Columbia River Water Use Plan

Revelstoke Flow Management Plan

Mid Columbia River Ecological Productivity Monitoring

Implementation Year 9

Reference: CLBMON-15b

Columbia River Water Use Plan Monitoring Program: Middle Columbia River Ecological Productivity Monitoring

Study Period: September 2014 -May 2015

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PROGRAM NO. CLBMON-15B

MIDDLE COLUMBIA RIVER ECOLOGICAL PRODUCTIVITY MONITORING, 2007-2015

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ACRONYMS AND ABBREVIATIONS

µS	microsiemens
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
Caro Labs	Caro Environmental Laboratories (Kelowna, B.C.)
CFU	colony forming unit
chl-a	Chlorophyll-a
CV	Coefficient of variation
Didymo	*Didymosphenia geminata*
DO	Dissolved oxygen
EPT	*Ephemeroptera* (mayflies), *Plecoptera* (stoneflies), *Trichoptera* (caddisflies)
FFF	fall fluctuating flow
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
PCA	principal component analysis
RVI	relative variable importance
SD	standard deviation
UTM	Universal Transverse Mercator
WUP CC	Columbia River Water Use Plan Consultative Committee

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DEFINITIONS

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

Term	Definition
Aerobes	Organisms that require >1-2 mg/L dissolved oxygen in their environment
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	The production within the benthos originating from both periphyton and benthic invertebrates
Bioavailable	Available for use by plants or animals
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
Diel	Denoting or involving a period of 24 hours
Epilithic algae	Algae that grow on hard inert substrates, such as gravel, cobbles, boulders
Eutrophic	Nutrient-rich, biologically productive water body
Flow	The instantaneous volume of water flowing at any given time (e.g.1200 m^3/s)
Freshet	The flood of a river from melted snow in the spring
Functional Feeding group	(FFG) Benthic invertebrates can be classified by mechanism by which they forage, referred to as functional feeding or foraging groups
Heteroscedasticity	Literally “differing variance”, where variability is unequal across the range of a second variable that predicts it, from errors or sub-population differences.
Heterotrophic	An organism that cannot synthesize its own food and is dependent on complex organic substances for nutrition.
Inflow plume	An inflow seeks the layer of matching density in the receiving water, diffusing as it travels. High TSS, TDS and low temperature increase water density.
Laminar	Non-turbulent flow of water in parallel layers near a boundary
Light attenuation	Reduction of sunlight strength during transmission through water
Linear Regression Model	Linear regression attempts to model the relationship between two variables by fitting a linear equation to observed data
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
Mesotrophic	A body of water with moderate nutrient concentrations
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

Term	Definition
Myxotrophic	Organisms that can be photosynthetic or can absorb organic materials directly from the environment as needed
Nano plankton	Minute algae that are less than 5 microns in their largest dimension
Pico plankton	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
Reducing environment	Devoid of oxygen with reducing conditions (-ve redox) e.g. organic sediments
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
Salmonid	Pertaining to the family *Salmonidae*, including the salmons, trouts, chars, and whitefishes.
Substrates	Substrate (sediment) is the material (boulder cobble sand silt clay) on the bottom of a stream.
Taxa Taxon	A taxonomic group(s) of any rank, such as a species, family, or class.
Thalweg	A line connecting the lowest points of a river, usually has the fastest flows
Zooplankton	Minute animals that graze algae, bacteria and detritus in water bodies

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CLBMON 15B Status of Objectives Management Questions and Hypotheses After Year 9

Objectives	Management Questions	Management Hypotheses	Year 9 (2015) 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?	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. Theoretically, the spatial area supporting benthic communities should increase with minimum flows because productive habitat is directly dependant on submergence. The spatial area of productive habitat is determined by the BC Hydro operating regime. The operating regime creates three typical bands of growth that moved across the channel in relation to mean low flows and duration of daily high flows. During certain operating regimes, the total productive area is determined by factors such as high daily average flows, backwatering from Arrow Lakes Reservoir, and weather conditions. To explicitly determine the spatial area of habitat covered by minimum flows, a more complex spatial model is required that considers all aspects of the operating regime due to the strong correlations between submergence and the total area of productive habitat. Developing this spatial model will allow more specific conclusions and will provide useful information for considering alternative operating regimes. A preliminary concept for a spatial model is presented in this document and will be developed in the coming years.
	Q.2. What is the effect of implementing minimum flows on the area of productive benthic habitat?	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. Given no other operating constraints, we conclude that minimum flows in combination with daily, weekly, monthly, and annual operating regimes positively affect the total biomass within the MCR. Peak or total biomass was greatest in permanently wetted areas adjacent to the channel edge at average low flows and in areas directly below average low flows. The overall benefits of minimum flow are greatest under the following conditions: • Periods of low daily flows that exceed 24 hours with high or freezing average daytime temperatures. • Repeated exposure events in excess of 12 hours, particularly during more extreme temperatures

CLBMON 15B Status of Objectives Management Questions and Hypotheses After Year 9

Objectives	Management Questions	Management Hypotheses	Year 9 (2015) Status
	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$_{3A}$: There are no changes in accrual rates of periphyton at channel elevations that remain permanently wetted by minimum flow releases.	Ho$_{3A}$: The hypothesis is accepted. Accrual rates in permanently wetted areas that occurred in the mid-channel, with the highest water velocity and depth during high flows did not appear to have a different accrual rate under current minimum flows management when compared to pre-implementation of minimum flows. Physical characteristics such as velocity, light, and substrate were more important determinants of periphyton accrual than minimum flows within these areas. Thus, minimum flows are expected to have minor effects on accrual. Peak flows associated with REV 5 or other high water events may reduce periphyton accrual rates and standing crop in permanently submerged habitats.
		Ho$_{3B}$: There are no changes in accrual rates of periphyton at channel elevations that are periodically dewatered during minimum flow releases.	Ho$_{3B}$: The hypothesis is accepted, but only under certain conditions. We conclude that minimum flows do not affect areas that are periodically dewatered, located above the minimum flow line, but they have had an effect in areas that were regularly exposed before the minimum flow operating regime because increased accrual would have occurred as observed in time series sampling in the spring and fall. Daytime submergence, seasonal patterns, algal immigration from Revelstoke Reservoir and operating cycles were also important determinants of periphyton accrual and must also be considered.
	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$_{4A}$: 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.	H4$_{A}$: The hypothesis is rejected, but only under certain operating conditions. Permanently submerged areas were the most productive and diverse, but frequently submerged varial zone areas also had some level of productivity and diversity. The area of productive invertebrate habitat was bounded by average daily low flows and its upper limit was determined by average daily submergence. Specifically determining the benefits of minimum flows is not currently possible because of other confounding factors such as the duration of daily high flows. Without any other operating constraints, minimum flows do affect the total abundance, biomass, and diversity of benthic communities because they establish a minimum area of productive habitat and ensure there are organisms for recolonization in addition to those provided by tributary inflows. However, other factors such as the life history strategies of different benthic invertebrates or periphyton species may also be equally or possibly even more important to overall productivity.

CLBMON 15B Status of Objectives Management Questions and Hypotheses After Year 9

Objectives	Management Questions	Management Hypotheses	Year 9 (2015) Status
		$Ho_{4B:}$ There are no changes in abundance/biomass/diversity of benthic invertebrates at channel elevations that remain permanently wetted by minimum flow releases. $Ho_{4C:}$ There are no changes in abundance/biomass/diversity of benthic invertebrates at channel elevations that are periodically dewatered by minimum flow releases.	$Ho_{4B:}$ The hypothesis is accepted. We conclude that minimum flows have not affected abundance/biomass/diversity in permanently wetted areas. However, our data suggest that other aspects of operation, such as high peak flows associated with high water events may also be important determinants of invertebrate production. Thus, consideration of all aspects of flow regulation must occur in conjunction with minimum flows to understand potential effects. $Ho_{4C:}$: The hypothesis is accepted, but only under certain conditions. We conclude that minimum flows do not affect areas periodically dewatered (i.e., above minimum flow), but they probably had an effect in areas that were regularly exposed before the minimum flow operating regime because the data suggest that benthic invertebrate abundance, diversity, and biomass are positively associated with submergence or time in the water. Daytime submergence, seasonal patterns, and operating cycles were also important determinants of benthic accrual and must also 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_5: 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_5: This hypothesis is rejected, but only under certain operating conditions. Food for fish was assessed using a Fish Food Index (FFI) in 2013 and the total biomass of EPT and Dipteran taxa in 2014 and 2015. The FFI 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 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. • Repeated exposure events in excess of 12 hours Substrates submerged for 450 to 500 hours during daytime hours (10 to 11 hours per day) had the greatest availability of preferred fish food items, which are generally EPT and Dipteran. EPT and Dipteran biomass was greatest in areas submerged for at least 750 to 1000 hours over at least 46 days, regardless of depth. Both periphyton and invertebrates showed similar responses, suggesting that overall productivity and food for fish are directly affected by the operational cycles that create either submerged or dry conditions, where increased periods of submergence result in an overall increase in productivity. In addition to the area wetted by minimum flows acting as a species reservoir, tributaries such as 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 heavily influenced by variable flow 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 the MCR. The objective of the 142 m^3/s minimum flow strategy is to enhance the productivity and diversity of benthic communities in the MCR by increasing the permanently wetted area by an estimated 32–37% (Golder 2012). The goal of the ecological productivity monitoring program CLBMON-15b is to provide long-term data on benthic productivity of MCR using artificial substrate samplers that assess how minimum flow influences benthic communities and availability of food for fish. This summary report presents data and findings from years 1 through 9 of the study period. 2007 to 2010 data was collected pre-implementation and 2011 to 2015 data was collected post-implementation of minimum flows, noting that a fifth generating unit (REV 5) was added in December 2010, which increased the maximum flow discharge from 1699 to 2124 m^3/s. This report summarizes the findings of all study sessions to date, with a focus on fall 2014 and particularly, spring 2015.

Minimum flows benefit MCR benthic invertebrate and periphyton communities by ensuring that a channel area remains wetted and productive at all times. Habitat conditions of MCR included the permanently submerged zone and two zones with varying degrees of submergence. The permanently wetted zone showed high productivity and accrual rates despite periodic thinning by high water velocities. Immediately above the minimum flow elevation was the most productive zone, the lower varial zone. The final zone was the less productive upper varial zone, located in areas of increased exposure above the lower varial zone. Over the years of study, the boundaries between these three zones shifted in response to growth conditions provided by the operational flow regimes over the preceding 30 – 70 days. Benthic productivity in all zones was directly influenced by physical factors such as velocity, light, and substrate stability, but in varial zones, submergence times were the most important determinants of benthic productivity. For both periphyton and invertebrates, productivity was greatest at mid-channel elevations extending from just below the elevation of minimum flow to slightly above it in the lower varial zone.

Distinguishing between the benefits of minimum flows and variation in the operating regimes observed over the study period was difficult. Daytime submergence and high average daily flows were key factors in determining benthic productivity. Varial zone areas submerged for at least 9 to 12 hours per day (400 to 500 hours over the 46 day deployment period or 36-45% of the time) were typically as productive as those in areas constantly submerged by minimum flows. However, productivity in these higher varial zones was dependent upon key factors such as daytime air temperature and operating regime. Submergence times in excess of 1000 hrs (or 40 days) appear to show an increase in productivity over those submerged for less time. Further, the benefits of minimum flows were lessened by other factors, most notably backwatering from Arrow Lakes Reservoir that submerged habitats in the varial zone substrates that would otherwise have desiccated. In the absence of other operating constraints, minimum flows benefit the benthic productivity in MCR, but alternative operating regimes that have higher average daily flows without permanent minimum flows may also create habitat conditions that are equally productive.

Overall benthic community structure was stable at the family group taxonomic level across all sites of variable submergence, with similar representation between years.

However, when MCR periphyton data were examined at the genera or species level, distinctions between years, seasons, and flow changes emerged. For example, fall 2013 data showed a much higher than normal proportion of the periphyton derived from species exported by Revelstoke Reservoir, while fall 2014 data showed unusually strong filamentous green algae in the lower varial zone and very high productivity in the Reach 3 upper varial zone with backwatering. Similar patterns of inter-annual variation were observed for invertebrates, although the specifics reasons were more challenging to elucidate.

Benthic invertebrates were more sensitive to exposure than periphyton. Exposure events of as little as 24 hours during high daytime temperatures caused substantial stresses and die-off in the benthic community, such as those observed in the spring of 2011. For periphyton, exposures exceeding 36-48 hours were usually required before similar effects were observed. Mortality from exposure of either invertebrates or periphyton is most dependent upon weather patterns at the time of the event.

Peak production in 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, particularly in the spring when growth rates are slow.

Substrates submerged for 10-11 hours/day in daylight hours had the most preferred fish food items, which generally 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 (70-90% of the time).

In this study, submergence was consistently identified as the single most important determinant of benthic production in the MCR. Thus, 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 daytime hours. However, many factors affect the total area of productive habitat and need to be considered in conjunction with the effects of minimum flows. Factors such as Arrow Lakes Reservoir backwatering, operational flow patterns, high peak flows (exceeding 1800 m^3/s), seasonal cycles, and species tolerances were all important determinants of benthic productivity and should be considered when reviewing future operational flow regime guidelines. A proposed spatial model to determine the total area and quantity of production in MCR has been presented and will be further developed over the coming years of the study. Spatial modelling of MCR is needed to better elucidate the specific benefits provided by implementation of minimum flows.

Keywords:

Middle Columbia River, Ecological Productivity, Minimum Flows Management

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Appendix A – Supplemental Results

Appendix B – Digital Data

The digital appendix contains summary statistics of data in Excel.

1.0 INTRODUCTION

Aquatic habitats in the Middle Columbia River (MCR) are heavily influenced by variable flow releases from the Revelstoke Dam (REV), and to a lesser extent, by tributary inflows and backwatering from Arrow Lakes Reservoir (ALR). In December 2010, BC Hydro added a fifth generating unit (REV 5), which increased the maximum possible flow discharge of REV from 1699 to 2124 m^3/s.

The Columbia River Water Use Plan supported implementation of a year-round minimum flow of 142 m^3/s to mitigate the effects of variable flows released from the Revelstoke Dam. Studies of minimum flow sought to understand how physical and biological variables affect fish habitat and productivity in MCR (WUP, BC Hydro 2005). One component of the WUP involved assessing how the productivity and diversity of benthic communities would change through implementation of a minimum flow operating regime. It was hypothesized that increasing 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 improve fish abundance (WUP, BC Hydro 2005).

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

In the study years prior to implementation of a minimum flow (2007 – 2010), the water release from the 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. Since REV 5 and minimum flows were initiated (2011-2014), flows have ranged from 142 m^3/s to 2124 m^3/s. The extent of submergence of river substrates was therefore determined by the variable water releases, in combination with backwatering from the downstream Arrow Lakes Reservoir (ALR) into portions of MCR as far as just upstream of Big Eddy, a large deep pool near Revelstoke.

Some of the predicted trends of the new operating regime include a general increase in the frequency of high flows with corresponding increases in river elevations and velocities immediately downstream of the dam, and a general increase in average daily discharge during low demand periods (BC Hydro 2006). These trends will result in a greater variability in flows. The operating regime or 'operations' of the dam have direct influence on both periphyton and benthic invertebrate production downstream of Revelstoke Dam.

The results from the Ecological Productivity Monitoring will be integrated with other BC Hydro monitoring programs, including Physical Habitat Monitoring, Fish Population Indexing Surveys, Juvenile Habitat Use and Adult Habitat Use. The findings from these monitoring programs will be collectively used to evaluate if minimum flows provide benefits for fish, and if there is an advantage to the establishment of a long-term minimum operating release requirement for Revelstoke Dam.

These data will serve to quantify long-term trends in the productivity of periphyton and benthic invertebrates and will provide valuable information pertaining to the ecological health of the riverine environment downstream of the Revelstoke Dam.

This report summarizes years 1 through 9 of the monitoring program, focuses on the spring 2015 (Year 9) sampling season, and presents findings from fall 2014 for comparative purposes. At this time, the project is proposed to transition from understanding the specific effects of submergence due to minimum flows (i.e., pre and post) and important environmental factors (e.g., velocity, light, and depth), to understanding the spatial effects of the operating regime on productivity. A spatial model, previously prepared for the Lower Columbia River is presented conceptually to provide an initial framework within which to consider productivity in a spatial sense (Schleppe et al., 2015).

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) in MCR
- To assess the response of benthic community taxa (periphyton and invertebrates) of MCR to a minimum flow release from Revelstoke Dam and REV 5 operations
- To investigate and quantify the relationship between habitat attributes and benthic composition, abundance, and biomass with the section of 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). We developed a conceptual model, presented in Figure 1-1, to address the second and third objectives, and to understand the potential interactions of the complex factors affected by changes in flow. At this time, there is a basic understanding of the relative importance and role of each parameter; the model highlights the many variables and complex interactions that can influence benthic productivity and ultimately food for fish. It should be noted that life history has been added to the table, and while this has been considered part of community in the past, recent works suggest that it is an important factor that directly affects communities, suggesting it should be considered separately (Kennedy et al, 2016). Highlighted areas indicate what data is being collected to address the management questions, noting that specific life histories have not yet been considered to date. At the forefront of the model are BC Hydro operations that determine quantity and duration of water release. Altered flows directly influence several factors such as velocity, turbulence, depth, submergence, scour, etc. and therefore have a direct effect on benthic productivity.

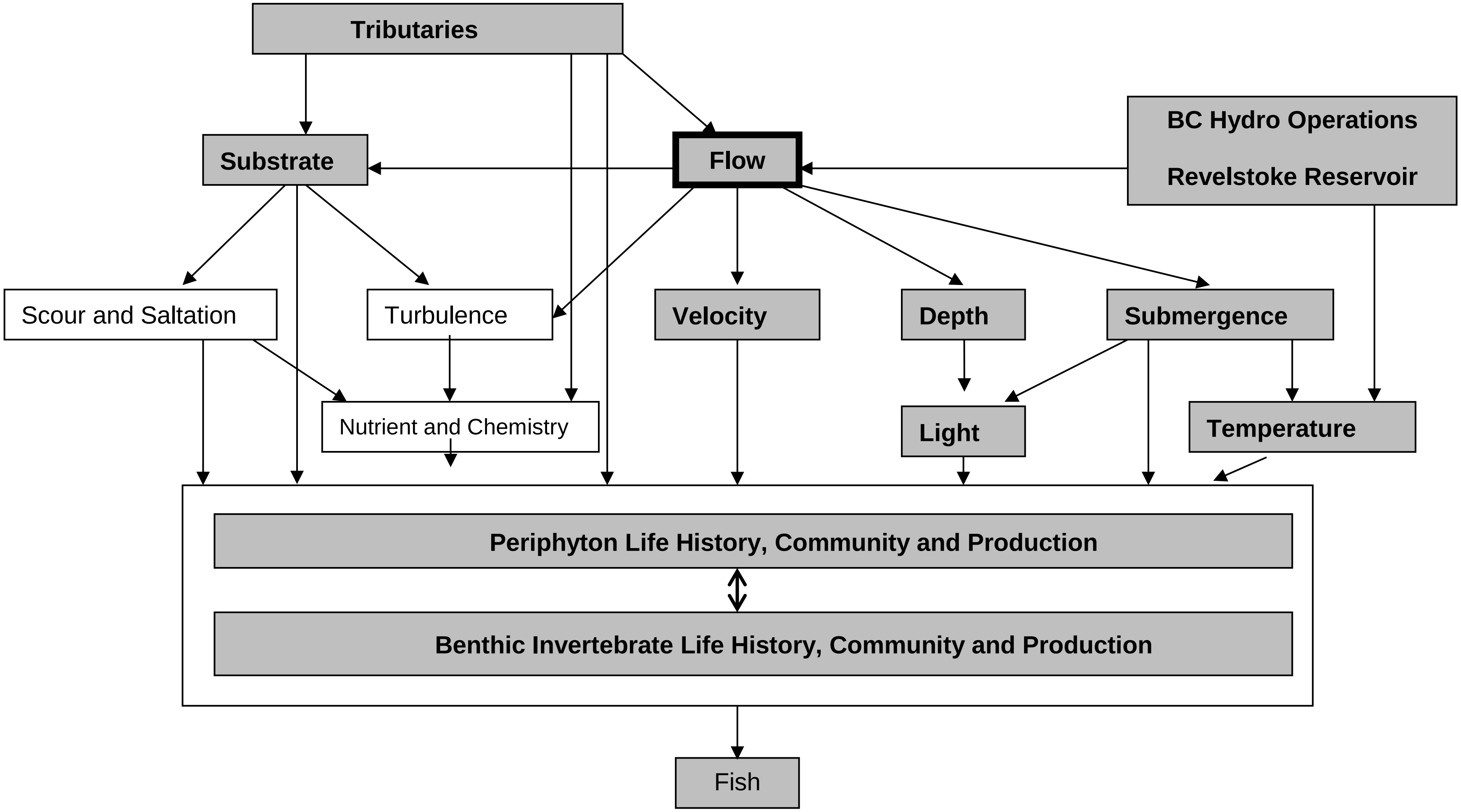


Figure 1-1: **Conceptual interactions model of habitat variables and benthic production as they relate to food for fish in MCR. Parameters shaded in grey, with bolded text represent parameters assessed in this study.**

To comprehensively address the three main objectives, five management questions with related hypotheses were developed. Table 1-1 lists each of the management questions/hypotheses (BC Hydro 2010), 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 Terms of Reference, that the evaluation of minimum flow release is to include the operational changes associated with REV 5 operations (BC Hydro, 2010).

Simple statistical models were used to understand the physical responses of periphyton and benthic productivity to flows. In a complex system like the MCR, the effects of minimum flows and REV 5 flows could not be isolated from each other and the larger flow regime. In lieu of this approach, we identified relationships between benthic production and spatial features that are directly influenced by flows including area of wetted habitat, and frequency and duration of submergence. From this, the effects of the operating regime including minimum flow are inferred. 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 intent of the data collection is to facilitate the extrapolation of benthic and periphyton productivity in the river as a whole and to enable estimation of the spatial area of productive habitat in 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 may affect benthic productivity in 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?	Ho$_1$. The implementation of the 142 m^3/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 deployed across the spectrum of flows/elevations of the MCR. Data collection includes: • Abundance –periphyton & invertebrates • Diversity – taxonomy indices for periphyton and invertebrates • Production/Biomass – chl-a, AFDW/DW, biovolume, benthic invertebrate biomass • Natural Substrate Comparisons
Q2. What is the effect of implementing minimum flows on the area of productive benthic habitat?		Productive habitat area is considered using the analogous measure submergence as a surrogate for minimum flow. Statistical models using a variety of parameters describing submergence are tested for the different measures of production. Future data analysis will attempt to directly link submergence time to the total spatial area of productive benthic habitats
Q3. What is the effect of implementing minimum flows on the accrual rate of periphyton biomass in 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 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 spectrum 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 HTPC plate counts 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 that test the effects of submergence on periphyton peak biomass. Future data analysis will attempt to directly link submergence time to the periphyton productivity in three areas of the river, those permanently submerged, those in varial zone areas, and those in floodplain areas of MCR.
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 m^3/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 spectrum 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. Future data analysis will attempt to directly link submergence time to the invertebrate productivity in three areas of the river, those permanently submerged, those in varial zone areas, and those in floodplain areas of MCR.

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.	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.

Note: AFDW/DW = ash-free dry weight/dry weight; Chl-a = chlorophyll-a; HTPC = heterotrophic plate count

2.0 METHODS

2.1 Study Area and Sampling Locations

The MCR consists of Reaches 4 through 1 of the upper Columbia River adjacent to the town of Revelstoke, encompassing approximately 38.5 km between the Revelstoke Dam and the Upper Arrow Lake Reservoir (ALR) near Galena Bay. This study focused on Reaches 4 and 3, which exhibit more riverine-like conditions than 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 approximately 1 to 5 m depending upon flows. It 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 2010). 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 due to the unique habitat it provides.

