.000	0.000	0.588
Log Total Abundance	5.460	0.379	-1.230		0.398	5.000	106.000	2.000	0.216
Log Total Abundance	5.440		-1.260	-0.112	0.385	5.000	107.000	2.830	0.143
Log Total Biomass	1.640		-1.290		0.235	4.000	129.000	0.000	0.639
Log Total Biomass	1.630		-1.300	0.056	0.230	5.000	132.000	2.840	0.154
Log Total Biomass	1.630	0.121	-1.290		0.228	5.000	132.000	2.940	0.147

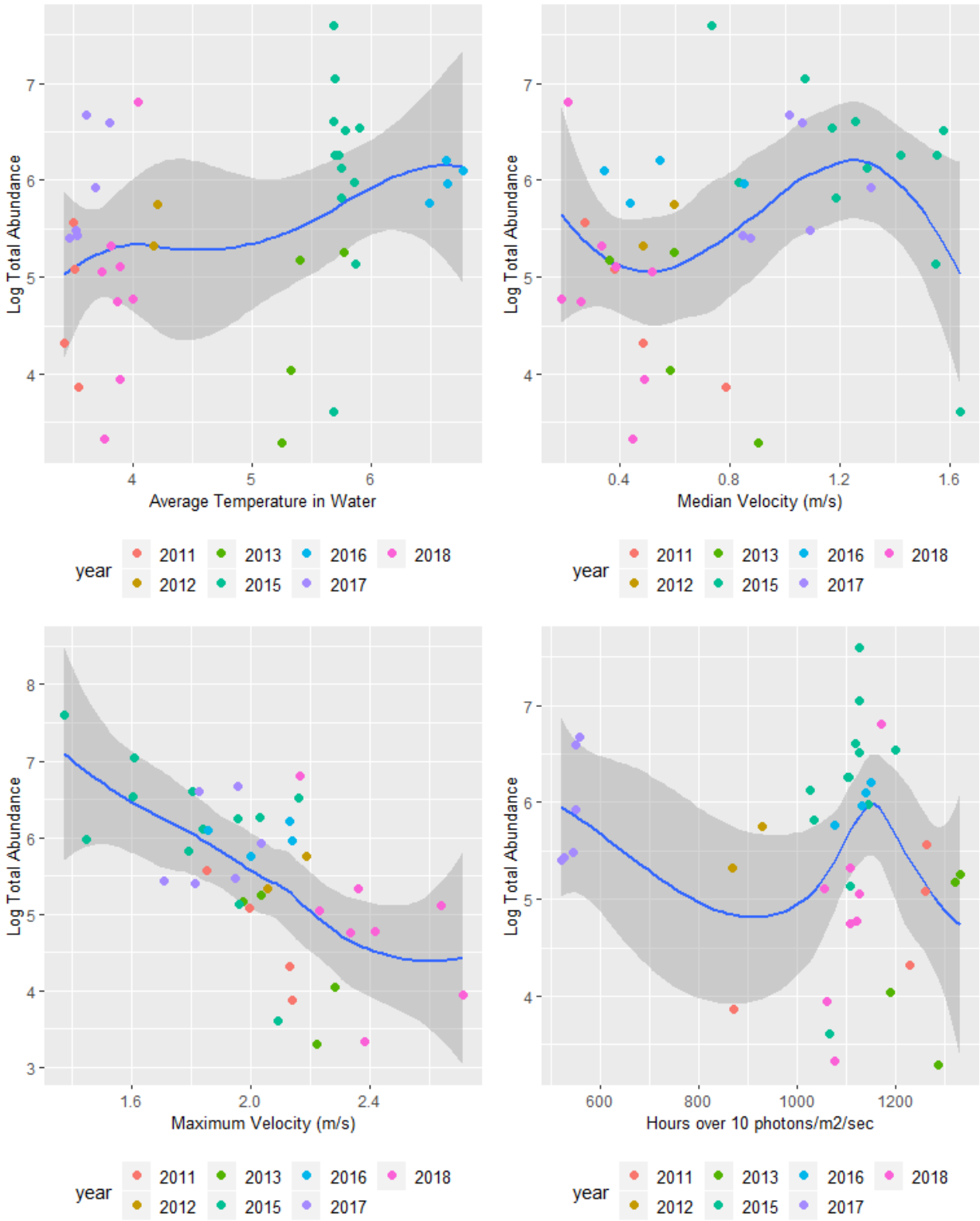

Figure A61 Log (abundance) vs. environmental and operationalvariables by year, R4 riverine samplers. Grey ribbon is the standard deviation for LOWESS line.

