

Columbia River Project Water Use Plan

Revelstoke Flow Management Plan

Mid-Columbia River Ecological Productivity Monitoring

Implementation Year 11

Reference: CLBMON#15b

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

Study Period: 2017

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PROGRAM NO. CLBMON-15B

**MIDDLE COLUMBIA RIVER ECOLOGICAL PRODUCTIVITY
MONITORING, 2007-2017**

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ACRONYMS AND ABBREVIATIONS

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



DEFINITIONS

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

Term	Definition
Accrual rate	A function of cell settlement, actual growth and losses (grazing, sloughing)
Autotrophic	An organism capable of synthesizing its own food from inorganic substances, using light or chemical energy
Benthic	Organisms that dwell in or are associated with the sediments
Benthic production	Production originating from both periphyton and benthic invertebrates
Catastrophic flow	Flow events that have population level consequences of >50% mortality
Cyanobacteria	Bacteria-like algae having cyanochrome as the main photosynthetic pigment
Diatoms	Algae that have hard, silica-based "shells" frustules
Eutrophic	Nutrient-rich, biologically productive water body
Freshet	The flood of a river or stream from melted snow in the spring
Functional Feeding group	(FFG) Benthic invertebrates can be classified by their foraging mechanisms as functional feeding or foraging groups
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.
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
Microflora	The sum of algae, bacteria, fungi, <i>Actinomyces</i> , etc., in water or biofilms
Morphology, river	The study of channel pattern and geometry at several points along a river
Picoplankton	Minute algae that are less than 2 microns in their largest dimension
Peak biomass	The highest density, biovolume or chl-a attained in a set time on a substrate
Periphyton	Microflora that are attached to aquatic plants or solid substrates
Phytoplankton	Algae that float, drift or swim in water columns of reservoirs and lakes
Ramping of flows	A progressive change of discharge into a stream or river channel
Reach 3	The section of river extending from the Jordan River to the Illecillewaet River
Reach 4	The section of river extending below Revelstoke Dam to the Jordan River
Riffle	A stretch of choppy water in a river caused by a shoal or sandbar
Riparian	The interface between land and a stream or lake
Substrates	The bottom material (boulder cobble sand silt clay) of a stream or lake.
Taxa Taxon	Taxonomic group(s) of any rank, such as a species, family, or class.
Thalweg	A line connecting the lowest points of a river, usually has the fastest flows

**Suggested Citation:**

Schleppe, J., R. Plewes, H. Larratt, A. Duncan. 2018. CLBMON-15b Middle Columbia River Ecological Productivity Monitoring, Annual Report 2016. Okanagan Nation Alliance with Ecoscape Environmental Consultants Ltd. & Larratt Aquatic Consulting Ltd. 71 pp.

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Keywords:

Middle Columbia River, Ecological Productivity, Minimum Flows Management



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ACKNOWLEDGEMENTS

Numerous employees of BC Hydro have been instrumental in the successful implementation of this project, including Guy Martel, Trish Joyce, Jason Watson. They have provided helpful suggestions and discussions that have assisted in our understanding of the complexities of MCR. We also want to thank Michael Zimmer, Project Manager for ONA and other Ecoscape personnel, whom over the years have greatly contributed to this project. Sue Salter of Cordillera Consulting processed and identified the benthic invertebrate samples. Dr. Jason Pither provided valuable support with statistical analyses and data interpretation in 2010 through 2012. Dr. John Stockner contributed valuable QA/QC by providing confirmation of periphyton identifications in 2010 - 2012. The field crews of Golder Associates Ltd. and Triton Environmental Consultants Ltd. are also acknowledged for the collection and field-processing of fish stomach samples that were used in previous years. Finally, we acknowledge our families and spouses who continue to be understanding of the commitments required to successfully undertake this project.



CLBMON 15B Status of Objectives Management Questions and Hypotheses After Year 11

Objectives	Management Questions	Management Hypotheses	Year 11 (2017) Status
<p>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.</p>	<p>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?</p>	<p>Ho₁: The implementation of the 142 m³/s minimum flow release does not change the spatial area of productive benthic habitat for periphyton or benthic invertebrates in the MCR.</p>	<p>Ho₁: The hypothesis is rejected, but only under certain operating conditions. The spatial area supporting benthic communities increased with minimum flows, predominantly in Reach 4, but also in Reach 3 during periods when ALR reservoir did not create backwater conditions. The spatial area of productive habitat is determined by the BC Hydro operating regime because the operating regime is directly responsible for the wetted history. 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. The spatial model developed during 2017 and 2018, currently considers chlorophyll-a and invertebrate biomass. The results of the model indicate that minimum flows increased productivity during periods of low ALR reservoir elevations, and the minimum flow effects were more apparent for periphyton and invertebrates in Reach 4 than in Reach 3.</p>
	<p>Q.2. What is the effect of implementing minimum flows on the area of productive benthic habitat?</p>	<p>Ho₂: The implementation of the 142 m³/s minimum flow release does not change the total biomass accrual rate of periphyton in the MCR.</p>	<p>Ho₂: 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. ALR backwatering increases the total area of productive habitat in the MCR, but does not appear to alter the accrual rates.</p> <p>The overall benefits of minimum flow are greatest under the following conditions:</p> <ul style="list-style-type: none"> • Periods of low daily flows (400 to 600 m³/s) that exceed 24 hours with low humidity and >10-15°C or <0°C 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 11