Upper Reach 3 is immediately below Big Eddy, where the river turns 120 degrees and the channel thalweg occurs on the left bank with a floodplain area on the right bank. The right river bed 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. In lower Reach 3 below the bridges, the side braided channels are exposed when ALR water elevation 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 2010). Substrates in Reach 3 are finer than Reach 4 with sand, gravel and cobbles predominating throughout the reach.

The key tributaries that influence MCR are the Jordan and Illecillewaet Rivers. The Illecillewaet River is the largest tributary in the study area of MCR. The lower Illecillewaet receives secondary treated sewage effluent from the Town of Revelstoke.

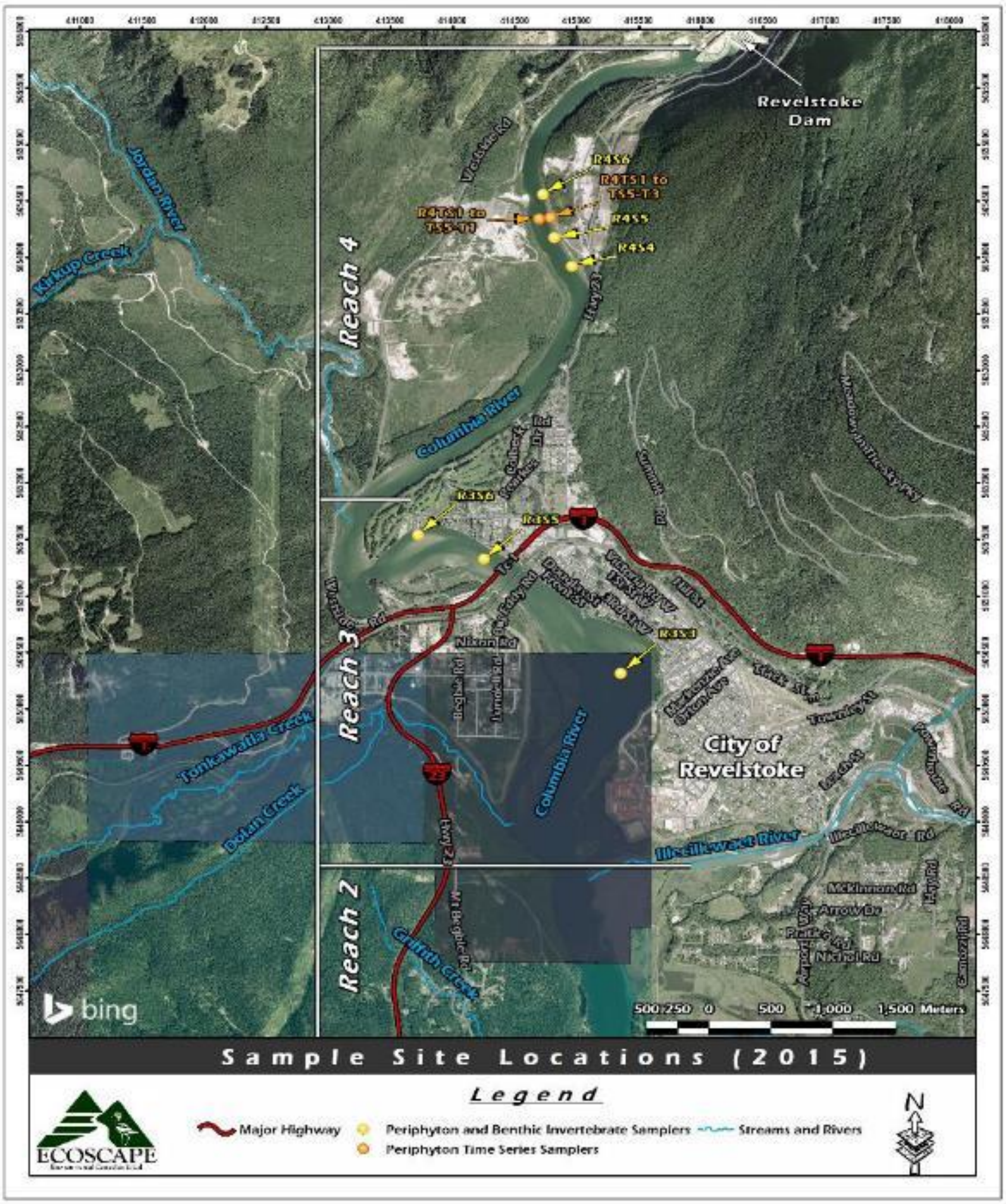


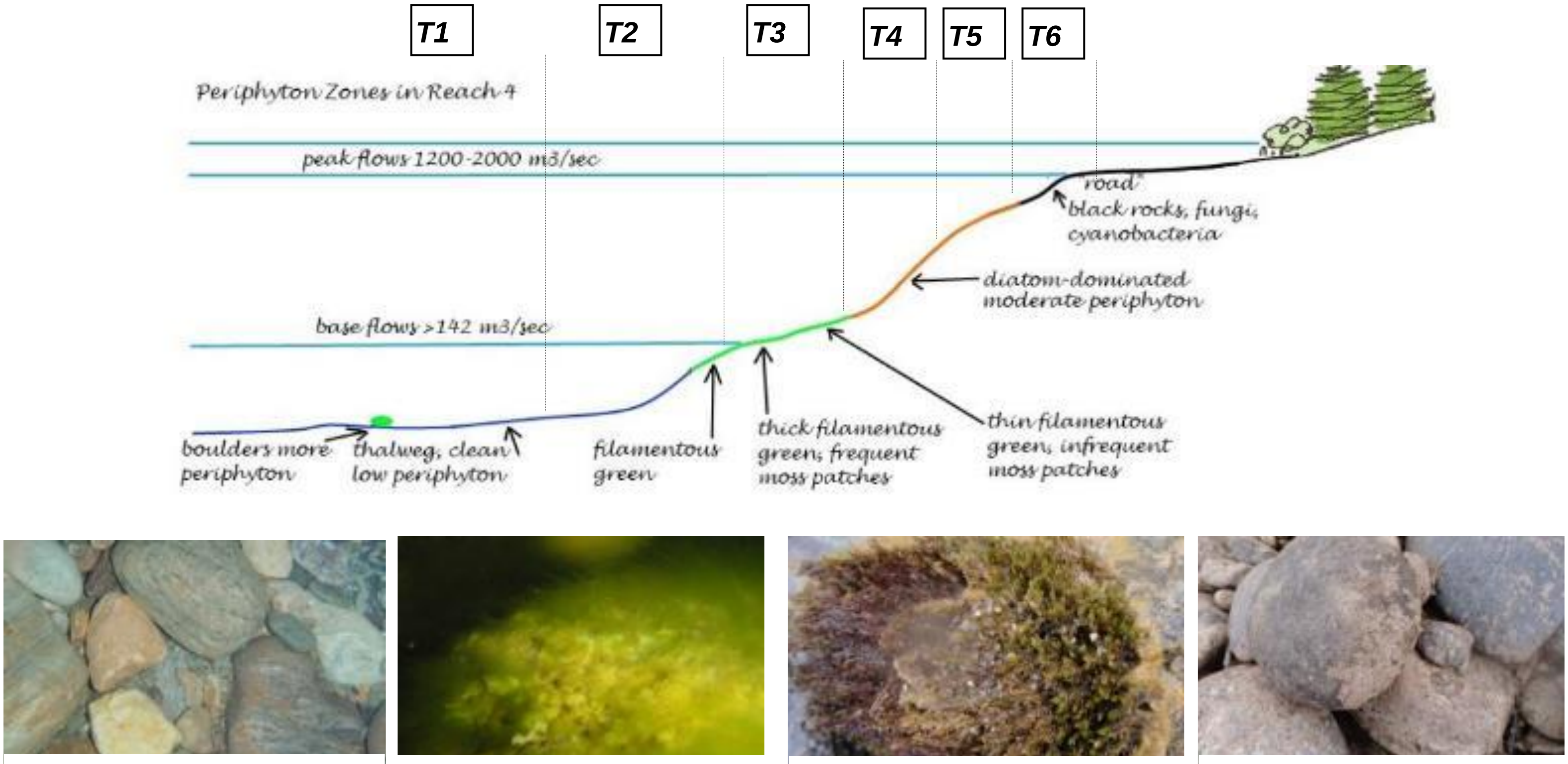
Figure 2-1: **Map of the study area and sampling locations. Site labels are fully defined in Table 2-1**

2.2 Periphyton and Invertebrate Community Sampling Using Artificial Samplers

2.2.1 Artificial Sampler Design and Deployment

Year 9 of the CLBMON 15-b study included spring (2015) sampling session, where artificial samplers were placed in the river and left for a minimum of 44 days in each session (Table 2-1), noting that fall 2014 data is presented for comparative purposes. Data for previous years are available in previous CLBMON15b reports, however the sample sites used in 2015 were consistent with previous years. 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 sampled at sites S4, S5, and S6. Finally, sites at Big Eddy (BE), bedrock (BR), and Backwater areas (BW) were also sampled.

Sampling sites at transects T1 through T6 were deployed in Reach 4 as shown in Figures 2-2 and 2-3. Transect position refers to the position of the sampler within the river cross-section. T1 samplers were positioned mid-channel, within or near the thalweg. T2 samplers were placed in slightly shallower areas than T1. Both T1 and T2 were typically permanently wetted at minimum flows. T3 through T4 were placed in the mid-channel and were wetted during moderate flow levels of 200 to 800 m^3/s. T3 and some T4 positions sampled the lower varial zone. T5 and T6 samplers were placed within the upper varial zone and were only wetted during higher flows from 1000 to 1600 m^3/s. 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 Reach 4 at the bedrock (BR) location were studied instead.



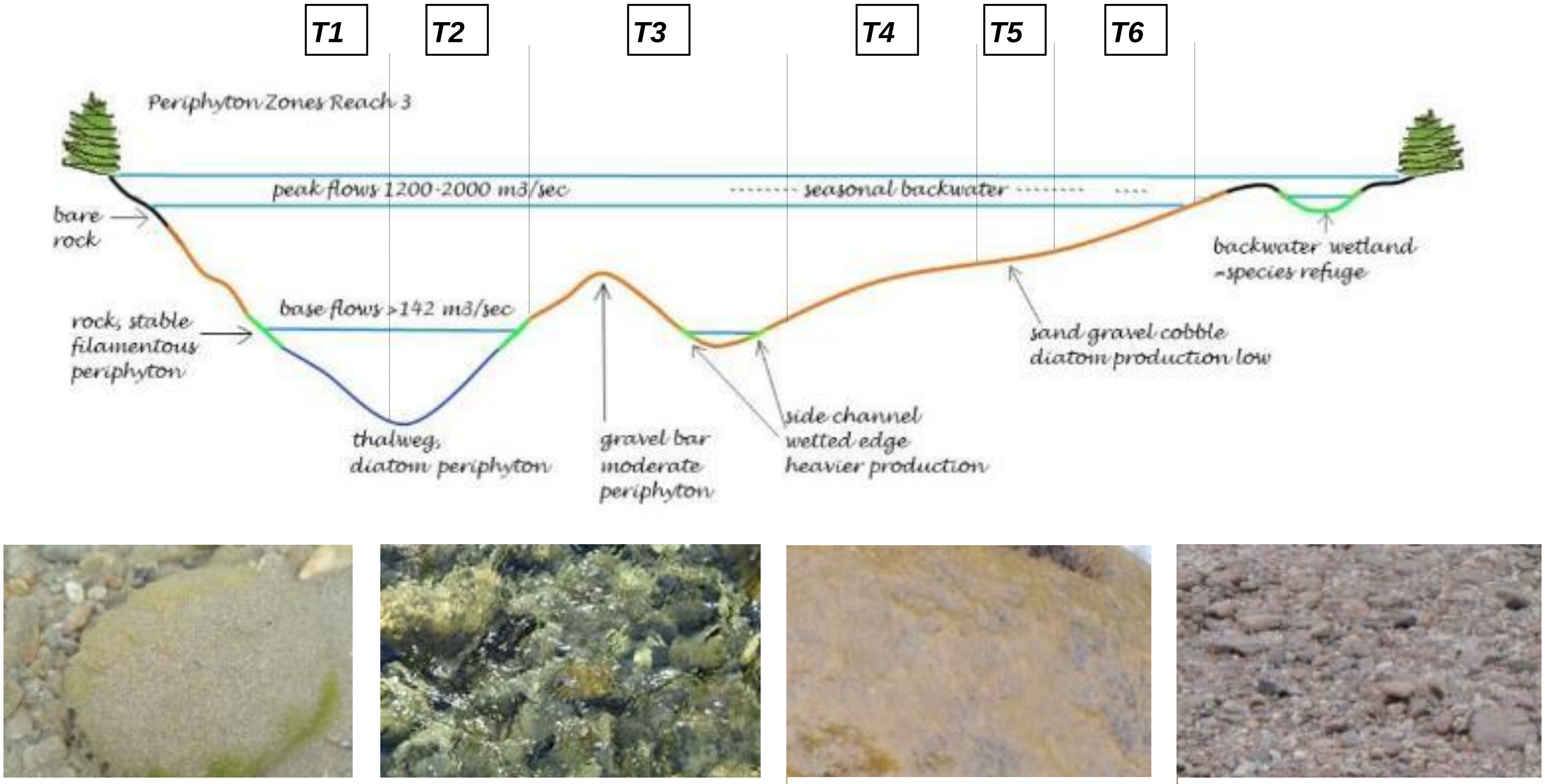
thalweg
(low periphyton

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 Reach 4**



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 Reach 3**

Samplers and associated rigging were assembled and during September 9 - 11, 2014 for the fall deployment and April 2015 for spring deployment. One day was spent preparing gear, followed by deployments in both Reaches 4 and 3, when flows were minimal to moderate. Figure 2-4 illustrates our standard artificial sampler design which did not deviate from previous years, with the exception of time series samplers. Time series samplers had 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.

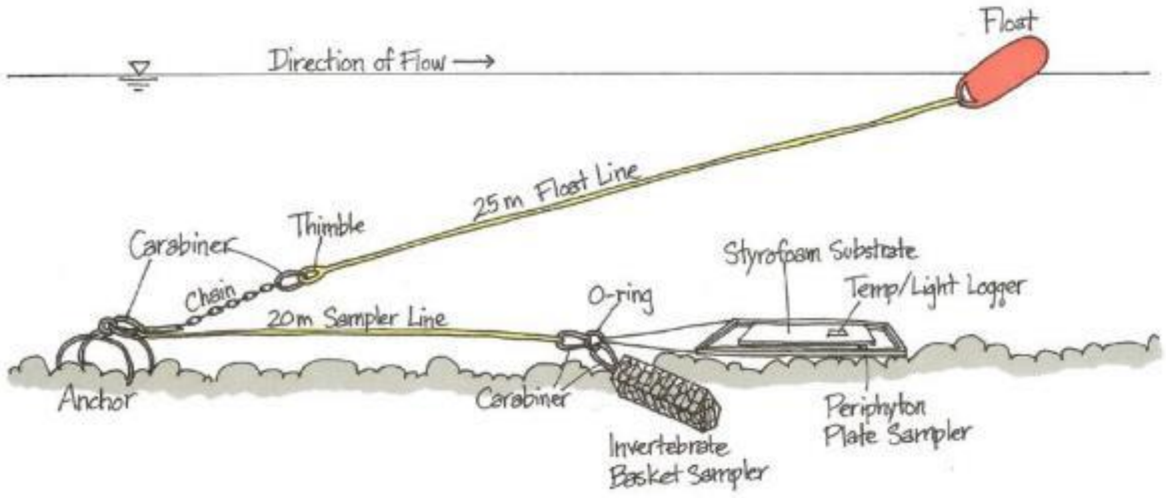


Figure 2-4: **Schematic drawing of the artificial substrate sampler used in MCR**

Table 2-1: Summary of samples collected from artificial sampler deployment and retrieval in fall 2014 and spring 2015

Season	Reach	Site/Habitat Type	Periphyton Samplers		Invertebrate Basket Samplers	
Fall (Sept 9th - Oct 30th)	Reach 4 (R4)	Site 6 (S6)	6	6 (100)[1]	6	6 (100)
		Site 5 (S5)	6	6 (100)	6	6 (100)
		Site 4 (S4)	6	6 (100)	6	6 (100)
		Bedrock (BR)	6	6 (100)	6	6 (100)
		Time Series (TS)	10	10 (100)[1]	10	10 (100)
	Reach 3 (R3)	Big Eddie (BE)	4	4 (100)	4	2 (100)
		Site 6 (S6)	6	6 (100)	6	6 (100)
		Site 5 (S5)	6	5 (83)	6	5 (83)
		Backwater (BW)	4	3 (75)	4	3 (75)
		Site 3 (S3)	6	6 (100)	6	6 (100)
2014 Totals			**60**	**58 (96)**	**60**	**58 (96)**
Spring (April 12th - May 27th)	Reach 4 (R4)	Site 6 (S6)	6	6 (100)[1]	6	6 (100)
		Site 5 (S5)	6	6 (100)	6	6 (100)
		Site 4 (S4)	6	6 (100)	6	6 (100)
		Bedrock (BR)	6	6 (100)	6	6 (100)
		Time Series (TS)	10	10 (100)[1]	10	10 (100)
	Reach 3 (R3)	Big Eddie (BE)	4	4 (100)	4	3 (75)
		Site 6 (S6)	6	6 (100)	6	6 (100)
		Site 5 (S5)	6	6 (100)	6	6 (100)
		Backwater (BW)	4	4 (100)	4	0(0)
		Site 3 (S3)	6	6 (100)	6	6 (100)
2015 Totals			**60**	**60 (100)**	**60**	**55(92)**

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 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. In 2010, time series samplers were deployed across the river at transect positions from T1 through T7. 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. Five time series samplers were deployed in Reach 4 in both transects positions.

Varial zone time series samplers represent conditions between T3 and T4 locations because they cannot be accurately placed, retrieved, and re-deployed at the same location/depth during sample collections. These time series samples are therefore considered to be representative of accrual in the varial zone rather than a discrete sampling location such as T3.

Time series samplers were retrieved once per week following deployment. During each weekly sampling, the light/temp loggers were wiped clean with a paper towel so light measurements from time series periphyton samplers could be compared with undisturbed loggers left in place for the entire study duration. 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 was not conducted after 2013.

2.2.3 Artificial Sampler Retrieval

Artificial samplers remained in the river for a total of 44-51 consecutive days in each season. This deployment period matches earlier MCR deployments and is within the incubation period required for attainment of peak biomass defined by Perrin (2004). Spring and fall samplers were retrieved either by boat, wading or by foot on May 27-28 2015 for spring and October 28 – 29 2014 for fall.

Four Styrofoam punches were randomly collected from each sampler in order to assess the following metrics: 1) chlorophyll-a to give an estimate of only 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 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.

During sampler retrieval, 1 litre composite samples of Reach 4 and Reach 3 river water were collected mid-river and analysed for drift algae originating from Revelstoke Reservoir during the fall and spring. Confirmation of the source of algae taxa were made by comparing these drift sample results to existing reservoir algae data and to their published growth habits (Wehr and Sheath, 2003).

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 any contents were rinsed into a labeled bucket with pre-filtered river water. The retrieved baskets were also placed in the labeled buckets until further field processing. During certain flow conditions, use of the net was conditional on safety of the crew and was not used in all circumstances, particularly 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 in order 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, placed in pre-labeled containers and preserved in alcohol for analysis.

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 QA/QC and initial taxonomic verifications provided by Dr. J. Stockner in 2011-2012. Fresh, chilled samples were examined within 48-hrs for protozoa and other microflora that are harder 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 undertaken. 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 lowest practical level following the Standard Taxonomic Effort list compiled by the Southwest Association of Freshwater Invertebrate Taxonomists (SAFIT) (Richards and Rogers, 2011) and recommendations from Environment Canada (McDermott *et al*., 2014). A reference sample was kept for each unique taxon found. A sampling efficiency of 95% was used for benthic invertebrate identification and was determined through independent sampling. Numerous 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

Water and air temperature data obtained from the HOBO light/temperature loggers was the primary dataset used to determine whether an artificial sampler was submerged. Four HOBO light/temperature loggers were placed in the upland areas above the high water level within Reaches 4 and 3 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. However, this analysis of submergence was only partially reliable as there were times during the deployment when the air and water temperatures were within 1.5 ºC of each other (Schleppe *et al.,* 2011).

To ensure that the determination of submergence was accurate, the entire database for each session was reviewed 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 to assess whether a plate was submerged: flow, 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 sites of exposure had notable highs, and we expect that localized effects such as metal frame heating may help separate similar temperature points between exposed and submersed samplers on sunny days. Data corrections were generally greatest on sites exposed to the air for longer periods.

2.3.2 Variables and Statistical Analyses

Non-metric multidimensional scaling (NMDS) was used to explore variation in benthic invertebrates and periphyton community composition. The Bray Curtis Dissimilarity measure was used for the periphyton analysis, while the Gower Dissimilarity measure was used for the invertrebrate analysis. A PERMANOVA (Oksanen, 2015) was used to determine if groups (either Pre/Post minimum flow, Year, Season, and Transect) were significantly different in composition. NMDS was run at the genus taxonomic levels for both periphyton and benthic invertebrates to investigate the effects of small and large scale taxonomic community differences within the study period. To further this analysis, a de-trended correspondence analysis (DCA) was attempted (but is not presented), and will possibly be presented and improved in future years depending upon direction of the project.

The full set of predictor data developed by Perrin and Chapman (2010) and those developed in 2010 were collected in 2011 through 2015. Temperature, light and submergence data were used to calculate a number of different predictor or explanatory variables that could test the effects of hydro operations on productivity in MCR (Table 2-2, Schleppe et al. 2011). Variables of time are often collinear, but all of the variables developed were initially considered. To reduce collinearity, multiple attempts at different model predictor combinations were considered to choose the most appropriate variables describing submergence without omitting any potentially influential factors that may affect productivity. An exploratory analysis of final production responses to explanatory variables (Table 2-2) was completed for raw and transformed data. The intent of this step was to reveal any general patterns or trends across transects or within response variables prior to any statistical analyses. Methods described by Zuur et al. (2009) were employed to examine multi-collinearity among explanatory variables based on variance inflation factors (VIF) and correlation coefficients, avoiding inclusion of highly collinear variables (correlations coefficients > 0.7) together in descriptive models. Most collinearity in predictors originated from variables of submergence and variables for light. The final set of predictor variables chosen were selected because they were the most interpretable and most useful to address key management questions without overly inflating the variance of models due to high collinearity. It should be noted that a variety of different predictor combinations have been presented in previous years reports, and although not directly tested, the trends observed in previous years for certain predictors should still be valid because of consistency in data between years.

Six response variables for both periphyton and benthic invertebrates were modeled. Periphyton responses included: 1) abundance, 2) biovolume, 3) chlorophyll-a, 4) percentage of community that is good forage, 5) species distinctiveness (Clarke and Warwick, 1999), and 6) Simpson's Index. To determine the percentage of the community that is good forage, each species was categorized as good, fair, fair-large, fair-poor, and poor. Subsequently, the total biovolume of all “good” forage species was determined and divided by the total biovolume for each site. Similar models for invertebrate production and diversity metrics were also prepared and included: 1) abundance, 2) biomass, 3) Simpson's Index, 4) Hilsenhoff Biotic Index, 5) species distinctiveness, and 6) total biomass of (good forage) *Ephemeroptera, Plecoptera*, *Trichoptera*, and *Dipterans* to estimate the effect on food for fish. Diversity and production data were transformed using either log10 or square root in order to adhere to the assumptions of least-squares multiple regression (i.e. normal distribution of residuals and heteroscedasticity of residuals). These six responses were modelled for the full set of predictor variables. Seasonal data is complicated because it interacts with many of the other predictor variables, and was therefore considered independently using a separate suite of models to reduce the need to utilize complicated interactive effects within the models.