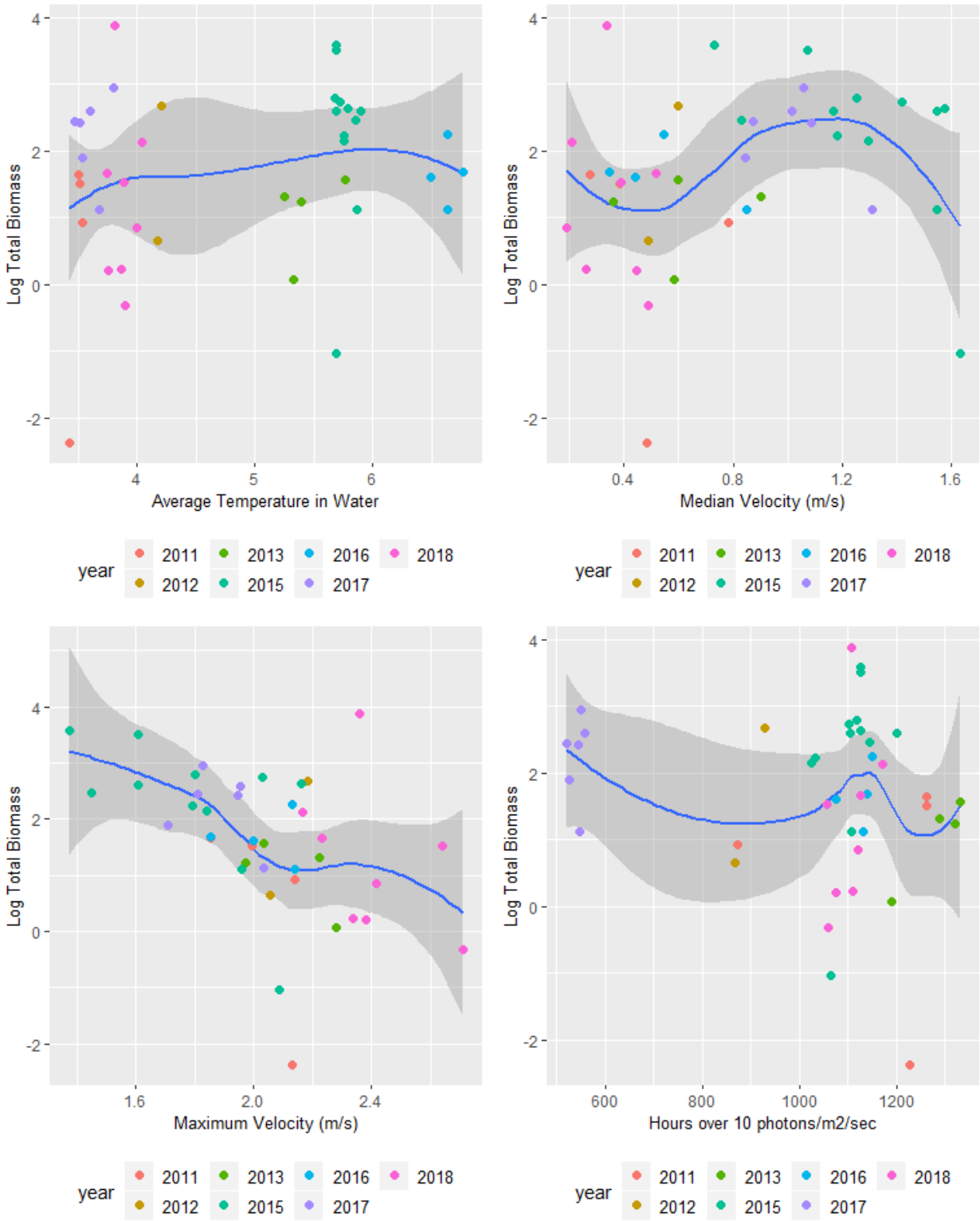

Figure A62 Log (biomass) vs. environmental and operationalvariables by year, R4 riverine samplers. Grey ribbon is the standard deviation for LOWESS line.