Hilsenhoff Biotic Index (HBI) is typically used as a measure of oxygen concentration in organic loading of rivers, relating water quality conditions to benthic invertebrate distributions where higher index values are indicative of low dissolved oxygen conditions and hence poor water quality. This index factors the sensitivity of different taxonomic groups to low oxygen conditions. To some extent, low oxygen conditions originating from poor water quality are similar to extremes associated with substrate dewatering. The Hilsenhoff Biotic Index is calculated as follows:

$$HBI = \sum x_i t_i / n$$

Where: x_i is the number of individuals within a taxon,
t_i is the tolerance value of the taxon (from published literature), and
n is the total number of organisms in the sample (Plafkin et al. 1989).

The relative support for the effects of these 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 2012) to compete models based on Δ AICc values and AICc weights (w_i), 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), which 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).

A fish food index previously used to assess the effects of minimum flows on food for fish was not calculated in 2014. Although useful, for this report the total biomass of EPT and Dipterans were used as an alternative and was investigated to see if similar trends existed using raw data versus a more complicated index for comparative purposes. Since the Fish Food Index was heavily weighted towards EPT and Dipteran species as they are the typically the most preferred food across multiple species, this alternative was considered as an alternative measure for calculating food for fish. The biggest difference between methods is the Fish Food Index considers biomass, preference, and abundance, whereas this method only considers biomass.

Traditional regression methods such as stepwise multiple regression consider only one model as correct, even if alternative models are equally plausible. The model averaging approach is more objective because it simultaneously evaluates the merits of all the different working hypotheses relating operations, including minimum flow, to invertebrate and periphyton production (Johnson and Omland 2004). By objectively evaluating multiple alternative hypotheses, we are more likely to achieve an accurate understanding of how operations influence benthic production.

All statistical tests were conducted using R (R Development Core Team 2015), and model averaging was completed using the R package “MuMIn” (Barton 2009). In all analyses, independence of each sampler was assumed both within each transect and across sites. This assumption does not reflect the hierarchical sampling structure of Year / Reach / Site / Transect previously established. This model is improved from previous years because high collinearity among predictors has been addressed. Further, models treated Year, Reach, and Site as random effects. Transect was not considered as an independent variable because it is merely a categorical representation of depth which is highly correlated with light and submergence variables. It is acknowledged that this approach may not entirely address all of the variation within or between sites due to the hierarchical nature of the sampling but since the study focus is on understanding key trends rather than using models predictively, this should have little effect on conclusions reached. Finally, we acknowledge that each of the identified predictors likely plays some role in production and it is difficult to select the most appropriate predictor in cases when two are highly correlated but affect biological productivity differently. This is why different predictor / explanatory variable model combinations have been considered throughout the time period of this assessment and previous reports provide valuable insight into some of the information relied upon within this annual report.

Table 2-2: Variables used in the prediction of periphyton and benthic invertebrate response in relation to BC Hydro operations and physical conditions during deployment. The full set of variables developed in 2010 were prepared for 2015. Environmental predictors used in the final models presented in 2015 are shown in bold, while the non-bold variables were considered but subsequently removed.

Variable	Definition
max_daily_light	Average daily maximum light intensity (lux)
Num_Days_Incubated	Number of days of deployment
tot_exp_hrs	Total time exposed (hrs) or out of the water
mean_exp_hrs_per_day	Average time exposed (hrs) or out of the water
min_exp_hrs_per_day	Minimum number of hours spent out of the water in one day
max_exp_hrs_per_day	Maximum number of hours spent out of the water in one day
max_cum_exp_hrs	Maximum cumulative (hrs) period of time exposed or out of the water
exp_ratio	Ratio of the total hours exposed to the total time deployed
num_time_sub_x	Number of times the site was submerged for more than nine continuous hours
tot_sub_time_hrs	**Total time spent submerged (hrs) in the water**
mean_sub_time_hrs_day	Average time (hrs) submerged or in the water
min_sub_time_hrs_day	Minimum number of hours spent in the water in one day
max_sub_time_hrs_day	Maximum number of hours spent in the water in one day
max_cum_sub_hrs	Maximum cumulative time (hrs) spent in the water
sub_ratio	Ratio of total hours submerged to the total time deployed
avg_daily_light	Daily light intensity averaged across the duration of time deployed
max_tot_daily_light	Total accrued light intensity over the duration of deployment (sum of all light intensity)
cum_max_int_sub	**Sum of the maximum observed light intensity each day over the course of deployment when submerged**
avg_day_cum_int_sub	The average daily light intensity average over the duration of deployment while submerged
sub_tot_light	Total accrued light intensity while submerged
tot_time_sub_light	Total time (hrs) spent in the light and water
avg_daily_time_water_light	Average time spent in the water and light per day over the duration of deployment
tot_exp_night	Total time spent exposed each night
mean_temp	Average temperature over the duration of deployment
max_temp	Minimum observed temperature over deployment
min_temp	Maximum observed temperature over deployment
avg_temp_sub	**Average temperature while submerged**
avg_temp_exp	Average temperature while exposed
avg_resElv	Average reservoir elevation over the duration of deployment
min_resElv	Minimum reservoir elevation over the duration of deployment
max_resElv	Maximum reservoir elevation over the duration of deployment
avg_flow	Averaged flow over the duration of deployment
min_flow	Minimum flow over the duration of deployment
max_flow	Maximum flow over the duration of deployment
velocity	**The average velocity of two data points observed at the sampler during higher flows (i.e., >1000 m^3/s)**
substrate_score	
distance_to_thalweg	**The thalweg of MCR was determined as the center of the channel at a normal operating range of 400 m^3/s to 800 m^3/s. The distance to the thalweg was then measured perpendicular from each site to the constructed thalweg line using GIS.**
Rel. Abundance Cobble / Boulder	Relative abundance of cobble and boulder substrates
Site Class	An initial attempt was made to classify observed site level effects. Sites tested included Backwater (BW's), Bedrock (BR's), and Main stem large (upstream large substrate Reach 4), and Main stem small (downstream Reach 3 and Big Eddy).
Rel. Abundance of Silts, Sands (Fines), and Gravels	Relative abundance of silts, sands, and gravels in MCR
Embeddedness Score	Embeddedness was assigned a score of 1 (0-5%), 2 (5-25%, 3 (25-50%), 4 (50-75%) or 5 (75-100%)

2.3.3 Time Series and Artificial Sampler Assumptions

Community losses along the edges of the artificial substrate were assumed to be negligible. The effects of edges on the artificial substrate, such as the edge between tape adhesive and artificial Styrofoam sampling substrate, were considered in the same manner. 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, lost Styrofoam may have necessitated collecting a sampler 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 samples is still considered to be small when compared to each sample as a whole, reducing any potential data skewing effects that may result from invertebrate grazing. Further, it is probable that invertebrate distributions around plates were clumped, reducing the potential for effects across multiple replicates. Finally, the populations of invertebrates in MCR were low relative to other large rivers, and we have not fully investigated the power of our sample size.

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 have made this assumption, data collected suggests that artificial substrate types and natural substrates do respond differently within MCR (Schleppe et al., 2012). Future investigations may be required to accurately relate artificial samplers to natural substrates. The advantages of artificial substrates include consistent surface area/substrate characteristics, and capacity for sampling beyond wadeable depths.

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 due to sloughing from rock turnover, etc. were excluded from collection. For invertebrates, this means that we have not considered emigration or immigration from within or between sites and that specific operational patterns have not unduly affected any one community or result in changing densities of invertebrates due to mortality over the duration of deployment. For periphyton, it is noted that in cases when 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 due to slough or scraping upside down. For invertebrates, damaged samplers were not analyzed as these samplers were biased due to damage. 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 we do not suspect that it biased the results. It is acknowledged that substrate mobility and periphyton sloughing/drift are important components of periphyton production in MCR.

3.0 RESULTS

3.1 Biophysical Characteristics of the Middle Columbia River

3.1.1 Light and Temperature in Submerged areas of MCR

Overall water temperature ranges in Fall 2014 and Spring 2015 were similar to temperatures collected in 2010 through 2014 (Figure A-1). Numerous small spikes in temperature were observed, similar to other years. Reservoir conditions upstream are the most probable factor affecting the daily variation in observed temperature because downstream river temperatures were most dependent upon upstream reservoir conditions and the temperature/flow of tributaries (Larratt et al., 2011; Olson Russello et al., 2015). During the fall deployment period, temperatures usually vary between 10 to 15 ºC at the start and 5 to 7 ºC at the end. During the spring, initial river temperatures were cooler and ranged from 3 to 5 ºC at the start, and increased near the end of deployment to 8 to 10 ºC. Temperatures in the Jordan River were likely a contributing factor to the variation in temperature observed in Reach 3, but the extent of this effect has not been thoroughly investigated. Temperatures of exposed plates in the fall varied between periods of higher or lower air temperatures than the water, while in the spring air temperatures usually exceeded water temperatures.

Light intensity patterns during spring 2015 were similar to 2010 – 2014. In the turbulent, low turbidity MCR flows, light intensity on submerged samplers increased from deep sites at T1 locations to shallow sites at T6 locations in the fall (Figure A-2) and spring (Figure A-3). When samplers were in shallow water, they received more energy to support periphyton production, but these sites were also most likely to be exposed during the variable operating regime. Peak light intensities occur around noon, a period when flows are usually high. Light intensities were substantially greater when samplers were exposed, and were highest at the T6 locations where exposure was the most frequent. Fall light intensities were less than half of those observed during spring deployment due to proximity to the solstice. Results from the fall of 2014 were unchanged from the mean of earlier years, with the possible exception of the shallowest T6 position because Reach 3 was backwatered through the fall 2014 deployment (Figure A-2). Spring light intensities were similar to previous years (Figure A-3).

Figures A-4 and A-5 present the fall and spring light logger data when the samplers were exposed. They show the expected reception of far more light than was received during the water-covered periods, and the greater available light in the spring. The differences between the results at the various transect positions would reflect a combination of aspect, riverbank shading and periphyton growth on the sensors.

3.1.2 Pattern of Flow in MCR

Several features in the MCR flow regime during the study period directly influenced productivity. The following key elements are presented in approximate chronological order:

- Minimum flows of 142 m^3s were maintained from 2011 onwards (Schleppe et al., 2013, for analysis of 2011 and 2012 data).

- 2011 and 2012 were extremely high water years resulting from a combination of higher than normal snowpack and possibly higher discharge from REV 5. Small morphological and biological substrate changes were observed. For instance, in 2010 there was a noticeable fungal/bacterial black coloration on substrates in Reach 4, 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 and 2012. The frequency of these events was greater in 2012 than 2011, 2013, 2014. 2015.
- 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 a.m. until 7 p.m. At all other times, flows were either ramping up or down from high or low flow periods (Figure A-6).
- High variability in high, low, and ramping flow periods was observed between years and seasons. Daily flow patterns were similar to previous years in spring and fall 2013, with the exception that daily high flows were lower (<100 m^3/sec difference) than what had been observed in 2007 – 2012 (Figure A-6). In spring 2015, the flows were slightly higher than average, and were slightly lower than average in fall 2014.
- The magnitude of flows in the fall of 2014 and 2015 were most similar to 2007-2010 and 2013, which were lower flow years than 2011 or 2012. Samplers deployed at deep sites (T1) were usually submerged at depths of 4 to 7 m during the day, whereas sites at T6 were only submerged in approximately 1 m of water during the day during 2014, compared to 2011-2012 when depths were 6 to 8 m at deep sites and 2 to 3 m at T6 during the daytime.
- The magnitude of flows in spring 2015 was relatively high. This resulted in slightly deeper depths at T1 locations (5 to 8 m) and 2 to 3 m at T6 locations.
- The Arrow Lakes Reservoir (ALR) elevation can result in extensive backwatering of Reach 3 from early June through October, and can extend into Reach 4 during the summer months (Figure A-7). Backwatering effects have been considered through the submergence variables, which do not distinguish between submergence due to backwatering and submergence due to flows in the model analyses. During 2014, backwatering occurred in Reach 3 throughout the fall deployment period so that Site 5 and Site 6 upper varial zone samplers were water-covered continuously. Benthic production benefitted from the water cover and below average flows. During 2015, Arrow Reservoir was at very low levels, and backwatering was reduced.

Comparing the 2014 fall and 2015 spring flows to the corresponding season pre and post implementation of minimum flows, the 2014 fall was similar to the pre minimum flows and the 2015 spring was similar to post minimum flows with high flows in the early morning. It appears that the 2014 fall flows tended to be lower than the average flows post implementation of minimum flows. Spring 2015 was similar to spring data from previous years. As this is a hydro-peaking facility, it is hard to generalize flow patterns (e.g. daily or weekly).

3.2 Periphyton

3.2.1 Overview of MCR Periphyton Biofilms

Periphyton consists of two broad groups of micro-organisms, photosynthetic algae and bacteria, and non-photosynthetic bacteria and fungi. Algal periphyton production only occurs while substrates are submerged and exposed to sunlight, while the bacterial biofilm component also grows in the dark (Lear et al. 2009). For both components, growth in MCR slowed dramatically and mortality progressively increased during periods of desiccation. Heterotrophic bacteria counts on the MCR artificial substrates deployed for 44-47 days during fall were relatively low compared to other large North American rivers at 0.2 – 5 $x10^6$ colony forming unit (CFU)/cm^2. These low counts likely reflect repeated desiccation (Schleppe et al. 2012).

In addition to the grown-in-place MCR periphyton, algae drifting in the river deposit on and contribute to periphyton productivity in MCR. Drift of viable phytoplankton cells originate from upstream Revelstoke Reservoir, and to a lesser extent, from Arrow Lakes Reservoir during backwatering. Many reservoir algae are physically distinct from true periphyton algae, while others can grow in both standing and flowing environments. These cells adhered to existing periphyton and at times, significantly augmented local productivity. Eight taxa commonly seen in MCR periphyton grow only in standing water (Table 3-1).

3.2.2 Yearly Comparisons of Periphyton Algae Sampling

The dominant diatom species in MCR were either rapid colonizing diatoms with firm attachment strategies, or drift species from Revelstoke Reservoir that adhered to the periphyton biofilm. Like in most large rivers, MCR species were dominated by diatoms representing between 82 and 98% 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 84% of the fall biovolume and 89% of the spring biovolume. Green algae accounted for 11% in the fall with large filamentous species, and 9% 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 0.8% in the fall to 1.2% in the spring. Although cyanobacteria were functionally and numerically important, they only accounted 0.1% of total biovolume in the fall and increased to 0.5% under spring conditions that favoured species with rapid reproduction rates. The resultant growth patterns are visible in Figure 3-1, where spring has less growth than fall, and R4 has less growth than R3. In both seasons, diatoms predominate and the contributions made by the broad algae types were consistent, resulting in no biologically significant difference in periphyton community composition.

Figure 3-1: Examples of spring and fall incubated Styrofoam from MCR Reach 4 and Reach 3, comparing mainstem sites, all with cobble /sand substrates. The increased periphyton growth on the upper varial zone (T5,T6) of Reach 3 (disks were dark with growth) over Reach 4 (disks remained lighter), results from increased submergence and subsequent growth in part due to Arrow Lakes Reservoir backwatering.

The taxonomic structure of all river periphyton communities displays a tendency for predominance by a small number of taxa. In 2011 to 2015, the range of river habitats investigated was expanded to include backwater, Big Eddy and bedrock, but many of the same species occurred as in mainstem sites. Over the years of study, ten dominant taxa, accounted for 81–99% of abundance (87-91 % of total biovolume) in the fall and 81–90% of abundance (86-92 % of biovolume) in the spring. The ten dominant taxa distribution was typical in fall 2014 and in spring 2015, accounting for 88% of abundance and 89-91% of biovolume.

The donation of Revelstoke Reservoir diatoms to MCR periphyton was highly variable from year to year, and will relate to production dynamics within the reservoir versus the timing of releases. Taxa that occurred in mid-river drift samples and therefore were donated by Revelstoke Reservoir accounted for 40-70% of biovolume in fall samples and 20-60% of biovolume in spring samples to date. Examples of dominant species are provided in Table 3-1. They include limnoplanktonic species that can only function suspended in the water column (e.g. *Asterionella*) but persist after they become snared on MCR periphyton, and those that can reproduce after attachment to the periphyton (e.g. *Tabellaria*). Interestingly, most of the limnoplanktonic types were only found in mainstem samples and not in the backwater and Big Eddy samples. This may relate to greater exposure to drifting algae along the mainstem. Similarly, fall R4 samples had 34% more planktonic drift taxa than R3 samples and spring 2015 samples had 43% more in R4 over R3 because the reservoir algae cells progressively settle out.

There were seasonal shifts in the dominant periphyton taxa in MCR, likely in response to water temperature, freezing conditions and flows. In all spring samples, the dominant diatoms included *Diatoma tenue, Achnanthidium minutissima* and *Synedra ulna* (adhering variety) along with large concentrations of rapidly reproducing single-celled blue-green and green algae. In spring 2015, *Didymo* and *Cladophora* were more abundant than in the preceding three spring sample sets and this may correspond to warmer water in 2015. To date, spring samples had lower species diversity of 8 (T6) to 26 (T2) species/sample compared to fall samples at 11 (T6) to 31 (T2) species/sample. In fall samples, *Achnanthidium minutissima*, *Tabellaria fenestrata, Diatoma tenue* and *Synedra spp.* were dominant, and there was a greater contribution made by filamentous green algae, particularly in fall 2014. Although both seasons may show trends in periphyton community structure, they are not statistically discernible in the current data set.

Table 3-1: Range of biovolumes in MCR periphyton that are also phytoplankton taxa found in Revelstoke Reservoir and found in MCR drift samples, 2007 – 2015

Revelstoke Reservoir Taxa	Typical Growth Habit	% of periphyton biovolume in MCR		Found outside of mainstem
		Fall	Spring	
Ankistrodesmus falcatus	limnoplanktonic	0 - <0.1	0	No
Asterionella formosa	limnoplanktonic	0 - 47	0 - <0.1	No
Diatoma tenue var elongatum	planktonic	2 - 18	12 - 16	Yes
Fragilariforma spp.	limnoplanktonic	0 - 12	0.4 - 3	No
Fragilaria crotonensis	limnoplanktonic	0.1 – 1.4	0 – 0.1	No
Synedra acus, (large spp.)	limnoplanktonic	0.1 - 9	0.1 – 5	No
Synedra nana	limnoplanktonic	0 – 0.2	0 – 0.4	No
Synedra ulna (large sp.)	limnoplanktonic	0 - 2	0.5 – 1.2	Yes
Tabellaria fenestrata	planktonic or attached	2 - 12	0.3 - 1	Yes
Tabellaria flocculosa	planktonic or attached	3.5 – 4.1	0.2 – 0.3	Yes

Throughout MCR, 2015 spring samples showed a typical species assemblage but at higher cell density and much higher chlorophyll-a than in earlier years (Figure 3-2). This increase was also reflected in time series chl-a and in both cases, may relate to warmer water temperatures. There was a stronger effect of water temperature evident in the spring statistical models than in the fall models.

Light intensity data from spring 2015 was lower than spring 2011 or 2012, indicating greater water depth on MCR substrates in that year. Samples were not collected in spring 2014.

Generally, the R3 habitat is more productive than R4 and spring 2015 was no exception, with 1.32 x 10^7 cells/cm^2 in R3 and 1.01x10^7 cells/cm^2 in R4. These changes were likely driven by increasing sand concentrations in the R3 habitat. Substrate changes between R4 and R3 were also reflected in shifts among periphyton dominants. For example, species that were either adherent, colony-forming, or 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.*).

The distribution of algae groups through the range of transect depths was consistent between years and seasons, with declining diatom density but increasing cyanobacteria and flagellates moving from the T1 to T6. When all biovolume measurements were compared to chlorophyll-a (chl-a) results, similar curves emerged (Figure 3-2). Average periphyton productivity decreased with increasing exposure as the sampler positions progress 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 Reach 4 because only a select 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 in excess of 9 hours experienced rapid periphyton).

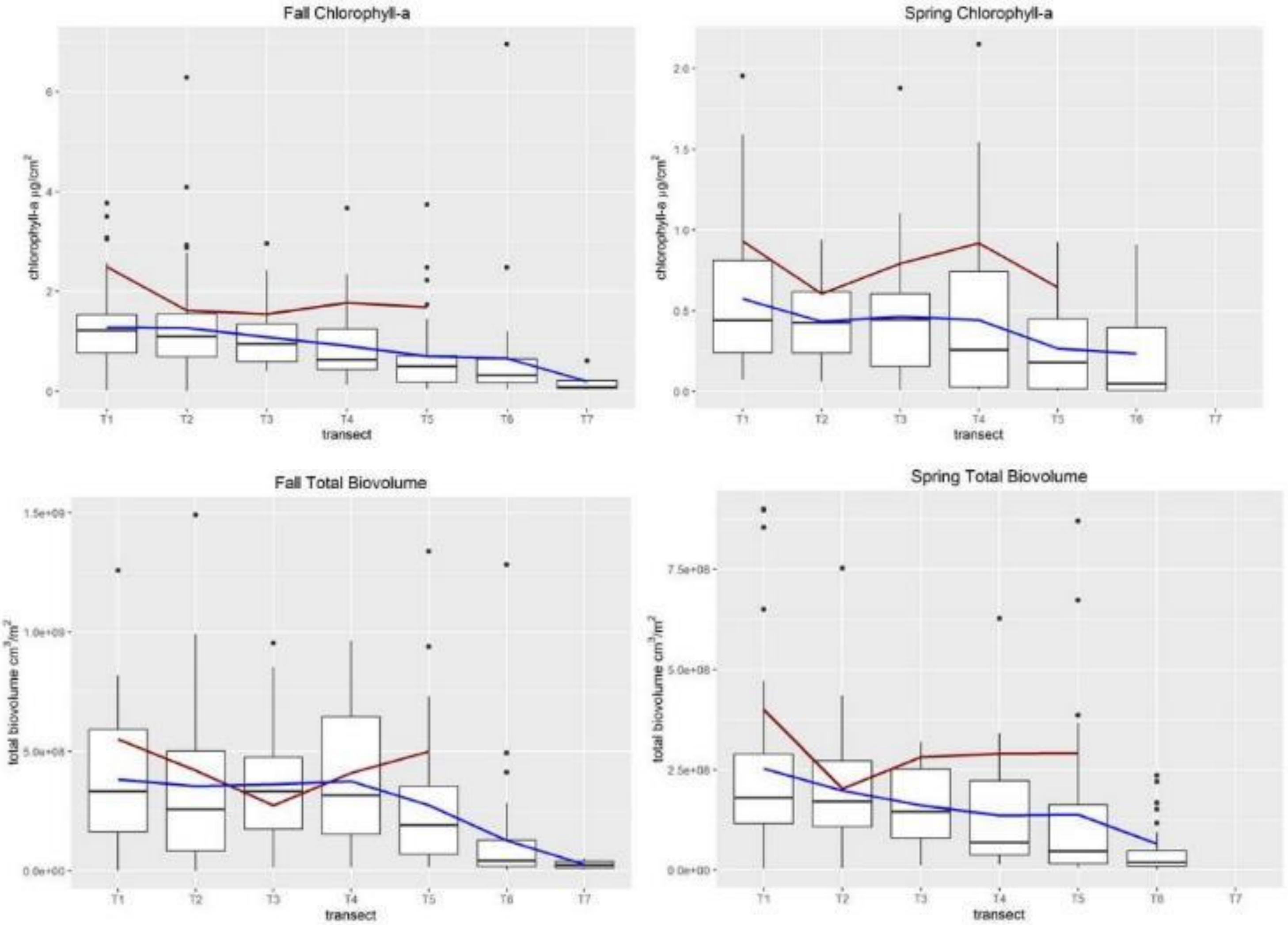


Figure 3-2: Total biovolume of MCR periphyton and chlorophyll-a in spring for 2010 to 2015 and fall for 2010 to 2014 by sampler location (T1 deepest in thalweg to T7 shallowest on floodplain). The blue represents the mean of all years and the red represents the mean for fall 2014 and spring 2015

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. Most of the organic material at heterotrophic-dominated sites was decomposer microflora and non-viable organic materials such as dead diatoms, leaf litter and detritus.

There were seasonal shifts in the dominant periphyton taxa in MCR. In all spring samples, the dominant diatoms included *Achnanthidium minutissima*, *Diatoma tenue* and *Synedra ulna* along with large concentrations of rapidly reproducing single-celled green and blue-green algae. In fall samples, *Tabellaria fenestrata, Diatoma tenue* and *Synedra spp.* were consistently dominant diatoms. With all microflora taxa included, MCR had 5 - 52 species per sample. Among the true algae, mean taxa richness was 10 ± 2 to 23 ± 6 taxa in the fall and 12 ± 4 to 20 ± 4 in the spring (Digital Appendix B). This suggests that species richness in MCR was lower than is typical for large rivers (Table 4-1). When species richness is assessed by transect locations, spring samples had lower average species richness of 13 (T6) to 19 (T2) species/sample compared to fall samples at 15 (T6) to 23 (T2) species/sample. All of these results indicate that spring periphyton samples were less diverse than fall periphyton samples.

Collection of AFDW (volatile solids) commenced in 2010. AFDW provides an estimate of all organic components of the biofilm plus detritus. Average MCR ash-free dry weight (volatile solids) samples remained in the typical range for large rivers but with considerable variation from year to year. AFDW has averaged about 0.57 mg/cm^2 in both seasons, but with wider variation in the fall than the spring. With both seasons and all years combined, AFDW remained near 0.49-0.59 ± 0.31-0.53 mg/cm^2 from T1 through T4, and peaked (0.86 ± 2.77 mg/cm^2) at T5 before declining to 0.49 ± 0.47 mg/cm^2 at T6. In most years, T5 appears to be a zone of organic accumulation or decomposition. Variations from year to year are likely flow-driven and they highlight the volatility of conditions in MCR. Field observations of reduced black banding suggest a decline in heterotrophic members of the biofilm in years with longer inundation of the flood plain areas (T5, T6). They may become displaced by algae as periods of substrate submergence increase.

Periphyton summary statistics are provided for all eight fall sample periods in the digital Appendix B. The year with the highest mean abundance values was 2007, while the year with the lowest mean abundance was 2012. The lowest mean total biovolume and chl-a were also in 2012, while the year with the highest mean total biovolume and chl-a was 2014.

Spring periphyton growth metrics were stable and low. For years 2011-2013, mean periphyton abundance was similar. However, in 2015 mean was higher compared to previous years. Similarly, mean chl-a and biovolume were also higher in 2015 compared to 2011-2013. The cause of this increase is not known, but may relate to early warm spring weather in 2015. In all four spring sample periods, average species diversity metrics were stable at 0.71 – 0.81 (Simpson’s index) and at 13 – 21 individual taxa. Overall, spring means and spring maximums among growth metrics were usually lower compared to fall samples from the same year (2011, 2012, 2013).

Year-round implementation of 142 m^3/s minimum flows and full in-service operation of REV 5 began in the winter of 2010. While species diversity was unchanged after the flow regime change, periphyton growth metrics were 6-20% lower, with 2012 having the lowest periphyton metrics and the highest flows to date (Table 3-2). However, fall 2014 growth metrics were high, led by greater filamentous green algae growth that benefitted from less shear under stable, lower flows in the Reach 4 T2 zone. These important algae were also prevalent in the spring 2012 samples but were lower in 2013 and again in 2015.

These large algae are slow-growing and their growth in R4 T2-T4 zone may continue to slowly increase over the years since minimum flows were implemented. This further confirms that flow management exerts a powerful influence on the MCR periphyton community. The area covered by minimum flows may be acting as a species reservoir with distribution to periodically exposed substrates when flows ramp up. The drivers behind these shifts in periphyton metrics are addressed in the statistical modelling section 3.2.5.

Table 3-2: Range of periphyton metrics in MCR R4 and R3 by season, 2007 – 2015

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	7.10E+05	3.67E+08	1.01	0.499	17.2	0.695
2012	2.76E+05	1.11E+08	0.47	0.400	21.6	0.704
2011 – 2014	5.68E+05	3.45E+08	1.00	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 – 2015	3.46E+05	1.66E+08	0.41	0.56	17.6	0.78

All growth metrics were higher in Reach 3 than Reach 4 in both spring and fall seasons. For example, over 8 fall sampling sessions, chl-a measured 1.31 ± 1.16 ug/cm^2 chl-a in R3 and 0.76 ± 0.53 ug/cm^2 chl-a in R4. When all samples to date for both reaches are compared, R3 had 17% higher cell abundance, 16% more biomass and 46% higher chl-a, than R4 averages. Similarly, in the 4 spring samples sessions, R3 had 12% higher cell abundance, 5% more biomass and 46% higher chl-a, than R4 averages.

There was no observable difference in the Simpson's index (0.79) or species diversity (18-19) between reaches, and this finding was confirmed by statistical modelling (next section). There are numerous mechanisms that account for similarities in species distribution in large rivers such as MCR. These include backwatering and high flow events that can shield and move benthic species to new substrate locations. Additionally, the T1/T2 area that remained wetted by minimum flows, together with 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.

Elevated flows can generate water velocities in the thalweg in excess of 2 m/sec (Schleppe et al. 2013). Since 2012 was the highest flow year to date for fall, the growth metrics at T1 positions in 2012 were compared to other years (Table 3-3). As expected with higher flows, thalweg T1 periphyton abundance and biovolume dropped significantly in both reaches during the fall in high flow years, while the flow effect in the spring was subtle and not statistically significant. Overall water velocities would have been higher in the narrower Reach 4 channel, possibly accounting for the larger fall periphyton declines compared to the wider Reach 3 channel, which was frequently backwatered. Higher flow velocities can increase sloughing of periphyton mats, and the greater water depth also lowers light penetration to the substrates.

Table 3-3: Effects of flow conditions on average periphyton productivity in Reach 3 and Reach 4 in the Thalweg (T1) zone

	T1 in Fall of Year	Flow conditions	Abundance cells/cm^2	n #	Biovolume um^3/cm^2	n #
R3	2010,11,13,14	typical flows	6.17 ± 2.48 x10^5	17	3.07 ± 1.85 x10^8	17

	2012	very high flows	2.87 ± 4.65 x10^5	3	1.18 ± 2.04 x10^8	3
R4	2010,11,13,14	typical flows	7.48 ± 3.00 x10^5	15	5.15 ± 1.82 x10^8	15
	2012	very high flows	2.36 ± 1.25 x10^5	4	1.04 ± 0.08 x10^8	4
	T1 in Spring of Year	Flow conditions	Abundance cells/cm^2	n #	Biovolume um^3/cm^2	n #
R3	2011, 2013	typical flows	5.12 ± 2.20 x10^5	11	3.53 ± 1.21 x10^8	11
	2012 2015	very high flows	5.06 ± 2.47 x10^5	13	3.31 ± 2.21 x10^8	13
R4	2011,2013	typical flows	4.10 ± 2.50 x10^5	9	2.2 ± 1.84 x10^8	9
	2012 2015	very high flows	3.56 ± 1.31 x10^5	7	2.08 ± 1.27 x10^8	7

A final aspect of MCR flow regime affected by both BC Hydro releases and by watershed hydrology is backwatering by Arrow Lakes Reservoir (ALR). This seasonal water cover should reduce 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 drop out 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. 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). Again, this finding was confirmed by statistical modelling presented in the next section.

The Reach 3 upper varial zone is the most variable region for periphyton productivity in 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 backwatering, resulting in far greater periphyton growth throughout the R3 upper varial zone (Table 3-4). Another important influence on the R3 upper varial zone is high flows. Very high flows in 2012 apparently curtailed productivity, while in spring 2015, high flows with backwatering into R3 allowed moderate productivity. These effects of backwatering are accounted for in the statistical models because they consider duration and timing of submergence.

Table 3-4: Upper varial zone (T5,T6) periphyton productivity in R3, 2010 - 2015

Fall R3 T5 & T6 of year	Flow conditions	Abundance cells/cm^2	Biovolume um^3/cm^2	N #
2010 and 2011	typical flows and backwatering	4.2 ± 2.4 x10^5	3.2 ± 2.0 x10^8	12
2012	very high flows, backwatering	0.90 ± 0.33 x10^5	0.22 ± 0.074 x10^8	6

2013	average flows, no backwatering	3.0 ± 1.8 x10^5	0.96 ± 0.53 x10^8	6
2014	lower flows, continuous backwatering	7.3 ± 3.4 x10^5	7.65 ± 3.5 x10^8	6

Spring R3 T5 & T6 of year	Flow conditions	Abundance cells/cm^2	Biovolume um^3/cm^2	N #
2011	typical flows and backwatering	4.2 ± 2.4 x10^5	3.2 ± 2.0 x10^8	6
2012	very high flows, backwatering	0.90 ± 0.33 x10^5	0.22 ± 0.074 x10^8	6
2013	average flows, no backwatering	3.0 ± 1.8 x10^5	0.96 ± 0.53 x10^8	6
2015	high flows, backwatering	2.01 ± 1.0 x10^5	1.03 ± 0.93 x10^8	6

3.2.3 Periphyton Accrual

Time series chlorophyll-a data have been collected since 2010, and it was selected as the measure of periphyton productivity to assess accrual because it is a standard measure of production, it is available for the longest period, and it is highly correlated (R^2 >0.8) with abundance and biovolume (Schleppe et al. 2011).

A repeated measures ANOVA was used to analyze chlorophyll-a accrual rates at the T1 and T3 locations within the channel for data across all years during the fall and spring (Table 3-5). The combined effects of transect, deployment duration and year explain a greater amount of variation for chlorophyll-a accrual in the fall compared to the spring (R^2 = 0.55 compared to R^2=0.25). Chlorophyll-a accrual rates were also greater in permanently submerged locations (T1) than in varial zone locations (T3) in both spring and fall (Figure 3-3), with some variation between years. Growth rates during the first few weeks were similar between permanently submerged and varial zone areas, but by the end of deployment, permanently submerged locations had achieved a greater quantity of chl-a. These data suggest that periphyton growth was linked to submergence patterns in both spring and fall.

Generally, the permanently submerged samplers at T1 benefit from continuous submergence, while the T3 samplers experienced greater substrate exposure and likely increased rates of mortality that slow accrual. Spring and fall chl-a accrual at T1 locations did not show a plateau typical of peak biomass after the 42 to 51 day deployment period. Rather, chl-a may continue to climb with incubation times exceeding 50 days. This is supported by very high chl-a and biovolume found on samplers that were incubated in MCR for 6 months (Schleppe et al., 2011).

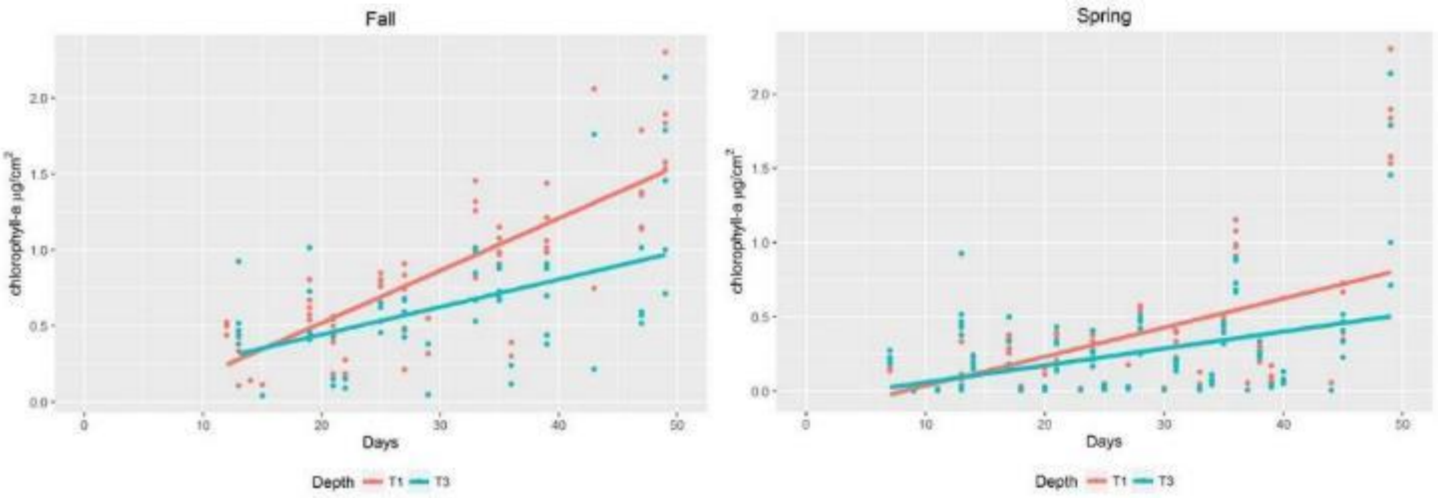


Figure 3-3: Chlorophyll-a accrual concentrations for transects T1 and T3 compared to days deployed in MCR for spring and fall for years 2010 - 2015. Note that the best fit regression lines have reduced predictive capability when submergence periods are less than 10 days and should be considered negligible (i.e., at time 0 productivity is 0).

Table 3-5: Summary of repeated measures ANOVA of chlorophyll-a accrual for all years in MCR. *Days in* is the deployment duration, independent of submergence. For the fall and spring repeated measures ANOVA model, the R^2 was 0.55 and 0.25, respectively.

Season	Factor	Sum	DF	F-Value	P-Values
Fall	Transect	1.10	2	11.06	0.001187
	Days In	11.95	2	120.14	1.42E-19
	Year	1.61	1	16.21	0.000102
	Transect : Days In	0.96	1	9.69	0.00234
	Transect : Year	0.019	1	0.20	0.658323
	Days In : Year	0.009	1	0.09	0.762715
	Transect : Days In :	0.019	1	0.19	0.661621
	Residuals	11.44	115		
Spring	Transect	2.00	1	18.02	3.33E-05
	Days In	0.59	2	5.28	0.022651
	Year	5.61	2	50.51	2E-11
	Transect : Days In	0.03	1	0.23	0.635571
	Transect : Year	0.11	1	0.95	0.331947
	Days In : Year	0.54	1	4.90	0.027975
	Transect : Days In :	.03	1	0.29	0.590576
	Residuals	22.43	202		

When chlorophyll-a accrual (time series) data to date are considered together, accrual rates were most affected by the flow regime during the preceding 30 to 70 days, with the most recent event tending to exert the greatest influence on overall productivity. Catastrophic events where mortalities exceeded 50% have been detected on several occasions over the duration of the assessment in periods of three or four days exposure during warmer weather. The periphyton standing crop drops to low levels after these events, essentially "resetting" productivity and community structure to a re-colonizing state of succession. These events occur most often during exposure periods that exceed 72 hours or last until channel substrate and interstitial spaces between the substrate is 100% dry, when temperatures are either above 20 °C or below -5 °C. Catastrophic events such as these have a far greater effect on short-term periphyton productivity than physical processes such as velocity or light intensity.

3.2.4 Periphyton Community Groupings

Community analyses of the full 2007 – 2015 database were completed at the genus level, because species under the same genus have the same environmental requirements (Hill et al, 2001). The NMDS analysis provided a good representation of the periphyton community with a stress index of 0.236. There was high inter-annual and seasonal variation with potential effects of implementation of minimum flow, operational flow patterns, plus some influence of changing taxonomists in 2010 (via a year effect) (Table 3-6). Many of these factors disappear when the data is analyzed at higher taxonomic levels. These results infer that large-scale shifts in periphyton communities did not occur. Rather, the data indicate that all differences were confined to shifts at lower taxonomic levels and were more typical of annual species shifts expected in all lotic environments as opposed to a direct periphyton community response to minimum flows.

Given the confounding effects of the change of the taxonomist and natural inter-annual variability on periphyton community, it cannot be concluded whether annual operations are independently affecting periphtyon community at the genus level. However, there is potential that annual operations are affecting periphyton community by the following mechanisms: creation of specific habitat conditions that favoured different taxa and/or because algal donation from Revelstoke Reservoir changed by year and by season.

For example, *Asterionella* was very common prior to 2010, but was rare in recent years and it has been identified as a key species affecting community similarity. *Asterionella* is exclusively a reservoir phytoplankton and can "bloom" in some seasons, and it can remain viable on a periphyton mat. Other phytoplankton exclusively from the reservoir *(e.g. Ankistrodesmus* and *Fragilariforma)* were also important. Other examples of taxa important to periphyton community metrics include small cyanobacteria that are fast growing taxa, and they appeared to influence some of the annual groups as well.

A de-trended correspondence analysis (DCA) suggests that annual variation is an important gradient (data not presented).

Table 3-6: Summary of the effects of year, season , flow condition, and transect on periphyton communities in the MCR

	Genus		
Factor	R Stat	F Stat	p val.
year	0.10	52.58	0.001
season	0.05	23.53	0.001
transect	0.06	6.17	0.001
Flow	0.19	52.40	0.001

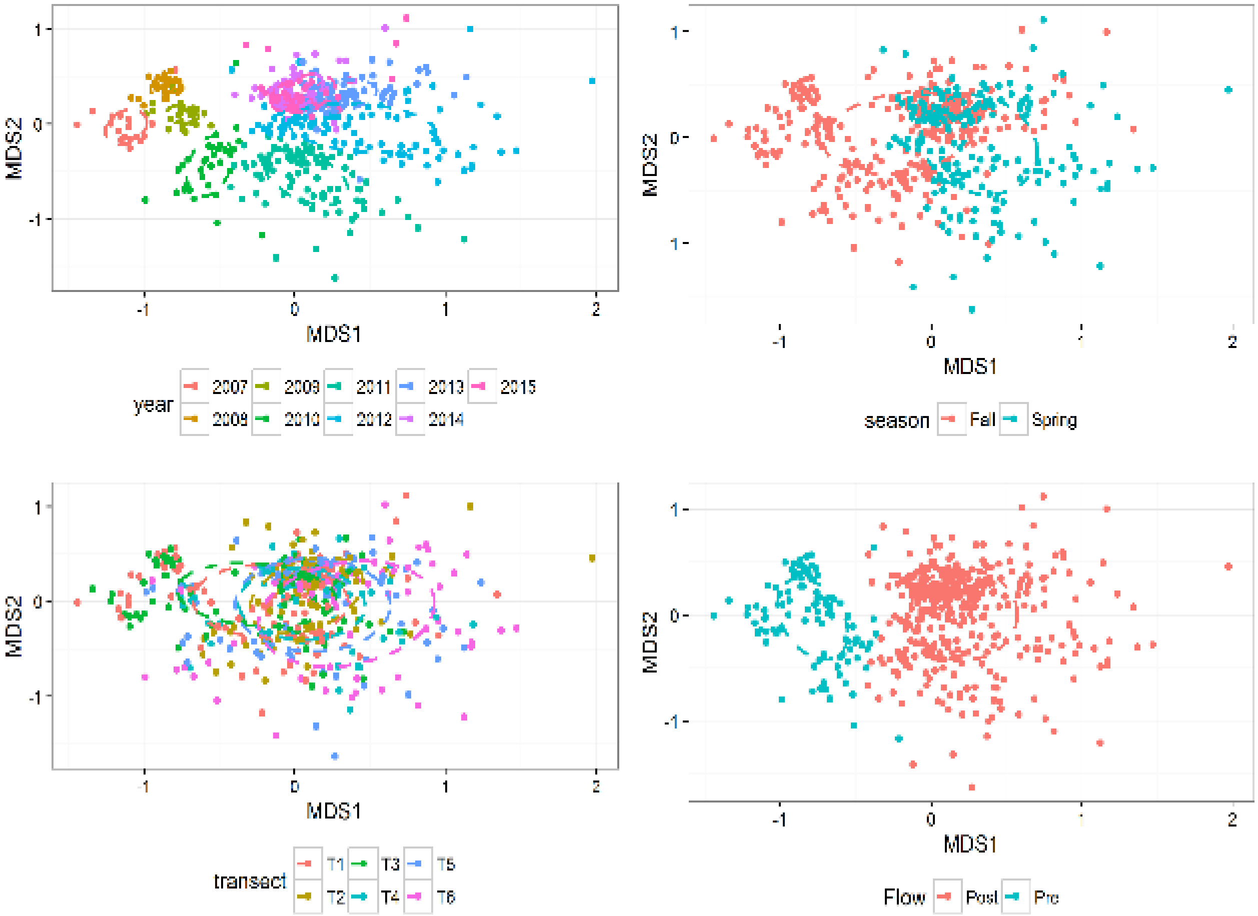


Figure 3-4: NMDS of periphyton abundance at the genus level, grouped by year, by season, by transect, and by implementation of minimum flowsfor data collected between 2007 and 2015. These figures suggest that there were distinct differences between years / flow periods, and smaller differences between seasons, and transect locations.

3.2.5 Periphyton Production Models

Results of periphyton production models are considered in a broad sense below. The intent is to understand the underlying processes that affect periphyton production rather than explain specific results of any given production response within a given season. This approach is advantageous because it considers multiple production responses (n=6), and facilitates future development of spatial models that can predict productivity under different flow scenarios.

A summary of the model averaged results are found in Table A-1.

3.2.5.1 Fall

This section considers the entire river cross section for transects location spanning the thalweg to the upper varial zone in the fall, while the next section considers only the spring periods. Model averaging clarifies the influence of the key drivers of periphyton production in the MCR system.

Several significant trends were observed across measures of periphyton production, most notably that production (abundance and biovolume) increased with increasing daytime submergence, and increasing cumulative light intensity (Figures 3-5 and 3-6). Periphyton abundance increased up to approximately 600 hours of submergence and then stabilized until approximately 1000 hours. After 1000 hours of submergence, it appears that there may be a second growth period, likely indicative of more stable submergence patterns. Additionally, substrate size may contribute to an increase in abundance but this trend is not as strong as submergence (Figure 3-5). Substrate exposure apparently increases periphyton mortality and reduces overall species richness.

Interestingly, preferred periphyton forage for invertebrates was most strongly associated with higher water temperatures and distance from the thalweg (Figure 3-6). The distance to the center of the channel also appeared to influence species distinctiveness and Simpson's index of diversity, where a more diverse assemblage was observed at sites farther from the center of the channel. This is likely the result of increased diversity observed on backwater sites, which are far from the thalweg and have high diversity because both diatoms tolerant of high velocities settling out from the drift and those species favouring calmer water were both prevalent.