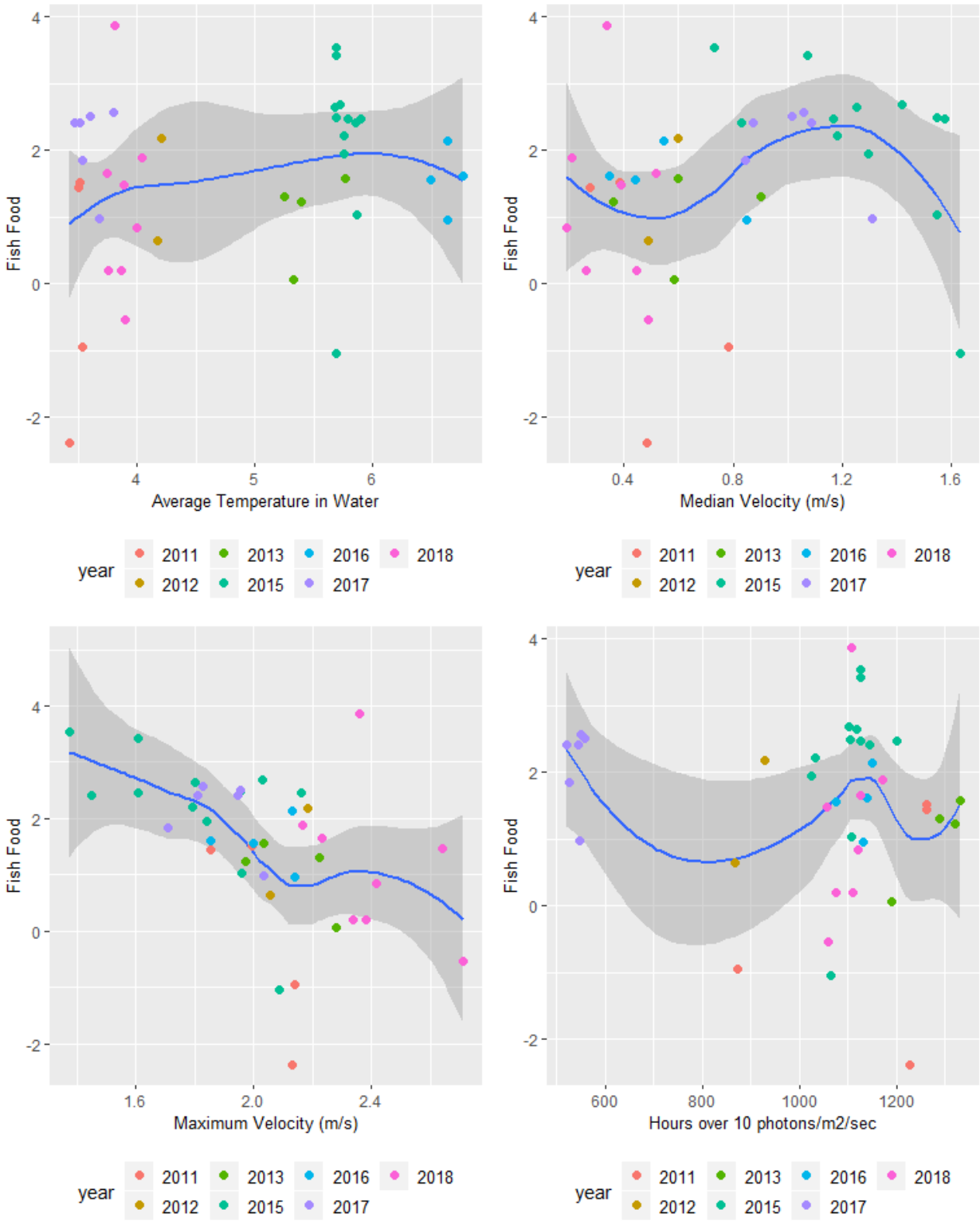

Figure A63 Log (fish food) vs. environmental and operationalvariables by year, R4 riverine samplers. Grey ribbon is the standard deviation for LOWESS line.

APPENDIX G PERIPHYTON AND INVERTEBRATE COMPARISION TO OTHER RIVERS

Comparison of MCR to other large rivers

Most of the artificial substrate periphyton data collected to date indicates that regularly wetted MCR substrates are moderately productive compared to similar substrates in other rivers of its size. However, the open-celled Styrofoam used in these trials may exaggerate production from 20% (Perrin et al. 2004) to as much as 400% (median = 200%) based on preliminary natural substrate samples from the upper varial zone (Schleppe et al. 2013). If the artificial sampler data are corrected by the median potential inflation of periphyton production, the corrected results indicate that MCR production is consistent with an oligotrophic or stressed river system (Table A38). Additionally, the natural substrate samples had far higher proportions of cyanobacteria, particularly in the sand from the cobble interstices in R4. The natural cobble samples also had higher proportions of the slower-growing filamentous green algae than the comparable artificial substrate samplers. Other researchers have found a similar under-representation of these algae groups on artificial substrates (Cattaneo and Amireault 1992).