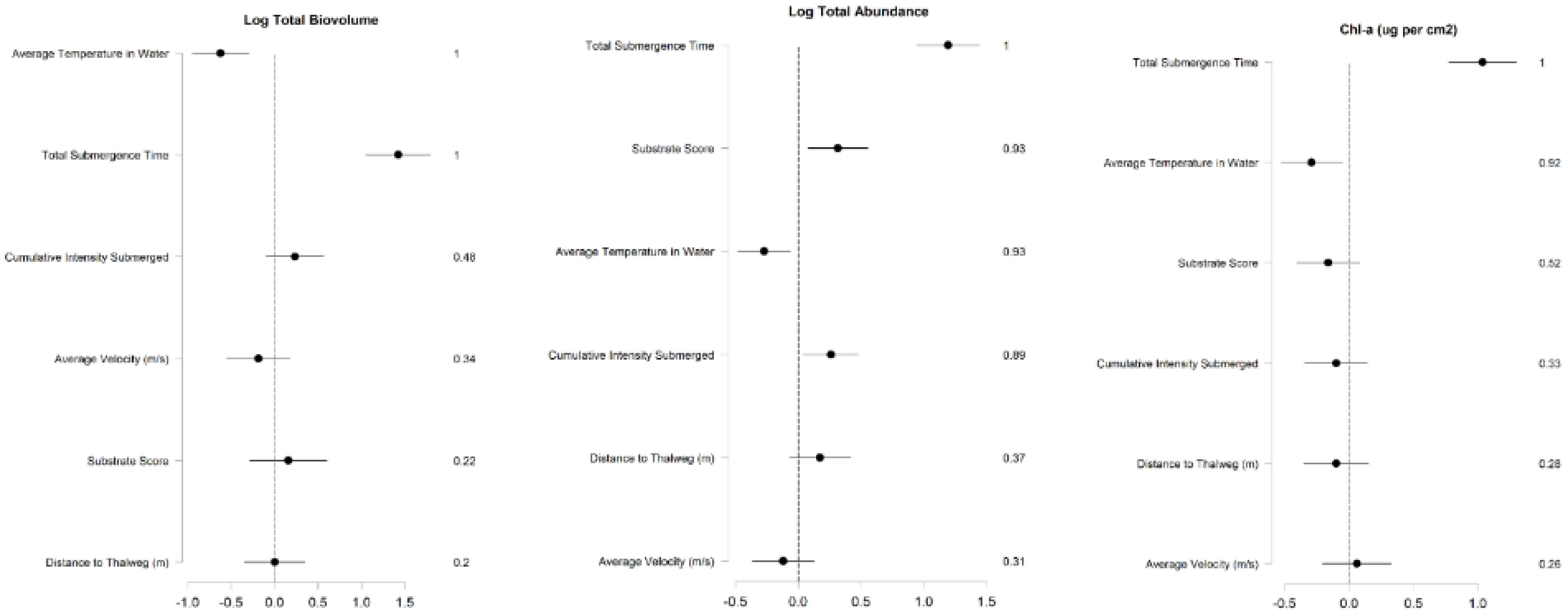


Figure 3-5: **Model averaged periphyton parameter coefficients and 95% confidence limits from model averaged linear mixed effects models for each given dependent variable. Each plot represents the probability of a given predictor, described on the left side of the plot, to be in the best AIC model (this probability is described by the RVI value on the right side of the plot). The predictors are also sorted based on this probability. Predictors have been standardized to allow direct comparison of coefficients (x-axis). The corresponding coefficient and its 95% confidence interval are represented on the plot. Those variables with 95% confidence intervals overlapping zero are considered of low significance as the direction of their effects are inconsistent among models.**

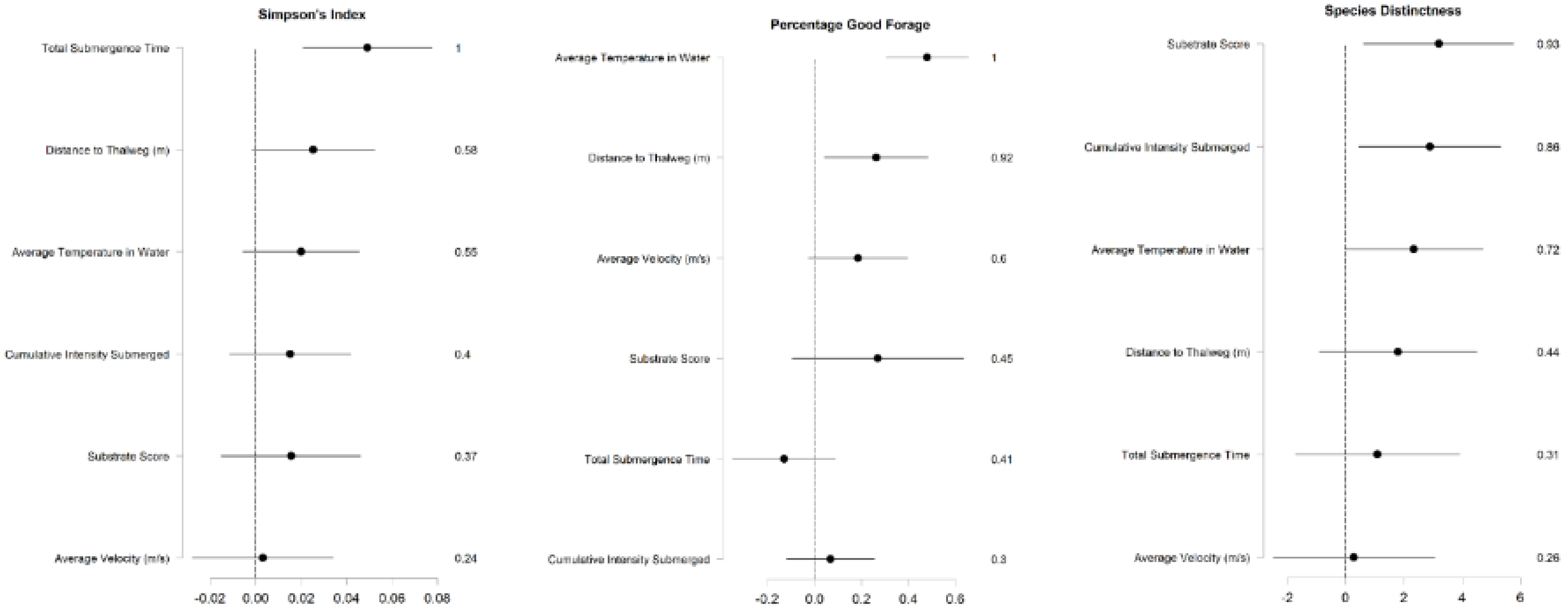


Figure 3-6: **Model averaged periphyton parameter coefficients and 95% confidence limits from model averaged linear mixed effects models for each given dependent variable. Each plot represents the probability of a given predictor, described on the left side of the plot, to be in the best AIC model (this probability is described by the RVI value on the right side of the plot). The predictors are also sorted based on this probability. Predictors have been standardized to allow direct comparison of coefficients (x-axis). The corresponding coefficient and its 95% confidence interval are represented on the plot. Those variables with 95% confidence intervals overlapping zero are considered of low significance as the direction of their effects are inconsistent among models.**

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3.2.5.2 Spring

Several significant trends were observed across all measures of spring periphyton production, most notably that production increased with increasing submergence in all production metrics. Like the fall results, spring periphyton abundance increased until approximately 600 hours of submergence and then stabilized until approximately 1000 hours. After 1000 hours of submergence, it appears that there may be a second growth period, likely indicative of more stable submergence patterns but this trend is not as clear in the spring as it is in the fall. Interesting, and different from the fall, abundance and biovolume decreased with cumulative light intensity, which is possibly an artifact of submergence, where varial sites have increasing light intensity in shallow waters during daytime submergence but death associated with exposure is resulting in reduced production (Figures 3-7 and 3-8). During the spring, species distinctiveness decreased with velocity and submergence time, and the percentage of good forage also decreased with increasing submergence. Simpson's index increased with increasing submergence and substrate size (Figure 3-8). The quantity of good available periphyton forage appeared to increase with increasing water temperatures, suggesting that annual trends in spring periphyton communities are influenced by temperatures increases, and are therefore affected by the timing of deployment (Figure 3-8). Since there are fewer data points available for the spring, determination of specific trends is more challenging. The most consistent trend appears to be the relationship between increasing measures of production and increasing submergence.

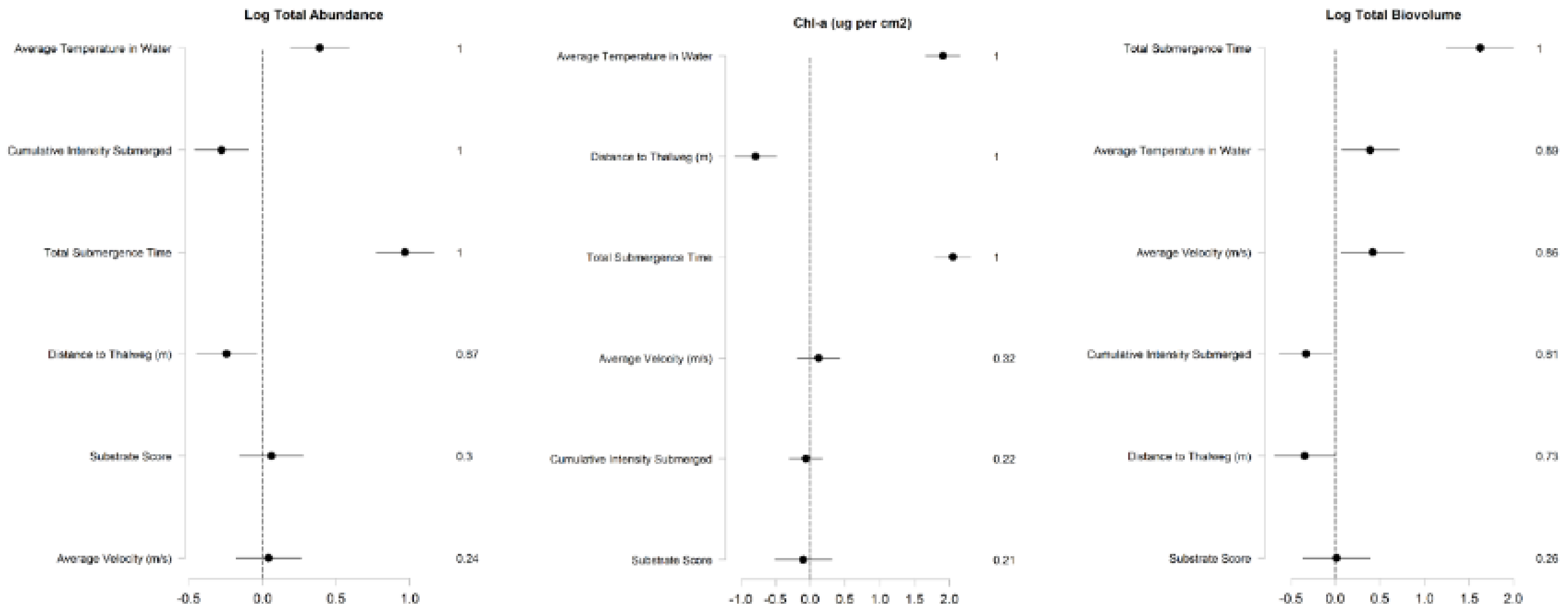

Figure 3-7: **Model averaged periphyton parameter coefficients and 95% confidence limits from model averaged linear mixed effects models for each given dependent variable. Each plot represents the probability of a given predictor, described on the left side of the plot, to be in the best AIC model (this probability is described by the RVI value on the right side of the plot). The predictors are also sorted based on this probability. Predictors have been standardized to allow direct comparison of coefficients (x-axis). The corresponding coefficient and its 95% confidence interval are represented on the plot. Those variables with 95% confidence intervals overlapping zero are considered of low significance as the direction of their effects are inconsistent among models.**

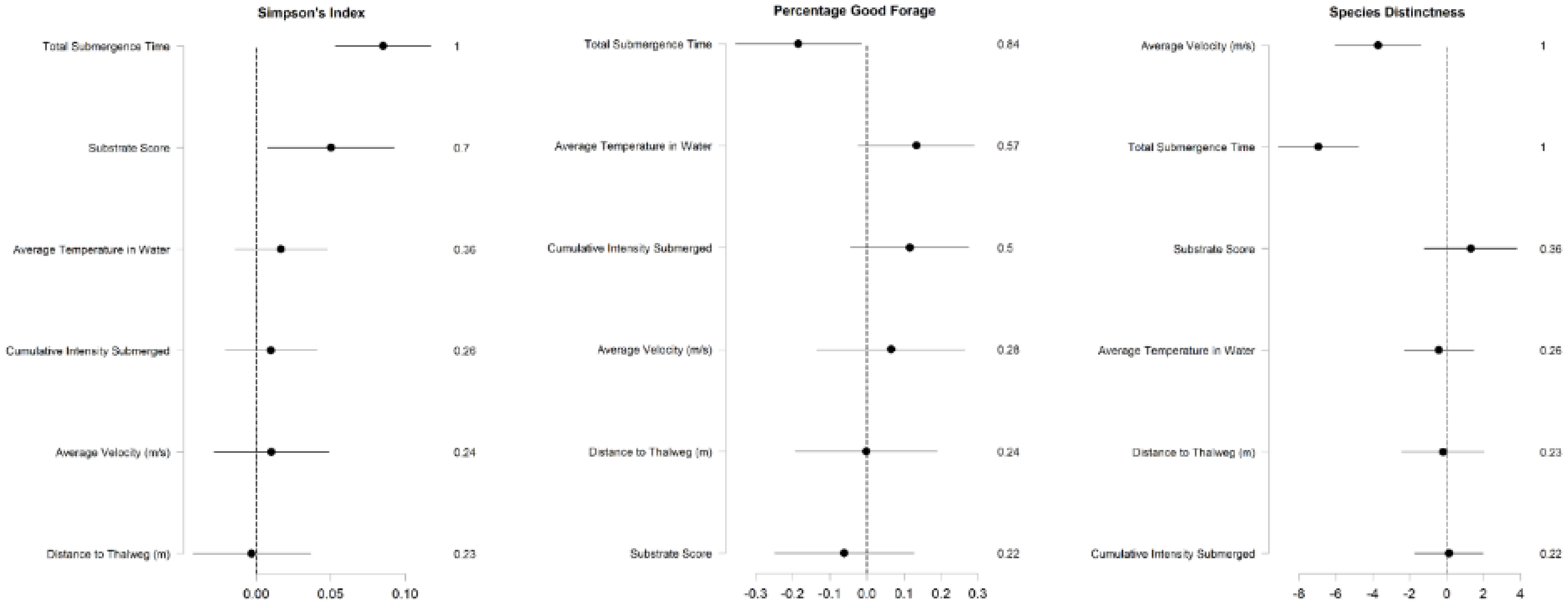

Figure 3-8: **Model averaged periphyton parameter coefficients and 95% confidence limits from model averaged linear mixed effects models0 for each given dependent variable. Each plot represents the probability of a given predictor, described on the left side of the plot, to be in the best AIC model (this probability is described by the RVI value on the right side of the plot). The predictors are also sorted based on this probability. Predictors have been standardized to allow direct comparison of coefficients (x-axis). The corresponding coefficient and its 95% confidence interval are represented on the plot. Those variables with 95% confidence intervals overlapping zero are considered of low significance as the direction of their effects are inconsistent among models.**

3.3 Benthic Invertebrates

3.3.1 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). Generally, members of *Hydra* sp., Chironomids, and small Tubificid worms were the most abundant, accounting for up to 75% of the total abundance in all years and seasons studied. Although not as numerically abundant, members of the EPT taxonomic groups relative biomass was high compared to their contribution to relative abundance (Appendix B). These trends were consistently observed in both spring and fall. In most samples, approximately 10 species made up over 90% of the total abundance or biomass 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. Standard deviations of abundance and biomass within a given year/season are consistently higher than the mean due to high levels of variation within the invertebrate data. Species richness also varied among years with the lowest values in fall months occurring in 2009-2010, and highest in sampling periods of 2011 and 2015. Species richness also appeared to be slightly greater in R3 than R4 in most years and was low and stable among years in the spring (Appendix B).

Benthic invertebrates were usually more abundant in the fall than in spring, and effects of flow, season, or year were not readily apparent. Chironomidae were much more prevalent than EPT taxa, and accounted for 30-75% of the total abundance in the spring or fall at any site. EPT taxa were most prevalent in 2013-2014, when they accounted for 2-5% of the total abundance in the fall and spring. Greater abundance of EPT taxa corresponded with years of higher average flow and associated increased submergence of substrates within varial zones. Although the Jordan River was not sampled in 2013 - 2015, it is considered an important source of invertebrates within Reach 3 and may partially explain the increased diversity observed in R3 sites.

Abundance, biomass, species richness, 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 (T5-T7). Contrary to these trends, Simpson’s indices were relatively consistent across all portions of the channel, and these indices are less prone to variations in abundance than more direct measures such as biomass.

3.3.2 Benthic Invertebrate Community Groupings

Community analyses of the full 2007 – 2015 dataset were completed at the Genus level. The stress index for the NMDS analysis was 0.227, which provided a good representation of the community data. Similar to previous years, data at the Genus level suggests that year, and the implementation of minimum flows are important determinants of the invertebrate community (Table 3-7, Figure 3-9). Season and patterns of submergence (transect) also appeared to affect the invertebrate community but their effects are not as pronounced.

Similar to periphyton, there was high inter-annual and seasonal variation. These seasonal and annual differences in weather conditions likely account for some of the variation, with reservoir operations also playing a role. The degree of influence of both of these factors, as they create a synergistic effect, is difficult to quantify.

In 2014, an attempt was made to determine which taxa were driving the invertebrate community variation between sites, years and transects. Using the function Envfit (Oksanen, 2015), taxa that significantly contributed to the overall variation (i.e., those with $r^2 > 0.03$) were determined. Trichopteran (Family *Leptoceridae*, Genus *Ceraclea sp*.) was the only significant taxon that is also considered important food for fish. This taxon exhibited high annual, seasonal and site variability. Other significant taxa were also identified, but they have lower food value for fish.

Table 3-7: Summary of the effects of year, season, reach, flow condition, and transect on benthic invertebrate communities in the MCR

		Order	
Factor	R Stat	F Stat	p val.
year	0.07	34.20	0.001
season	0.04	21.31	0.001
transect	0.04	3.82	0.001
flow	0.07	33.05	0.001

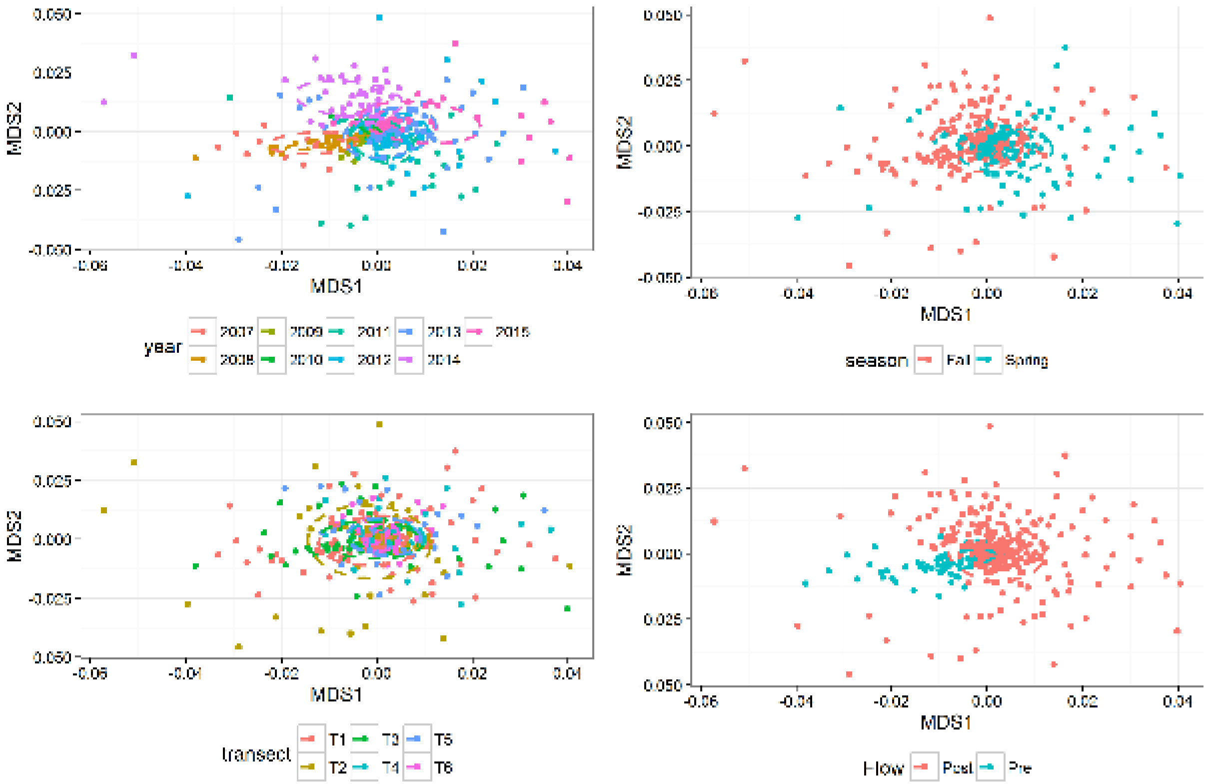

Figure 3-9: **NMDS of benthic abundance at the Genus level grouped by year, season, transect (T1- deep to T6-shallow), and implementation of minimum flows for data collected between 2007 and 2015.**

3.3.3 Benthic Invertebrate Production Models

The results of invertebrate production models are similar to that of periphyton. The study intent is to understand the underlying processes that affect invertebrate production rather than explain specific results of any given production response. This approach is advantageous because it allows evaluation of multiple production responses, and facilitates future development of spatial models that can predict productivity under different flow scenarios.

A summary of the model averaged results is found in Table A-2.

3.3.3.1 Fall

Production (abundance, biomass, EPT+D) increased with increasing daytime submergence (Figures 3-10 and 3-11). The biomass of EPT + Dipterans increased at a consistent linear rate for the first 300 to 750 hours and then appeared to increase exponentially at 750 to 1000 hours of submergence. Abundance and biomass also appeared to decrease with decreasing substrate score. This trend was driven by communities at bedrock locations, while the invertebrate communities were more similar in other areas. The HBI increased with both temperature and possibly increasing distance from the thalweg, likely the result of a combination of increasing exposure and a higher predominance of tolerant taxa such as dipterans found at the backwater and warmer locations or sites that are periodically exposed. Most other explanatory variables were not as important or reliable predictors of invertebrate production in the fall.

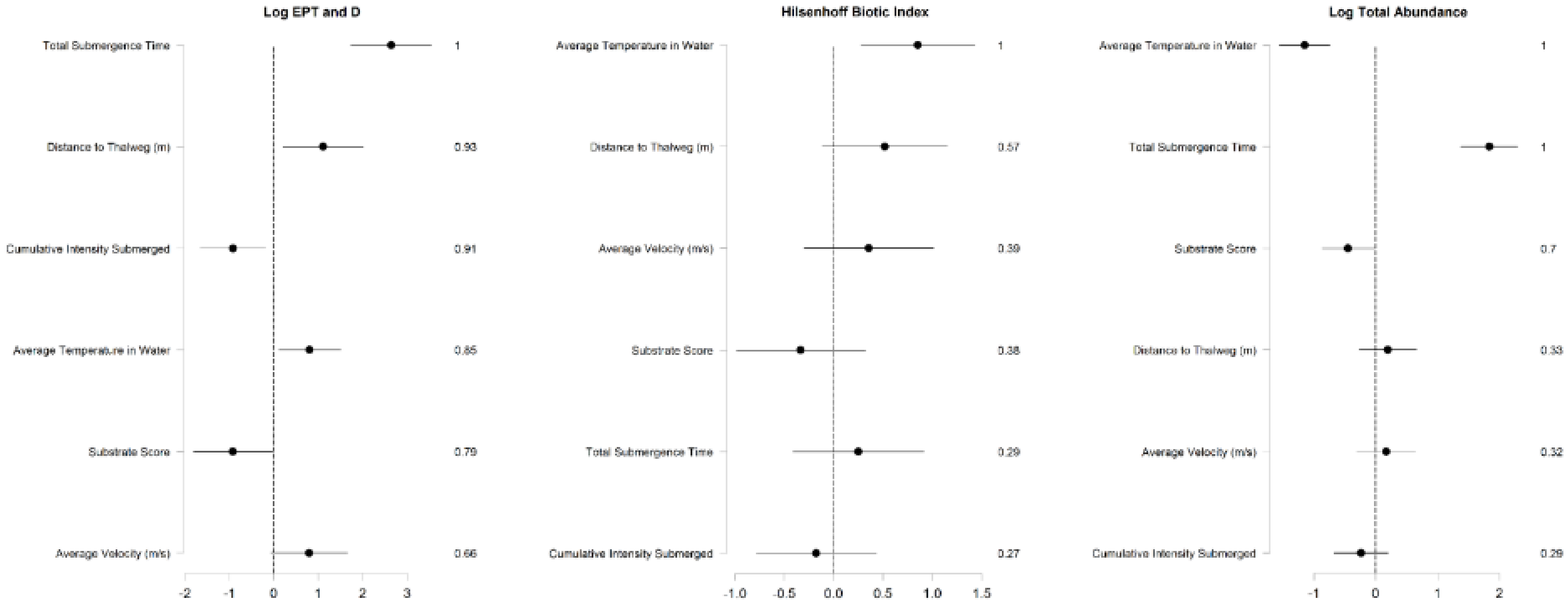

Figure 3-10: Model averaged benthic invertebrate parameter coefficients and 95% confidence limits from model averaged linear mixed effects models for each given dependent variable. Each plot represents the probability of a given predictor, described on the left side of the plot, to be in the best AIC model (this probability is described by the RVI value on the right side of the plot). The predictors are also sorted based on this probability. Predictors have been standardized to allow direct comparison of coefficients (x-axis). The corresponding coefficient and its 95% confidence interval are represented on the plot. Those variables with 95% confidence intervals overlapping zero are considered of low significance as the direction of their effects are inconsistent among models.