An oligotrophic or stressed river is expected to have <20 – 40 species richness (Table A38), whereas MCR had 5 - 52 species per sample. The relatively high species richness on inundated substrates may be a result of supplemental taxa imported with flows released from Revelstoke Reservoir. Over the years of study on the MCR habitats, ten dominant taxa accounted 72 -99% of periphyton biovolume, again suggesting a stressed system.

In summary, MCR production is probably low compared to other large unregulated rivers, particularly in regularly dewatered areas, where even the open-celled substrate samples show the low periphyton production expected of a stressed river system.

Table A38 Summary of average MCR periphyton metrics from spring and/or fall 2010 – 2018 deployments, with comparison to oligotrophic, typical, and productive large rivers

Metric	Oligotrophic or stressed	Typical large rivers	Eutrophic or productive	MCR Seasonal Averages -50-day deployment (values bolded in bracket = 6 month samples)
Number of taxa (live & dead)	<20 – 40	25 – 60	Variable	5 - 52 **(39-50)**
Chlorophyll-a ug/cm^2	<2	2 – 5	>5 – 10 (30+)	0.16 – 1.04 **(0.59-2.0)**
Algae density cells/cm^2	<0.2 x10^6	1 - 4 x10^6	>1 x10^7	0.25 – 0.56 x10^6 **(0.9 – 13.1x10^6)**
Algae biovolume cm^3/m^2	<0.5	0.5 – 5	20 - 80	0.97 – 3.12 **(0.6 - 5.9)**
Diatom density frustules/cm^2	<0.15 x10^6	1 - 2 x10^6	>20 x10^6	0.24 – 0.51 x10^6 **(0.2-1.0 x10^6)**
Biomass –AFDW mg/cm^2	<0.5	0.5 – 2	>3	0.50 – 0.59 **(0.35-3.5)**
Biomass –dry wt mg/cm^2	<1	1 – 5	>10	33 - 26 **(6-99)**
Organic matter (% of dry wt)		4 – 7		3.2 – 6.1 **(2 - 7)**
Bacteria count, HTPC CFU/cm^2	<4 -10 x10^6	0.4 – 50 ×10^6	>50×10^6 – >10^{10}	0.2 – 5 x10^6
Fungal count CFU/cm^2	<50	50 – 200	>200	<250 – 6000
Accrual chl-a ug/cm^2/d	<0.1	0.1 – 0.6	>0.6	0.062 - 1.6 shallow; 0.36 – 1.2 deep

Comparison data obtained from Flinders and Hartz 2009; Biggs 1996; Peterson and Porter 2002; Freese et al. 2006; Durr and Thomason 2009; Romani 2010; Biggs and Close 1998.

Throughout the 2007 – 2018 study period, periphyton communities in MCR occurred in three large zones created by the operating regime over the preceding 30 to 70 days as it interacted with the physical habitat. These zones are: 1) substrates that are permanently submerged with the minimum flow regime, 2) frequently wetted substrates in the lower varial zone, and 3) infrequently wetted substrates in the upper varial zone (Figure 2-2). Despite the establishment of these three distinct benthic communities with variable dominant species, both periphyton and invertebrate communities were relatively stable when viewed at the family taxonomic level. These zones are discussed in detail in the following sections.

Table A39 Comparison of benthic invertebrate communities in different river systems.

River	Average Annual Discharge (m^3/s)	Mean # of Invertebrates/m^2 (±SE)	Total # of Taxa	Diversity (Simpson's Index)	Most Abundant Taxa (percent abundance)
MCR (Revelstoke)	955	3092(±6122)	33	0.58	Orthocladius complex (28) Hydra sp. (24) Orthocladiinae (10) (9.4) Eukiefferiella sp. (6.6)
Fraser River (Agassiz)	3,620	829 (±301)	55	0.84	Orthocladiinae (62.7) Baetis spp. (7.2) Ephemerella spp. (5.4)
Thompson River (Spence's Bridge)	781	2108 (±1040.8)	48	0.44	Orthocladiinae (62.7) Baetis spp. (7.2) Ephemerella spp. (5.4)
Cheakamus River		1252 (±1149)	6	_	Ephemeroptera Plecoptera Diptera w/o chironomids

Data sources include, Reece & Richardson 2000, Triton Environmental Consultants Ltd. 2008 and this report.