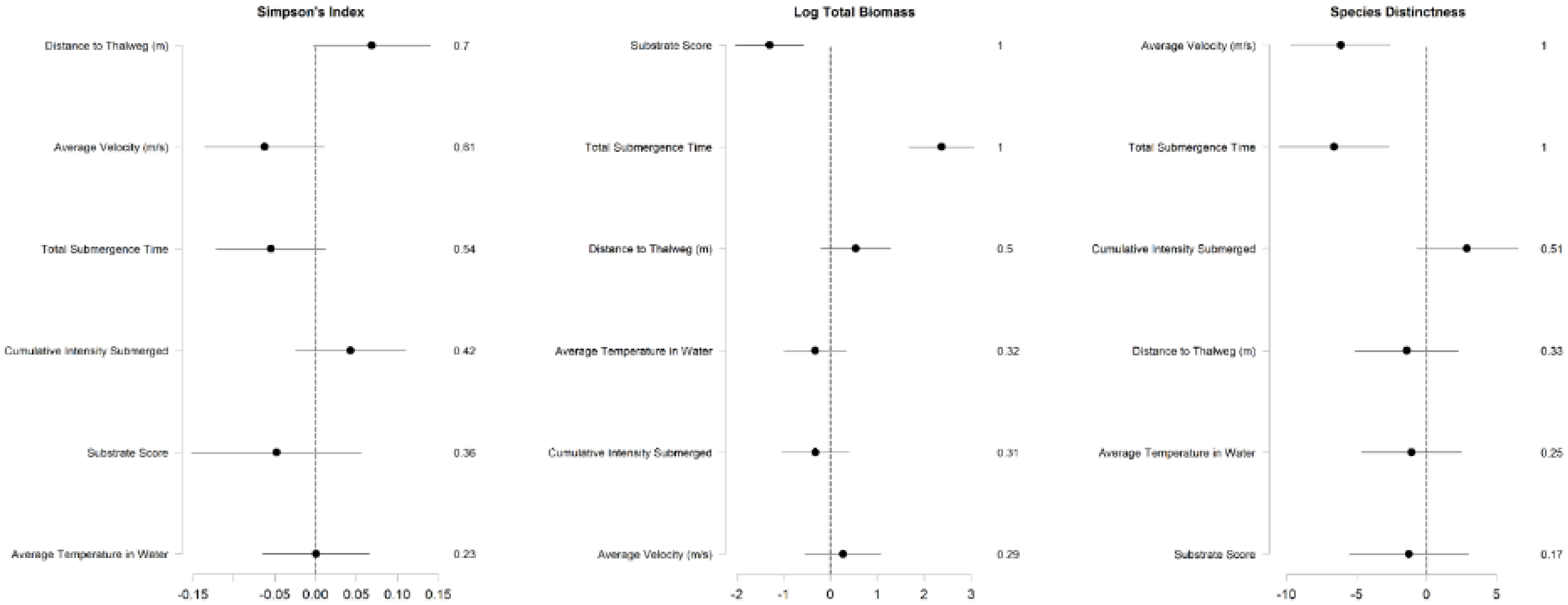

Figure 3-11: **Model averaged benthic invertebrate parameter coefficients and 95% confidence limits from model averaged linear mixed effects models for each given dependent variable. Each plot represents the probability of a given predictor, described on the left side of the plot, to be in the best AIC model (this probability is described by the RVI value on the right side of the plot). The predictors are also sorted based on this probability. Predictors have been standardized to allow direct comparison of coefficients (x-axis). The corresponding coefficient and its 95% confidence interval are represented on the plot. Those variables with 95% confidence intervals overlapping zero are considered of low significance as the direction of their effects are inconsistent among models.**

3.3.3.2 Spring

Production increased with increasing daytime submergence and temperature (abundance, biomass, and EPT & D) (Figures 3-12 and 3-13). The effects of temperature detected by the statistical models showed that years with warmer deployment periods are more productive than cooler years. Similar to the fall, the biomass of EPT+Diptera were gradually increasing for the first 300 to 750 hours and then appeared to increase at a large rate at 750 to 1000 hours of submergence. Abundance also appeared to increase with increasing distance from the thalweg, the result of the highly productive backwater areas. This finding is supported by the trend of increasing abundance, biomass and EPT+Diptera at sites with smaller substrates. Most other explanatory variables were not as important or reliable predictors of invertebrate production in the spring.

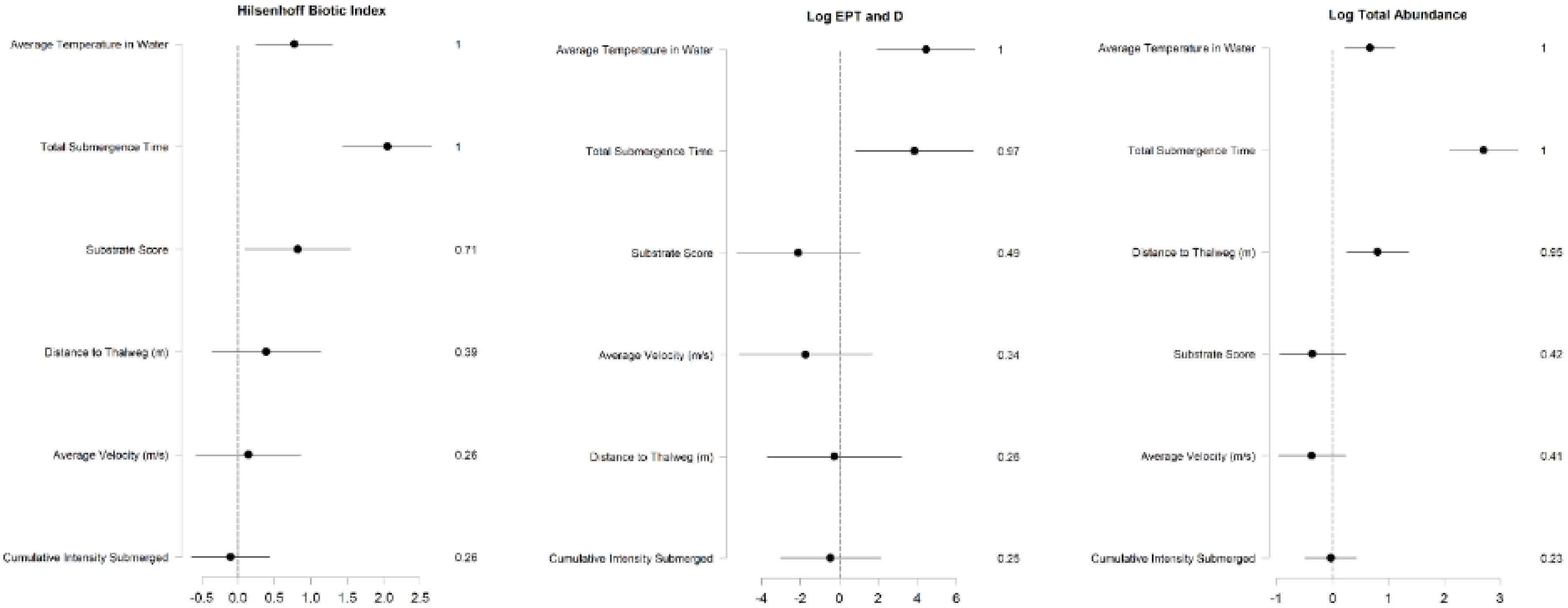

Figure 3-12: **Model averaged benthic invertebrate parameter coefficients and 95% confidence limits from model averaged linear mixed effects models for each given dependent variable. Each plot represents the probability of a given predictor, described on the left side of the plot, to be in the best AIC model (this probability is described by the RVI value on the right side of the plot). The predictors are also sorted based on this probability. Predictors have been standardized to allow direct comparison of coefficients (x-axis). The corresponding coefficient and its 95% confidence interval are represented on the plot. Those variables with 95% confidence intervals overlapping zero are considered of low significance as the direction of their effects are inconsistent among models.**

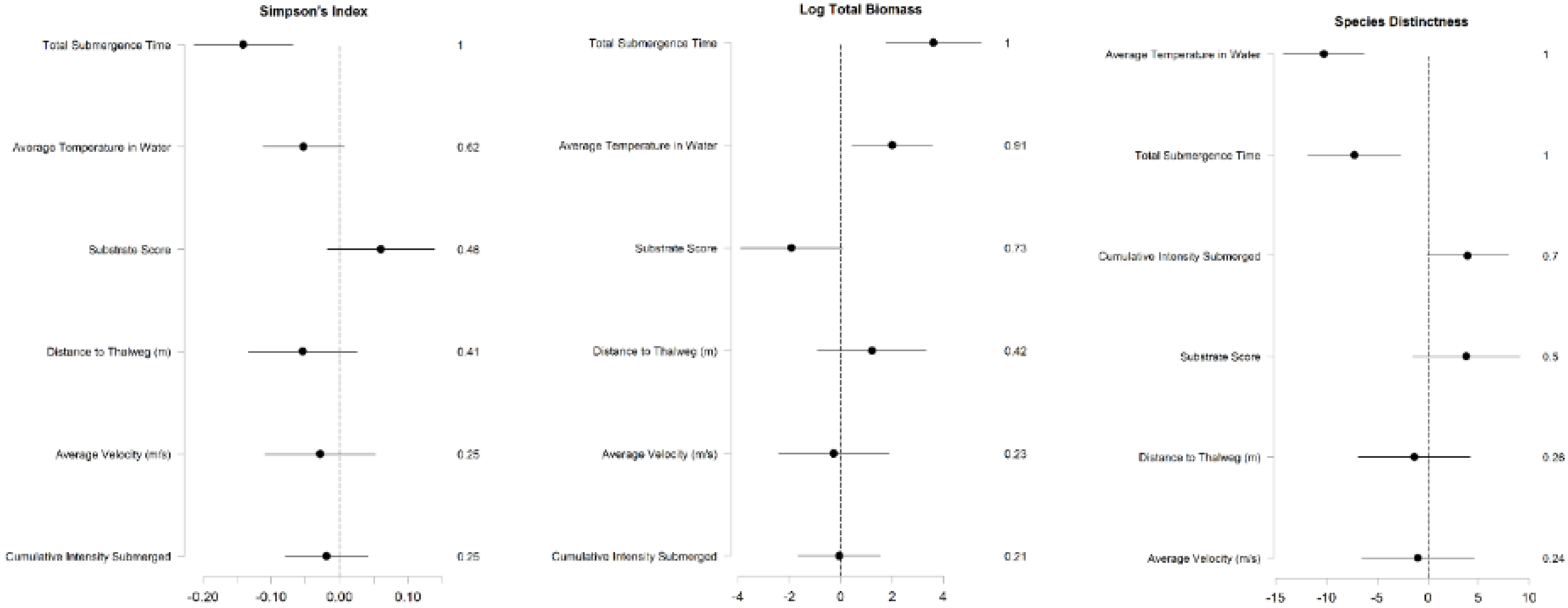

Figure 3-13: Model averaged benthic invertebrate parameter coefficients and 95% confidence limits from model averaged linear mixed effects models for each given dependent variable. Each plot represents the probability of a given predictor, described on the left side of the plot, to be in the best AIC model (this probability is described by the RVI value on the right side of the plot). The predictors are also sorted based on this probability. Predictors have been standardized to allow direct comparison of coefficients (x-axis). The corresponding coefficient and its 95% confidence interval are represented on the plot. Those variables with 95% confidence intervals overlapping zero are considered of low significance as the direction of their effects are inconsistent among models.

4.0 DISCUSSION

Over the ten years of this study, steady progress has been made toward answering the management questions, in addition to learning other complexities of MCR productivity that could not be foreseen when the study was initiated. This discussion summarizes our learning to date and concludes with a review of our current answers to the management questions.

4.1 Overview of MCR Habitat Zones and Conditions

Like 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). A long-term monitoring program of MCR periphyton and benthic invertebrates is on-going in the MCR to determine the effects of minimum flows and REV 5 flows. The key objective of the 142 m^3/s minimum flow strategy is to enhance the productivity and diversity of benthic communities in the MCR by increasing the permanently wetted area by an estimated 32–37% (Golder 2012). This discussion summarizes the findings from the 2007 to 2015 field surveys and subsequent analyses.

The typical daily pattern of flow in the MCR consists of high flows during the day and low flows at night, corresponding with peak power production and usage. Within this general pattern, flows are highly variable on a day-to-day basis. Freshet flows and storm events augment regulated flows and can cause periods with unusually high flows such as freshet 2012. Extreme events (flows in excess of 1800 m^3/s, or minimum flows of 142m^3/s that extend beyond 48 hours) occur regularly and can result in large-scale die-off of benthic communities. Based on the research conducted to date, we conclude that extreme events, coupled with routine BC Hydro operations, ultimately determine the benthic community structure and productivity within MCR.

Benthic communities in the MCR occurred in three large zones created by the operating regime over the preceding 30 to 70 days (2007-2015):

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, and positively correlated with increasing light intensity and substrate size. 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. Furthermore, time series data suggests that extreme high flow events that generated velocities in excess of 2 m/s coincided with thinning of the periphyton community 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 further periphyton thinning through abrasion (Gregory et al. 1991; Goudie 2006; Luce et al. 2010). Overall, the permanently wetted zone productivity is within the range expected for other large rivers that are oligotrophic or stressed (Table 4-1).

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), which 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 MCR. However, the time series chl-a accrual rate at T3 positions was significantly slower than T1 positions during most seasons and years. In the LCR, the total time spent in variable submergence prior to a more permanent submergence has also been shown to be an important factor affecting the time required to achieve peak biomass. Factors such as daytime submergence and substrate exposure were all-important predictors of both periphyton and benthic invertebrate community development in the lower varial zone. Recent works below the Glen Canyon dam in Colorado show similar results in a hydropeaking facility where abundance and diversity of EPT are reduced due to flow augmentation (Kennedy *et al*., 2016). These authors further suggest that specific life history traits such as riverside egg laying of insects that cement eggs may be more affected than those species that use different egg laying strategies.

4.1.3 Upper Varial Zone

The frequently dewatered 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 related to 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 in excess of 9 hours (Schleppe et al. 2012). Periphyton production halted when the substrates were dewatered during the day because normal cell processes couldn't continue 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 the importance of frequency of 12-hour submergence events and total incubation time in the water and light, identified in modelling data for the periphyton autotrophic index in previous years (Schleppe et al., 2013).

The floodplain zone 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. It 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 are typical of larger rivers (Doi, 2009).

4.1.4 Varial Zone Boundary Conditions

The boundaries between these zones were dynamic, and depended upon the average flow regime during the preceding 30-70 days, based on MCR and LCR time series data (Olson *et al.*, in prep). Growth within these zones occurred rapidly until least 6 months duration, when conditions were appropriate for benthic community development. The width of the productive lower varial zone expanded during stable flows in the 400 to 800 m^3/s range.

The ever-changing hydrologic patterns in the varial zone induced a benthic invertebrate community that was in a constant state of recovery following periods of exposure of >48 consecutive hours (Schleppe et al. 2012). Periphyton recovery was frequently faster than invertebrate recovery 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 drying (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 MCR, resulting in the observed homogeneity of the periphyton community structure throughout the varial zone. Invertebrate recovery after a catastrophic event could take several weeks (Table 4-2) or more (if at all) and may depend upon the life-stage of the invertebrates at the time of the event (Kennedy *et al*., 2016). BC Hydro operations create a larger, and more dynamic varial zone in the MCR than would otherwise be expected, and these operations may have a subsequently greater effect on populations than that observed in a natural system.

For many reasons, the rates of dewatering influence the mode of periphyton and benthic invertebrate recovery and likely interact with the life history of different species. In large rivers, rapid water loss such as ramping down hydro releases restricts or prevents recovery by *in-situ* reproduction and causes benthic recovery to be driven by recolonization from other sources (Stanley et al. 2004; Kennedy *et al.*, 2016). Periphyton originating from the Revelstoke Reservoir is therefore expected to be important to periphyton recovery while drift of invertebrates from tributaries is expected to be important to benthic invertebrate recovery in MCR, similar to other studies (Kennedy *et al.*, 2016).

The rate at which recovery occurs is also variable among the organisms present in the benthic communities of MCR. Periphyton biofilm recovery is dependent on their complexity. Biofilm bacteria are capable of division every 20-30 minutes and cyanobacteria every 6 – 24 hours. Five hours of saturating light per day can support a diatom division every 2-3 days in summer and every 4-6 days in winter (Capblanco and Decamps 1978; 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). Invertebrate life cycles vary by species, with some laying eggs multiple times per season, whereas others may only emerge once during any given year and each of these species uses a different reproductive strategy that may further affect colonization rates (Kennedy et al, 2016). This suggests that the effects of desiccation on either periphyton or invertebrates are function of tolerance and also species, their life history and reproductive strategies.

4.2 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 this 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 our 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 suggest that MCR production is consistent with an oligotrophic or stressed river system (Table 4.1). Furthermore, the natural substrate samples had far higher proportions of cyanobacteria, particularly in the sand from the cobble interstices in Reach 4. 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 4.1), 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. In summary, MCR production is probably low compared to other large rivers, particularly in regularly dewatered areas, where even the open-celled substrate samples show the low benthic production expected of a stressed river system.

Table 4-1: Summary of average MCR periphyton metrics from spring and fall 2010 – 2015 deployments, with comparison to oligotrophic, typical, and productive large rivers

Metric	Oligotrophic or stressed	Typical large rivers	Eutrophic or productive	MCR Seasonal Averages Spring – Fall (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+)	0.41 – 1.04 **(0.59-2.0)**
Algae density cells/cm^2	<0.2 x10^6	1 - 4 x10^6	>1 x10^7	0.35 – 0.56 x10^6 **(0.9 – 13.1x10^6)**
Algae biovolume cm^3/m^2	<0.5	0.5 – 5	20 - 80	1.67 – 3.12 **(0.6 - 5.9)**
Diatom density frustules/cm^2	<0.15 x10^6	1 - 2 x10^6	>20 x10^6	0.32 – 51 x10^6 **(0.2-1.0 x10^6)**
Biomass –AFDW mg/cm^2	<0.5	0.5 – 2	>3	0.56 – 0.59 **(0.35-3.5)**
Biomass –dry wt mg/cm^2	<1	1 – 5	>10	26.00 **(6-99)**
Organic matter (% of dry wt)		4 – 7		3.9 – 6.1 **(0.35-3.5)**
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	0.41– 0.79 mid (T3) 0.53 – 1.2 deep (T1)

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

4.3 Overview of Benthic Communities

The physical habitat condition on the MCR created three spatial zones of productivity during the study period: 1) those that are permanently submerged, 2) those in the lower varial zone, and 3) those in the upper varial zone. Despite the establishment of three distinct benthic communities with variable dominant species, both periphyton and invertebrate communities were relatively stable when viewed at the family taxonomic level. Benthic communities also followed annual and seasonal patterns of growth. Periphyton production metrics measured in the spring were usually less than half of the fall deployments. We expect this is because night outages 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). The MCR benthic community structure is stable but is still subject to seasonal variation, in addition to habitat condition over the preceding 2 to 6 months.

MCR periphyton communities were dominated by diatoms representing between 82 and 98% of the biovolume at all sample sites. Other species, such as 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 areas, periphyton communities transitioned from "producers" to "consumers", 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, likely in response to key drivers, particularly flows.

Benthic invertebrate communities were also dominated by taxa that are more tolerant of disturbance, such as chironomids (Tonking et al. 2009) which are often overrepresented in flow managed rivers (Bunn and Arthington 2002). EPT taxa and chironomids appeared to be more abundant along the edge of minimum flow (T2) or in the lower varial zone (T3), as suggested by our modelling of permanently submerged habitats in previous years (Schleppe and Larratt 2015). Although the major taxonomic group contributions of periphyton and benthic taxa remained the same, the dominant species varied with annual BC Hydro operations, weather conditions (e.g., freezing temperatures during night time low flows or hot weather and lower flows during daylight hours), other prevailing MCR conditions, and potentially with the interaction between life history strategies and hydropeaking operations (Kennedy et al, 2016).

Statistical modelling results identified two important factors that were determinants for both periphyton and invertebrate community development. First, submergence was a consistent and vital predictor of benthic production and diversity. Submergence metrics are probably the most important predictors of the benthic community because all of the best predictors for any metric of productivity for either periphyton or benthic invertebrates were associated with some measure of submergence or analogous measure of exposure. Second, physical parameters such as substrate type and velocity were identified as key factors determining periphyton and invertebrate community establishment. These physical parameters were more important determinants of community in permanently submerged habitat areas (Schleppe and Larratt 2015). Other physical factors that may also be important to benthic abundance and diversity that are yet to be investigated include frequency and magnitude of flow events. Large peaks in flow on other regulated rivers have been shown to decrease invertebrate species density, diversity and biomass (Robinson et al. 2004) and cause shear stresses sufficient to thin algal communities (Flinders and Hartz 2009).

4.4 Effects of Minimum Flows on Periphyton and Accrual (MQ 1,3,4)

Sections 4.4 and 4.5 address management questions (MQ) 1, 3 and 4 directly, while Section 4.6 covers MQ 5 and Section 4.7 deals with MQ 2. The questions are:

- MQ.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?
- MQ.2. What is the effect of implementing minimum flows on the area of productive benthic habitat?
- MQ3. 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?
- MQ.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?
- MQ5. 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?

Historically, BC Hydro avoided daytime dewatering and this operating regime was implemented prior to the establishment of 142 m^3/s minimum flows. After the initiation of this study, the REV 5 turbine also came online. Unfortunately, these events preclude clear before/after periods where we can study the benefits of minimum flows in isolation from other flow changes on the MCR. We therefore contrasted production in the regularly dewatered varial zones with production in the permanently wetted zones to address MQ 1 and 3.

The benefits of minimum flows were most evident in the periphyton communities at T2 and T3 locations because these locations occur directly above or adjacent to the wetted edge at minimum flows. Peak production was most apparent at T2 locations because higher velocities at T1 thalweg locations had higher sheer stresses that reduced the periphyton community. However, productivity at T3 locations was similar to T2 locations under the current operating regime of nightly low flow periods with daytime high flows frequently exceeding 800 m^3/s. The lower varial zone (T3/T4) was an important productive area bounded by minimum flows and a mobile upper limit created by average daily submergence during the preceding 30 – 70 days. Unlike the permanently wetted zone, productivity in the lower varial zone was entirely dependent upon submergence caused by the recent operating regime. Operations that result in minimal flows in excess of one week would cause extensive periphyton losses in the lower varial zone and require a recovery period of several weeks with consistent submergence. Productivity of the frequently dewatered upper varial zone (T5/T6) was consistently less than half of the high productivity zones.

The benefits of a permanently wetted channel area were also affected by prevailing conditions. For example, ALR backwatering, rain or high humidity, and cool air temperatures ranging from 5-10 ºC were all beneficial to periphyton viability on exposed substrates (Stanley at al. 2004). Conversely, dry weather with air temperatures below 0 ^{o}C (spring) or exceeding 15 ºC to 20 ºC (fall) all reduced periphyton viability on the exposed substrates.

The effects of season and peak flows were also important when considering the benefits of minimum flows. Minimum flows were particularly advantageous during the fall when rates of periphyton recovery were highest, while the benefits were less evident in the spring with slow periphyton recovery rates and high peak flows. Peak flows associated with REV 5 may reduce the benefits of minimum flows if they result in sheer stresses sufficient to thin established periphyton communities in the lower varial zones and thalweg.

In answer to MQ 3, establishment and accrual of periphyton communities in MCR occurred at slow rates similar to other large oligotrophic rivers (Table 4.1). The combined time series data collected across year, season and river depth suggest that accrual on MCR continued linearly to the end of the 46-51 day deployment period. Therefore, incubation periods of greater than 46 days are required to achieve peak periphyton biomass in MCR and may require more than 6 months to fully develop (Wu et al. 2009; Biggs 1989). Further, the daily, weekly, and yearly patterns of operation, Arrow Lakes Reservoir backwatering, and seasonal growth cycles can all affect accrual. Although improved periphyton production stemming from the implementation of minimum flows is already occurring, it is difficult to separate production benefits attributable to minimum flows from the effects of flows resulting from the recent and current operating regimes.

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. The role of shallows such as backwaters and back-eddies as a source of recruitment and maintenance of some planktonic and periphytic species cannot be doubted (Reynolds and Descy 1996; Butcher 1992). These areas are more abundant in Reach 3 than in Reach 4, and may cause Reach 3 periphyton to recover faster after catastrophic flow events. It is important to note that many of these areas may also act as impoundments to fish, resulting in mortalities, inferring that trade-offs are likely and should be considered in any flow management decisions.

Patterns of periphyton accrual and recovery in 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 periphyton for many kilometers below a dam (Doi et al 2008; Larratt et al. 2013). In MCR, this subsidy is important to standing crop and accrual rates. Contributions of phytoplankton to MCR periphyton may also occur from the Arrow Lakes Reservoir to Reach 3 during backwatering, but the few plankton hauls we have completed showed that 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 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 answer to MQ 4, these long-term trend data suggest that MCR periphyton communities may be more dependent upon the overall operating regime (daily, monthly, and annual patterns of flow release, ALR backwatering, etc.) than the specific effects of minimum flow because the normal operating regime determined the wetted edge of the channel during daytime periods, a key explanatory variable in our model.

4.5 Effects of Minimum Flows on Benthic Invertebrates and Accrual (MQ 1,3,4)

The responses of benthic invertebrates to minimum flows were very similar to periphyton. Productive habitat included permanently submerged habitat and areas in the lower varial zone adjacent to the edge wetted by minimum flows. Since invertebrate communities were directly dependent upon submergence and physical conditions of MCR for survival, the same explanation can be used to describe where and when invertebrate communities establish. Like periphyton, the area of varial zone productive invertebrate habitat is bounded by minimum flows and its upper limit determined by average daily submergence.

However, MCR invertebrate statistical models explain less variation than periphyton models, reducing our ability to understand specific trends. The following factors are thought to play a role: 1) the patchy distribution of invertebrates in space and time, 2) the potential sampling biases associated with the use of rock baskets retrieved from depths of 5 m at high velocities, 3) a low sample size to habitat area ratio when compared to periphyton, and 4) microhabitat factors or species specific life history and reproductive strategies that were not accounted for in our analysis. Further, invertebrates are more sensitive to desiccation than periphyton (Schleppe et al. 2012; Golder 2012). Invertebrate habitat was probably more heavily influenced by periods of daytime exposure than periphyton because of their reduced tolerances to desiccation. The spatial area of the lower varial zone available to invertebrates was probably smaller than that of periphyton. For these reasons, explicitly determining the effectiveness of minimum flows on improving benthic conditions for invertebrates is difficult, but it is known that minimum flows benefited the invertebrate community and that dewatering of habitat had a direct, negative effect on benthic abundance, biomass, and community composition. The permanently wetted area can function as a source of benthic organisms to re-colonize previously exposed habitat areas after extensive low flow events lasting longer than 24 hours.

4.6 Effects of Minimum Flow on the Availability of Food for Fish (MQ 5)

The area of productive MCR habitat is directly correlated with submergence. In answer to MQ5, our data suggest that the abundance, biomass, and overall availability of fish food (using the Fish Food Index (2013) or the EPT+Diptera responses in 2014-2015) were also directly dependent upon submergence. Fish food varies depending upon the species considered, and generally the EPT taxa and chironomids (Dipterans) are the most important forage for fish. It is for this reason that we have considered both a fish food index and created an EPT+D metric, to consider how fish food availability may be affected for different fish foraging groups. Generally, any increase in wetted productive habitat should cause a subsequent increase in fish food availability, provided there is sufficient populations for recolonization to occur. 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 models. For these reasons, minimum flows increased fish food availability, but other key influences on productivity such as frequency and duration of daytime submergence events must also be considered. Substrates submerged for 450 – 500 hours (10 – 11 hours/day) 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. When considering specific fish species, EPT taxa were most commonly observed in areas of boulder or cobble substrate, whereas overall benthic abundance was greatest at sites with finer substrates. This suggests that food for fish that forage on invertebrates should be greatest within areas of larger substrates. The interaction between minimum flow and substrate type is important. Further analysis is required to understand all the dynamics of fish species, and fish food interactions and how they relate to the implementation of minimum flows.

4.7 Spatial Area of Productivity (MQ 2)

The intent of implementing minimum flows is to increase the spatial area of wetted habitat and subsequently improve benthic community function at these locations. In answer to MQ 2, minimum flows will increase the area of productive habitat because they maintain a minimum area of wetted perimeter. Preliminary results from the HEC-RAS model showed an increase of 32 - 37% in the spatial area of wetted habitats in Reaches 4 and 3 with minimum flows when the ALR elevation was below 425 m (Golder 2012; K. Bray, BC Hydro, pers. comm. 2010). All MCR data suggest that productive benthic habitat was highly influenced by submergence parameters, including duration and timing of flow events. In fact, submergence (or metrics of it) may actually be the most important determinant of benthic communities in the MCR, most notably abundance, biomass, and food for fish. The most productive areas tended to occur at T2 through T3/T4, and depended directly on submergence. Thus, the wetted edge from minimum flows to slightly above in the varial zone is important and productive habitat. However, the size and position of productive varial zone habitats shifts depending upon the prevailing operating regime. Thus, minimum flows must make an overall contribution to benthic community abundance and diversity in areas subjected to minimum flows, but other parameters such as duration of daytime submergence were also important. However, our data also suggest that when the elevation of the ALR was higher, the benefit of minimum flows on the spatial area of productivity was lessened by the effects of backwatering that may extend throughout Reach 3 and into Reach 4. The specific relationships between ALR elevation and the effects of minimum flow have not been fully investigated, but determination of the spatial area of habitat must consider the effects of ALR backwatering as well as minimum flows.

In MCR, the total area of productive habitat in these three zones depends upon more than just minimum flows. The effectiveness of minimum flows at increasing the area of productive benthic habitat was difficult to determine given the highly variable flow regime, variable episodes of ALR backwatering and the timing of benthic life cycles and flow releases. Despite difficulties in determining the exact benefits in spatial area of productive habitats attributable to minimum flows, we conclude that minimum flow increased the spatial area of productive habitat because it provided a minimum wetted habitat area that is productive and basically was not as apparent before.

The spatial area of productive habitat in the MCR is a function of many factors, but submergence is the most important in varial zones. On the Lower Columbia River, a spatial model of productivity has been developed, where the patterns of varial zone growth were derived from works on this project (Schleppe et al, 2015). The spatial model considered two general factors, growth and death, where growth was directly dependent on submergence and death was directly dependent on exposure. Currently, sufficient data on the wetting and drying patterns in the MCR and through other references are available to generate a theoretical curve to address submergence. Data from this work can be used to develop the submergence aspects of the spatial model. With these components, it should be possible to build a spatial model that can directly test the questions regarding the spatial area of productivity.

Growth curves for periphyton in the MCR appear linear, as we couldn't derive a reasonable non linear function using MCR data for spring or fall. Typically, these curves are logistic in shape, at least theoretically. It is possible that time series deployments have not been left in the river for sufficient time to achieve peak biomass, meaning the peak occurs beyond the typical 49 to 50- day deployment. To further develop these curves, a logistic growth function will need to be developed for use in the spatial model, as a linear function will not settle on a peak biomass. Alternatively, a spatial model could use a linear function with an immediate asymptote at peak biomass, but this is not as consistent with a typical pattern of growth observed on the LCR. Thus, it is likely best to utilize the data in this report to develop a logistic growth function that considers the long term plate deployments that were collected in 2011 and 2012, as these provide information to support what peak biomass is. It is interesting to note that our data suggests that differential growth occurs in the varial zone versus permanently submerged areas. It is most likely that these difference occur due to exposure related mortality, since submergence is the most important predictor of productivity. This means that use of the growth curves from permanently submerged zones are most appropriate, as the spatial model will account for variable growth through the death function(s).

Collection of data to develop invertebrate growth curves were attempted in 2011, with little success. Further pursuit of this was thought to have a low success relative to the costs of sample acquisition. As a result, it is likely that theoretical growth curves will be needed to understand peaks. The spatial models developed for the LCR can act as guide, noting that it is probable that some adjustment of these curves is needed due to the significant difference in productivity between the MCR and the LCR.

Table 4-2 provides some initial consideration to generate death curves for periphyton. These data, combined with data from the LCR will be used to generate death curves for periphyton. For benthic invertebrates, there is data available from many sources, including the LCR and Kennedy *et al* (2016) that will be used to generate a reasonable spatial model. Both the initial invertebrate and periphyton death curves used in the LCR are presented below for reference (Figure 4-1).

Table 4-2: Approximate ranges of expected percent mortality of dominant periphyton in MCR Reaches 4 and 3 with substrate exposure time and corresponding recovery times Corresponding invertebrate mortality times will be shorter, and the recovery times more erratic than those for periphyton. Updated with 2015 information

Expected Percent Mortality							
Substrate exposure time per event	**<2 hours**	**2-10 hours**	**10-24 hours**	**24-48 hours**	**2-4 days**	**4-6 days**	**>6 days**
Day exposure, % loss	<10	10-30	30-40	40-60	40-70	70-95	95+
Night exposure % loss	none	0-10	10-30	30-50	50-70	70-80	80+
Corresponding Recovery Time (weeks)							
June – October	none	<1	1-2	2-3	3-5	5-8	.>8
November – May	<1	1-2	2-4	3-6	6-10	10-20	> 20

Data obtained from this study 2010 – 2014; Usher and Blinn 1990; Angradi and Kubly 1993; and Blinn et al. 1995, Hodoki 2005

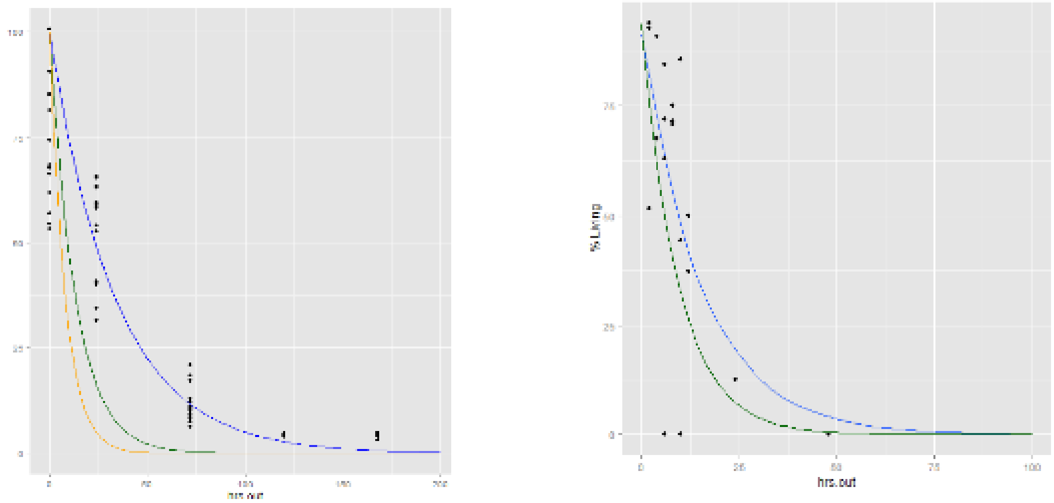

Figure 4-1: Periphyton decay curves for LCR are shown on the left (Schleppe et al., 2015). The green line represents spring and fall seasons for abundance and biovolume, the orange line represents the summer and winter seasons abundance and biovolume, and the blue line represents the decay of chl-a in all seasons. Benthic Invertebrate Death Curves for LCR are shown on the right (Schleppe et al., 2015). The blue line represents the Spring and Fall seasons, and the green line represents the Summer and Winter seasons.

Future development of the spatial model may also consider other factors at peak biomass, such as substrate size, velocity, and light intensity for example. The following is the initial model that will be used as a template, for the development of a model specifically for the MCR. If possible, a new component will be added to the spatial model that considers biomass at peak productivity, where the more physical aspects of production become important. In addition, data from Kennedy *et al*. (2016) may be considered for other aspects of the model.

4.8 Spatial Model Development for MCR

To explicitly determine the productivity within a spatial area of habitat covered by different flow regimes (i.e. minimum flow), a more complex model is required. This section outlines and defines the various component formulae of the growth and death phase functions in the predictive spatial models that are proposed for the MCR, as well as the combined model for describing total production across a section of river or within a river polygon in a given time period. First, we define which processes are occurring for a given period and how the different components of these processes relate to each other. Then, we describe how all the components fit together to determine the total production for any given river segment that is evaluated.

4.8.1 Model Notation

The following notation for all response variables of production has been used to clarify the relationships between various processes. Since the output of all functions are density responses (units/m^2), the derivation of formulae is identical between responses with only the coefficient values differing among them. For periphyton, it is likely we will consider chl-a, and derive total abundance and biovolume using chl-a (including some sample years where we have both abundance and biovolume from time series). For benthic invertebrates we will likely consider benthic biomass, total abundance and food for fish (EPT+D), each in their respective units.

- $C(t)$ – 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

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

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

4.8.2 Model for an Individual Polygon

In a regulated flow regime, two distinct processes are important in determining river production in the varial zone after any given period time: growth and death. In any 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 concurrently; rather there are consecutive periods of growth and death that vary only 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. Any given river polygon can move between growth (submergence) or death (exposure) independently of all other river polygons at any point in time and the state of a river polygon submergence is entirely dependent upon the regulated flow. A river 1D or 2D model will be used to determine the state of submergence for any given river polygon at any given time period on an hourly basis.

4.8.2.1 Growth Phase for an Individual Polygon

Growth within any given time period will occur between time $t = t_a \dots t_b$, 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 $c_i(t_a)$, which 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 $c_i^g(t)$, which 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) $c_i(t_b) = c_i(t_a) + c_i^g(t_b - t_a)$

4.8.2.2 Logistic Growth

At the time of submergence, t_a, growth is initiated using a logistic growth function. The productivity response (e.g., abundance or biomass for instance), $\mu_i(t_{a-1})$, 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) $c_i(t) = \frac{asym}{1+exp^{(xmid-h(t))/scal}} \cdot s_i \qquad \text{if } t_a \leq t < t_b$

We note here that the parameter $asym$, $xmid$ and $scal$ for the same river polygon varies 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.

4.8.2.3 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 $c_i(t_a)$, which may be zero or a positive number up to peak biomass.

At any point during this period we denote how much of the response has been 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:

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

in which case

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

For periphyton, the start of the death or loss phase can be offset by a fixed amount of time (starting values discussed above) if certain seasons or time frames are expected to be able to tolerate small periods of exposure. This is easily incorporated by modifying the start time t_a used in these equations.

4.8.2.4 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:

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

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:

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

4.8.3 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. In order 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 $t = t_a$:

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

4.8.4 Spatial 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 those polygons that are permanently submerged within the river, it is assumed that peak production for that metric has been achieved, whereas in varial zones where polygons are alternately submerged and exposed, the starting value is assumed to be zero until submergence occurs. For this reason, the minimum period of time that

can be considered in any given operational scenario must, at minimum, span the time period necessary for peak production for that given response to be reached.

2. All river cells are considered independent of all other river cells, meaning that growth, death or peak biomass in any cell has no direct effect on any other given river cell. This means that factors such as invertebrate drift due to natural migration or effects direction associated with flow regulation (via changes in velocity) are not accounted for.
3. As mentioned above, the most appropriate time period to consider is hourly, and all associated functions have been derived assuming that production will be calculated on an hourly basis. We have assumed that for any 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 to some extent and presumably emigration rates are species dependent. Further, the rates of ramping may affect emigration rates, where high ramping rates result in more rapid elevation changes within the river, resulting in a reduced ability for invertebrates to move, whereas lower ramping rates 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 are not likely sufficient to overly influence predicted estimates of production responses within the proposed spatial models.
5. Growth and death curves do not differ with weather or between years. It is important to note that high annual variation in growth has been observed, but the specific reasons for the variability are not well understood, making it difficult to account for the variability.
6. That production is greater than zero upon the first hour of growth phase and is equal to the minimum predicted growth at hour 1 in logistic regressions for each season. This is necessary 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 function is being used to transition between seasons when decreasing production occurs. Realistically, this process is governed by processes of natural slough, and we do not currently have any data to reflect this. This process could be easily added to the spatial model to further develop seasonal transitions.
8. To develop the spatial model, data has been collected since 2007 for a variety of different projects on the Columbia River for both BC Hydro and Columbia Power Corporation. The data collected in these assessments will all be considered as one data set. From this data set, predictive growth and death functions will be developed that are directly linked to submergence times. It is important to note that high annual variation has been observed on these systems, and the data has

been highly condensed to consider only one growth or death curve for each season. A full investigation of the potential consequences of dataset reduction like this has not been considered, but is likely an important factor.

9. The model assumes that different life history strategies do not affect overall production. This means that rates of population growth, death, and juvenile recruitment for instance are not affected by any other parameter than submergence and that all species respond the same. Recent works indicate these relationships may exist (Kennedy et al. 2016), and could be considered in this model, if they could be related to submergence. However, as the model becomes more complicated (i.e. more parameters are added), the more computer hardware and associated programming are needed to maintain the dataset.

5.0 RECOMMENDATIONS

The following are recommendations intended to further the development of the proposed spatial model.

Table 5-1: Recommended Project Directions and Actions for 2016 to 2018

Category of Recommendation	Timeline and Specifics to Consider	Relationship to MQ's
Growth and Death Functions	2016 - Finalize growth and death functions	Determine area of productive benthic habitat (MQ's 1,3,4)
River Model	2016-17 - Obtain calibrated river 2-D model from BC Hydro. Develop appropriate cell or patch size. Run model and generate outputs. Select appropriate study areas (likely R3 and R4 sample sites, noting that R4 sites may be subset to run different model iterations on a smaller scale and reduce computing overhead.	Determine area of productive benthic habitat (MQ's 1 and 2)
Spatial Productivity Model Development	2016-17 - Use of more or less conservative growth and death functions. Use of a secondary function at peak biomass that considers other factors (e.g., substrate, light intensity, velocity if using river 2 D), etc.). Develop model for only spring and fall, or use theoretical curves for time periods where data is not available. Consider other important parameters that could be added (e.g., life history traits such as egg laying strategy).	A spatial productivity model will give numeric values to answer MQ 2

Table 5-1: Recommended Project Directions and Actions for 2016 to 2018

Category of Recommendation	Timeline and Specifics to Consider	Relationship to MQ's
Spatial Productivity Model Results Analysis	2016 - Generate a specific set of questions; considering computer overhead, and time needed to run each iteration (i.e. Are the selected metrics most appropriate? Are the predictions for time series curves realistic? Should light intensity be estimated for specific periods of time to improve peak biomass predictions? Should key life history traits for different species groups be considered? Should a delayed death start be considered for periphyton in cooler, wetter seasons?	A spatial productivity model will give numeric values to answer MQ 2

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APPENDIX A DATA TABLES AND FIGURES

Light and Temperature Figures

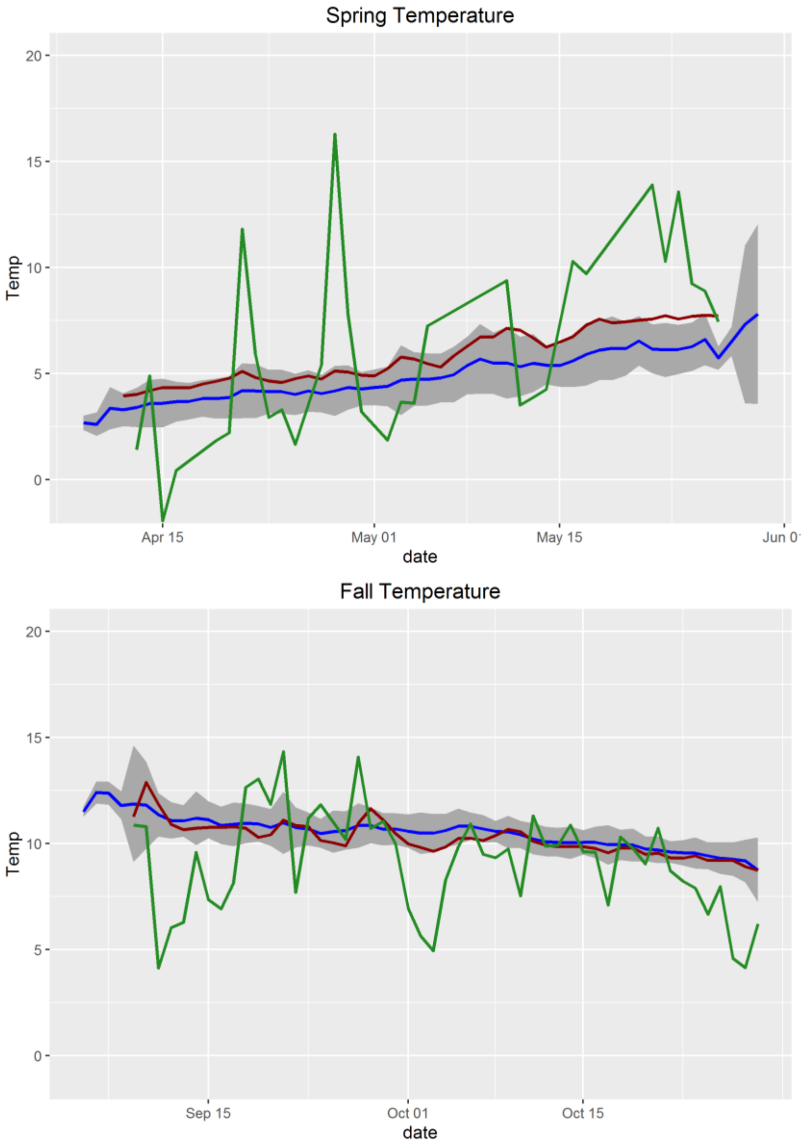

Figure A-1: The pattern of daily water temperature in MCR during the fall and spring study periods. The blue line represents the mean water temperature of submerged samplers from 2010 to 2014 (Fall) / 2015 (Spring) and red line represents the mean 2015 (Spring) or 2014 data (Fall) from all submerged samplers. The green line represents the average temperature of exposed sites in 2015 (spring) and 2014 (fall). Data were pooled for fall periods between 2010 – 2014 and for spring periods between 2011 – 2015 (±SD in grey).

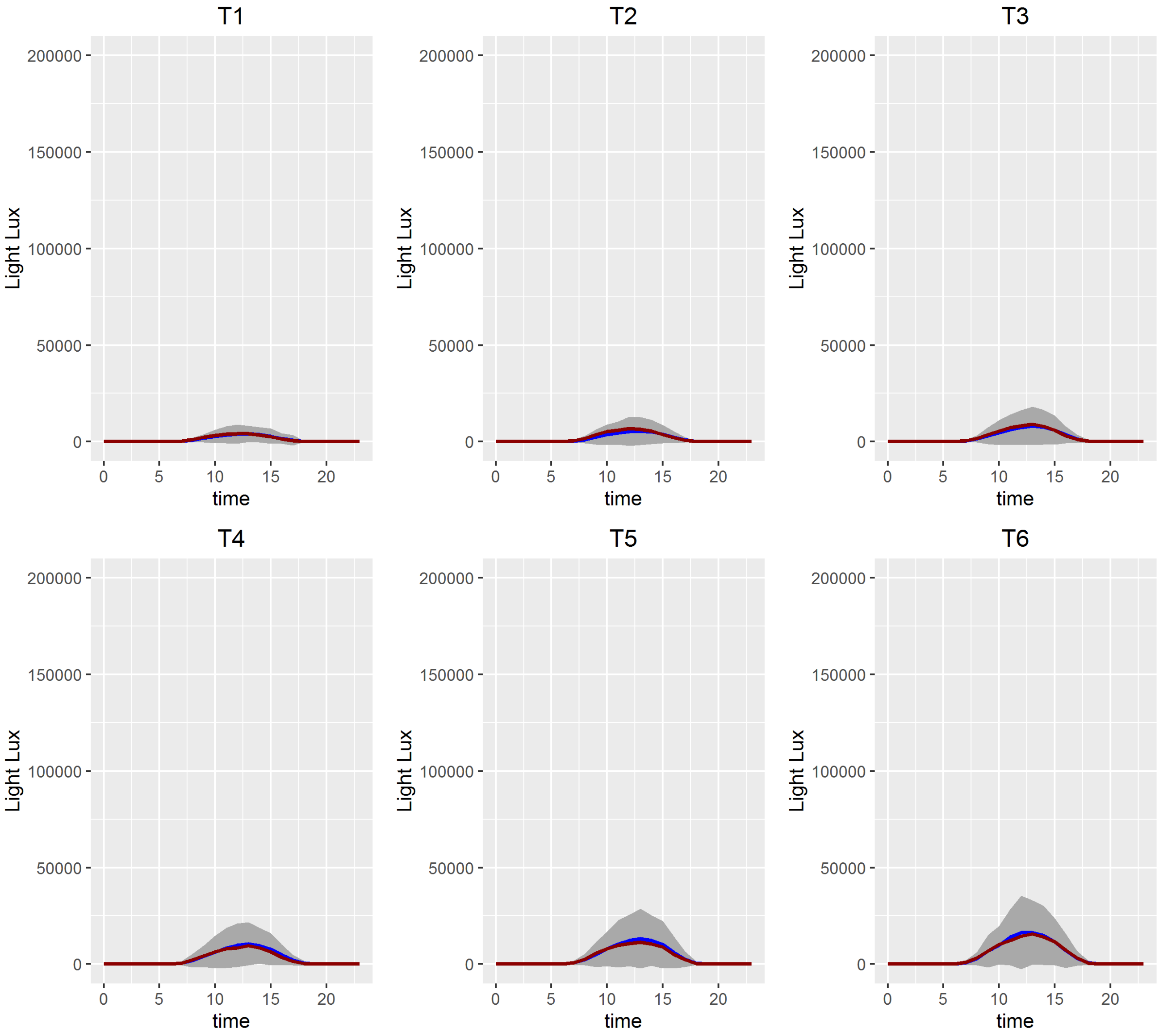

Figure A-2: Fall daily pattern of light intensity (lux) while samplers were water-covered in MCR at varying depths, where T1 is the deepest and T6 is the shallowest for samplers. The blue line represents the mean from 2010 to 2014 (±SD in grey) and red represents the mean 2014 fall data from all submerged samplers. The x-axis is time in hours of the day (0:00 to 24:00).

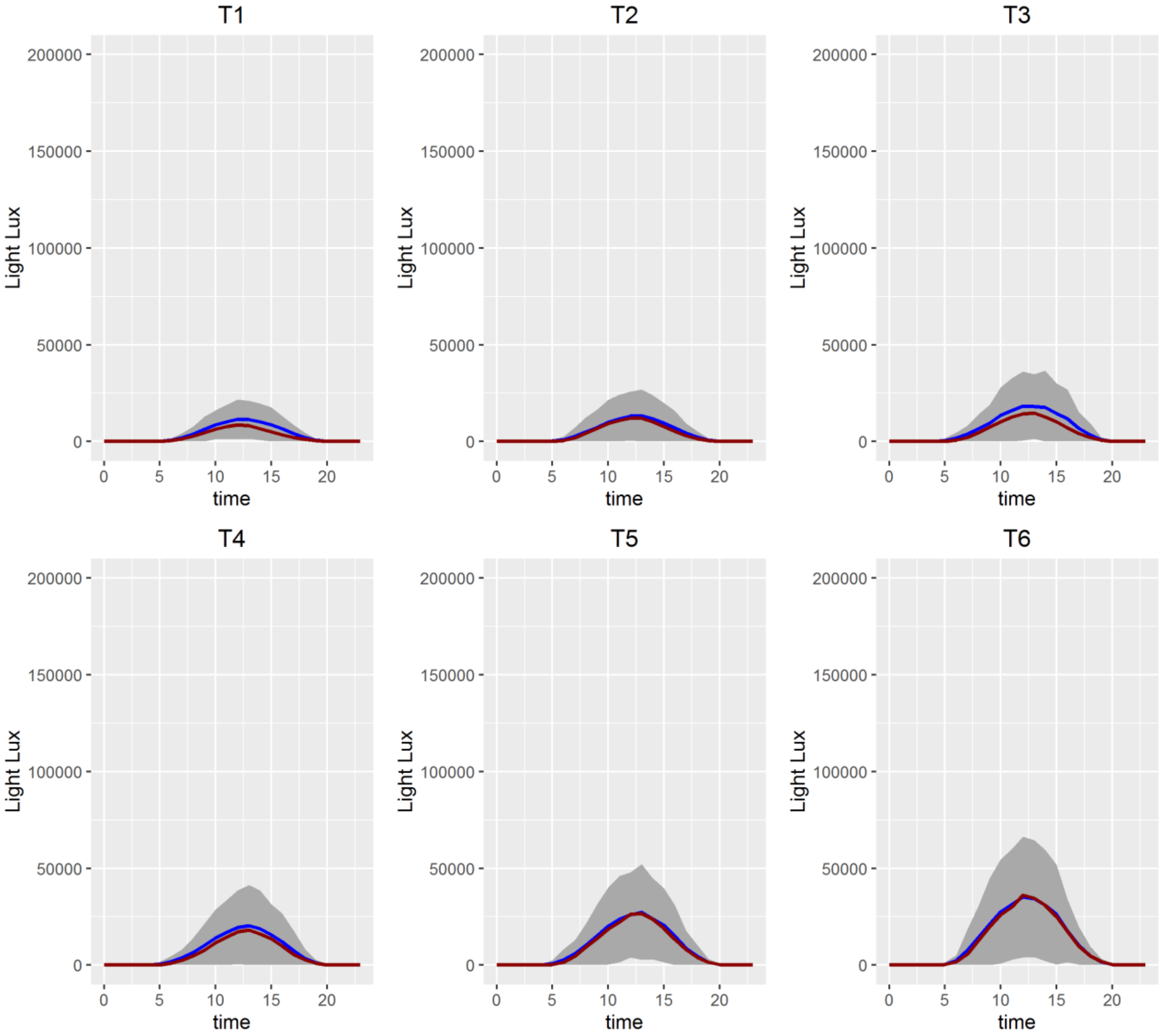

Figure A-3: Spring daily pattern of light intensity (lux) while samplers were water-covered in MCR at varying depths, where T1 is the deepest and T6 is the shallowest for samplers. The blue line represents the mean from 2011 to 2015 (±SD in grey) and red represents the mean 2015 spring data from all submerged samplers. The x-axis is time in hours of the day (0:00 to 24:00).

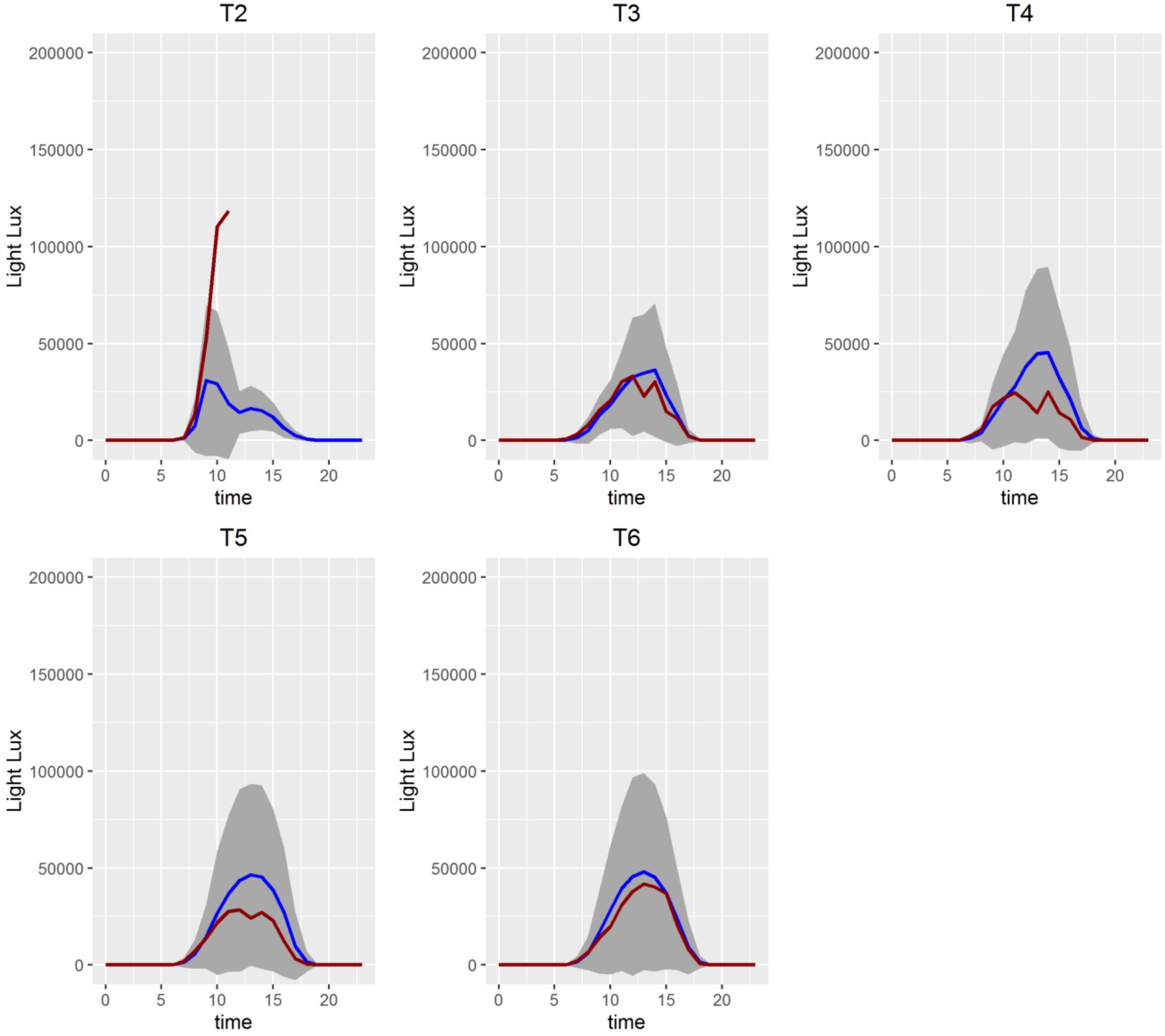

Figure A-4: Fall daily pattern of light intensity (lux) in MCR while samplers were exposed (out of the water), where T1 is the deepest and T6 is the shallowest for samplers. The blue line represents the mean from 2010 to 2014 (±SD in grey) and red represents the mean 2014 fall data from all exposed samplers. The x-axis is time in hours of the day (0:00 to 24:00).

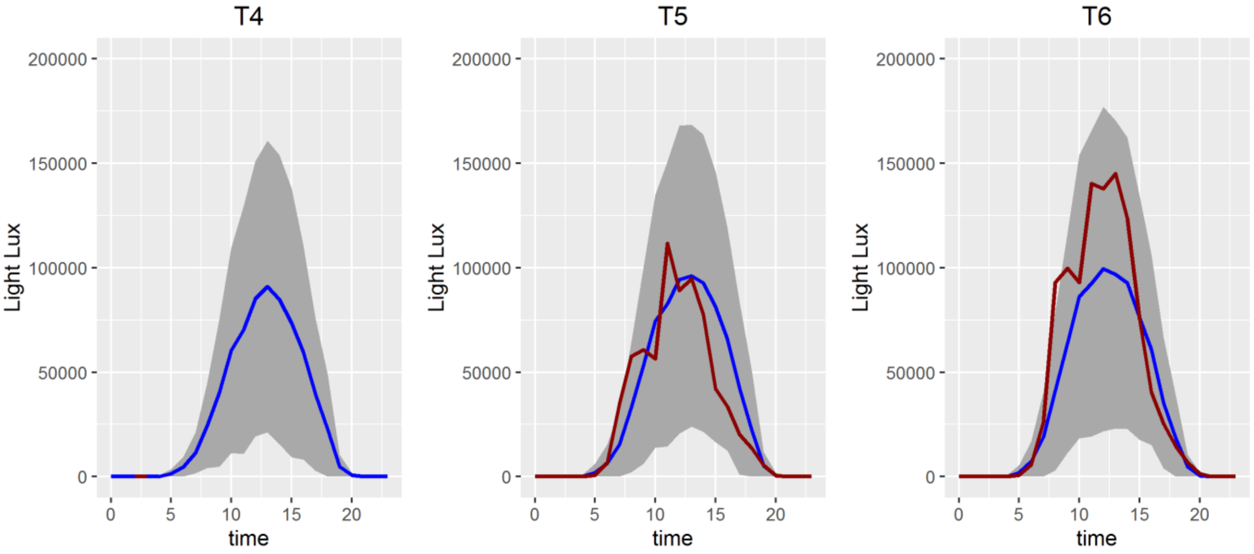

Figure A-5: Spring daily pattern of light intensity (lux) in MCR while samplers were exposed (out of the water), where T4 is the deepest and T6 is the shallowest for samplers, noting T1 through T3 were continuously submerged. The blue line represents the mean from 2011 to 2015 (±SD in grey) and red represents the mean spring 2015 data from all exposed samplers. The x-axis is time in hours of the day (0:00 to 24:00).

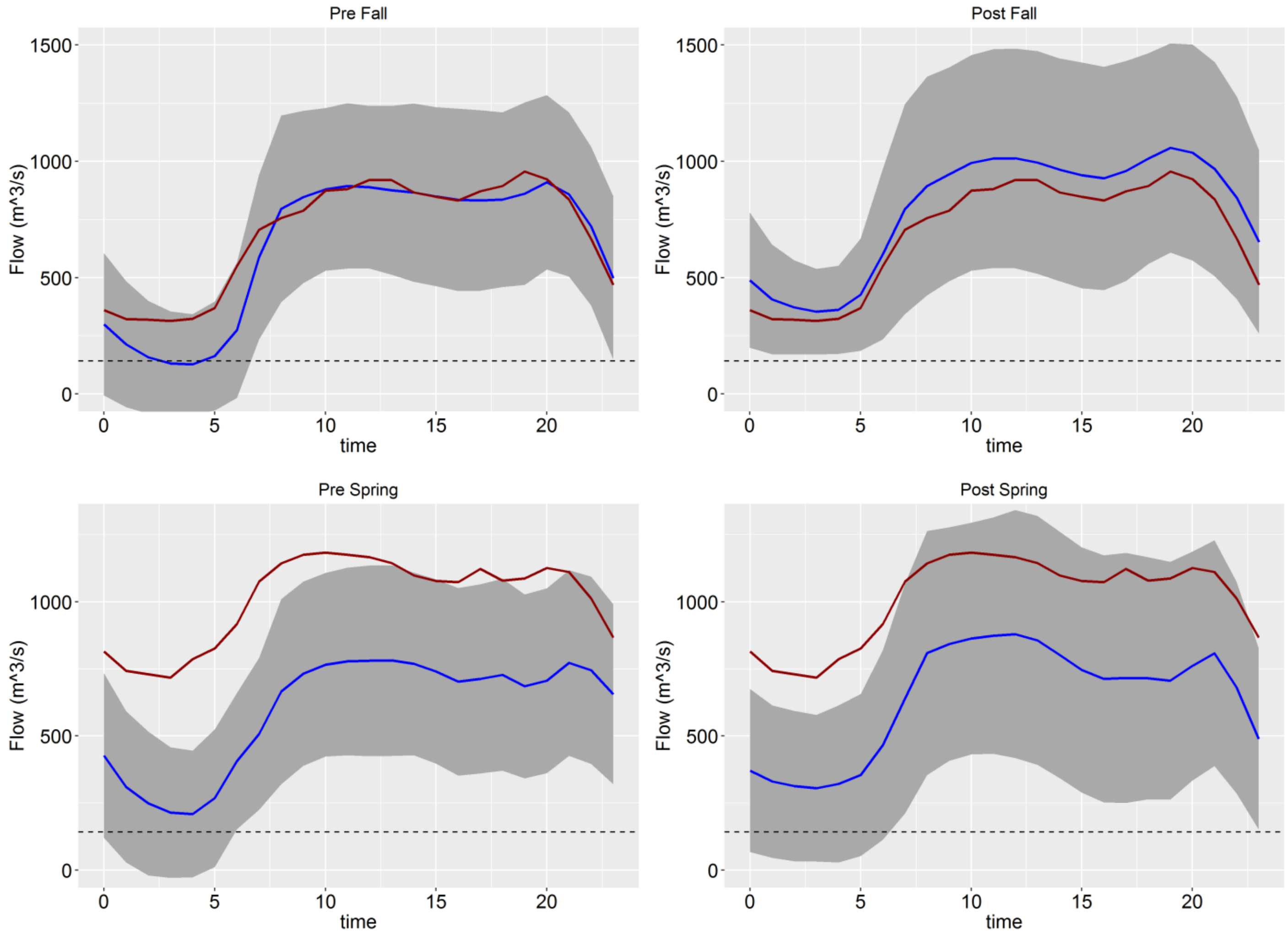

Figure A-6: The pattern of daily flow in MCR during the fall and spring study periods in pre (2007-2010) and post implementation (2011-2015) of minimum flows. Average hourly flow from 2015 (Spring) and 2014 (Fall) are shown in red, while the average of all data pooled is shown in blue (pre, post) are shown in dark 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.

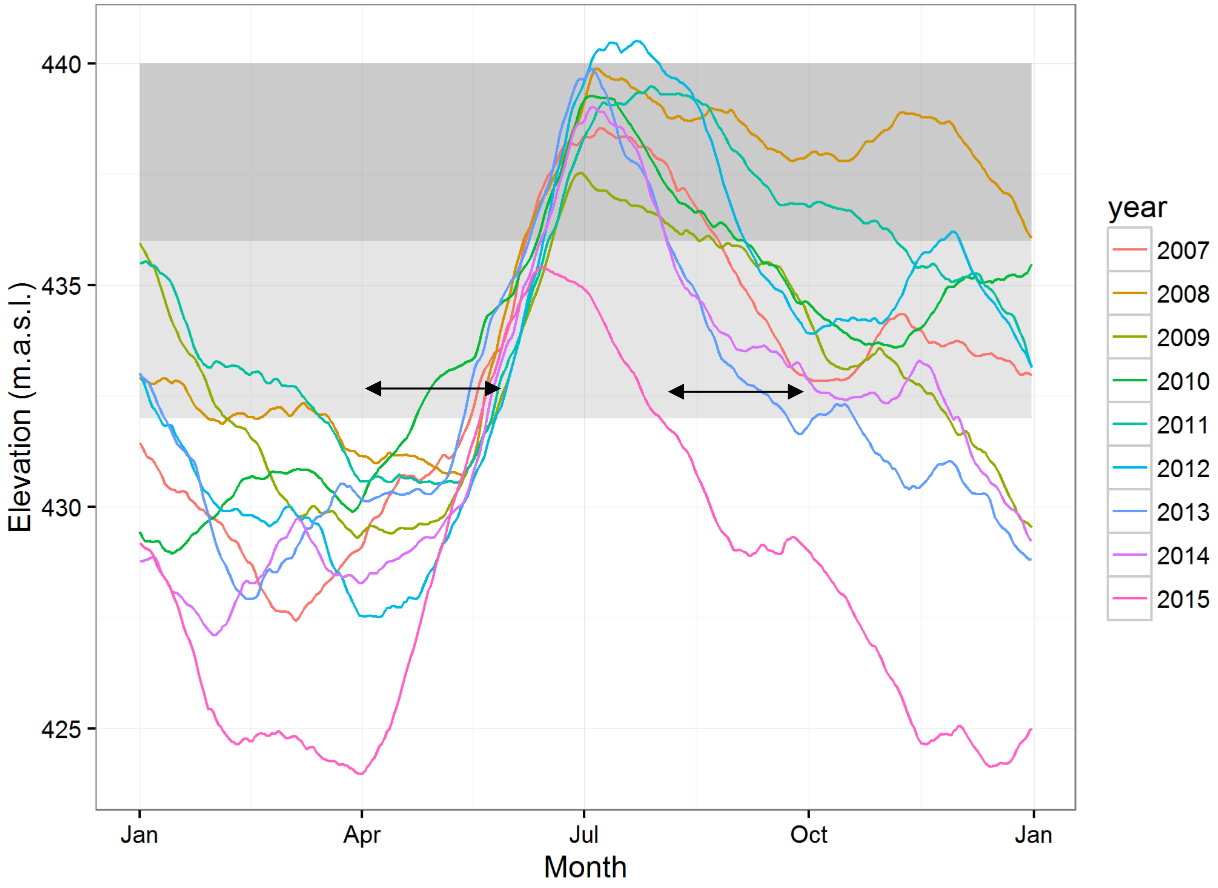

Figure A-7: Backwatering of Arrow Lakes Reservoir (ALR) into MCR Reach 3 and Reach 4 with typical spring and fall deployment periods occurring between the arrows. The vertical axis shows elevations in the normal operating range of ALR. Light grey shading denotes R3 was backwatered; dark grey shading denotes R3 and R4 were backwatered.

Periphyton Production Models

Table A-1 provides a summary of the model averaging results. A total of 64 models were competed using model averaging for each response in the spring and fall. In general, there were 6 to 10 plausible models for each response in the spring and fall.

Table A-1: Summary of the number of plausible models identified using model averaging (those with a ∆AIC <3) and the range of pseudo R^2 values for selected models for samplers across all transects.

MCR - Full Transect	Fall		Spring	
Periphyton Response	# of plausible models	range of pseudo R^2	# of plausible models	range of pseudo R^2
Abundance	3	0.47 – 0.48	3	0.54
biovolume	9	0.38 – 0.39	4	0.56 – 0.58
chlorophyll-a	9	0.39 - 0.40	4	0.81
% good forage	14	0.19 – 0.22	16	0.03 - 0.07
Simpson's Index	22	0.05 – 0.09	9	0.18 – 0.20
Species Distinction	9	0.06 – 0.09	5	0.43 – 0.44

Benthic Invertebrate Production Models

Table A-2 provides a summary of the model averaging results. A total of 64 models were competed using model averaging for each response in the spring and fall. In general, there were typically 7 to 11 plausible models for each response in the spring and fall. Since invertebrate distributions are more variable, and more samples are required to obtain better representation than periphyton, it is not surprising that more plausible models were identified for periphyton than for invertebrates.

Table A-2: Summary of the number of plausible models identified using model averaging (those with a ∆AIC <2) and the range of pseudo R^2 values for selected models for samplers across all transects.

MCR - Full Transect	Fall		Spring	
Benthic Response	# of plausible models	range of pseudo R^2	# of plausible models	range of pseudo R^2
Abundance	7	0.56 – 0.57	5	0.54 – 0.55
Biomass	12	0.38 – 0.40	6	0.25 – 0.29
Good Forage (EPT and D)	4	0.42 – 0.44	8	0.24 – 0.26
Hilsenhoff Biotic Index	9	0.05 – 0.08	7	0.40 – 0.43
Simpson's Index	19	0.11 – 0.12	19	0.25 – 0.29
Species Distinctiveness	10	0.22 – 0.24	8	0.38 – 0.41

APPENDIX B DIGITAL DATA TABLES AND FIGURES