Objectives	Management Questions	Management Hypotheses	Year 11 (2017) Status
	<p>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?</p>	<p>Ho_{3A}: There are no changes in accrual rates of periphyton at channel elevations that remain permanently wetted by minimum flow releases.</p> <p>Ho_{3B}: There are no changes in accrual rates of periphyton at channel elevations that are periodically dewatered during minimum flow releases.</p>	<p>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. The 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 minimal effects on accrual. Peak flows associated with REV 5 or other high water events appear to reduce periphyton accrual rates and standing crop in permanently submerged habitats.</p> <p>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 do have 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.</p>
	<p>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</p>	<p>Ho_{4A}: The implementation of the 142 m³/s minimum flow release does not change the total abundance / biomass / diversity of benthic invertebrates in the MCR.</p>	<p>H_{4A}: 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 comparable levels 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. 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.</p>



CLBMON 15B Status of Objectives Management Questions and Hypotheses After Year 11

Objectives	Management Questions	Management Hypotheses	Year 11 (2017) Status
	trend in benthic productivity?	<p>Ho_{4B}:</p> <p>There are no changes in abundance/biomass/diversity of benthic invertebrates at channel elevations that remain permanently wetted by minimum flow releases.</p> <p>Ho_{4C}:</p> <p>There are no changes in abundance/biomass/diversity of benthic invertebrates at channel elevations that are periodically dewatered by minimum flow releases.</p>	<p>Ho_{4B}:</p> <p>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 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.</p> <p>Ho_{4C}:</p> <p>The hypothesis is accepted, but only under certain operating conditions. We conclude that minimum flows do not affect areas periodically dewatered located above the minimum flow elevation, but they probably had an effect in areas that were regularly exposed before the minimum flow operating regime because the data indicate that benthic invertebrate abundance, diversity, and biomass are positively associated with submergence. Daytime submergence, seasonal patterns and operating cycles were also important determinants of benthic accrual and must also be considered.</p>
	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?	<p>Ho₅:</p> <p>The implementation of the 142 m³/s minimum flow release does not change the availability of fish food organisms in the Middle Columbia.</p>	<p>Ho₅:</p> <p>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 to 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.</p> <p>The overall benefits of minimum flow are greatest under the following conditions:</p> <ul style="list-style-type: none"> • Periods of low daily flows that exceed 24 hours with freezing or high average daytime temperatures; • Dewatering periods greater than 12 hours. <p>Substrates submerged for 450 to 500 hours (10 to 11 hours per day over approximately 45 days) during daytime hours had the greatest availability of preferred fish food items, which are generally EPT and Diptera. EPT and Dipteran biomass was greatest in areas submerged for at least 750 to 1000 hours over at least 46 days. Both periphyton and invertebrates showed similar responses, suggesting that overall productivity and food for fish is directly affected by the operational cycles that create either submerged or 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.</p>

EXECUTIVE SUMMARY

Aquatic habitats in the Middle Columbia River (MCR) are heavily influenced by 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 m³/s from Revelstoke Dam (REV) to the MCR. One objective of the minimum flow strategy is to enhance the productivity and diversity of benthic communities in the MCR by increasing the permanently wetted area. The goal of CLBMON-15b Ecological Productivity Monitoring is to provide long-term data on benthic productivity in the MCR using artificial substrate samplers to assess how minimum flow influences benthic communities and availability of food for fish. Data were collected from 2007 to 2010, pre-implementation of minimum flows, and from 2011 to 2017, post-implementation of minimum flows. Concurrent with the implementation of minimum flows, a fifth generating unit (REV 5) was added in December 2010, increasing the maximum flow discharge from 1699 to 2124 m³/s. This report summarizes the findings of all study sessions to date, with a focus on Spring 2017 and on the development of a spatial model.

Minimum flows provide benefits to benthic invertebrate and periphyton communities in the MCR by ensuring a portion of the channel area remains wetted and productive at all times. However, the benefit of minimum flows is dependent on flow management. The spatial productivity models developed confirmed that the benefit of minimum flow is dependent on the extent of ALR (Arrow Lakes Reservoir) backwatering and the time of year, with benefits limited to periods where ALR is not backwatered in Reach 3 (which starts approximately 11 km downstream of the dam). Minimum flows provide more of a benefit to productivity in Reach 4 (closer to the dam) compared to Reach 3. Minimum flows benefit productivity most during periods when average daytime flows (~500 to 1200 m³/s) over the preceding 30 to 70 days are lower (e.g., 400 to 600 m³/s versus 1200 to 1600 m³/s). 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 m³/s flow, provided that flows of 400 to 600 m³/s occurred every day for at least 9 daytime hours.

Habitat conditions of the MCR occurred in three distinct zones of varying submergence - the permanently submerged zone, the lower varial zone and the upper varial zone. The permanently wetted zone showed high periphyton 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 upper varial zone was the less productive, located at elevations that were frequently dewatered. Over the 11 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 to 70 days.

Flows during the week preceding sample collection had the greatest effect on the species composition of benthos. Benthic productivity in the permanently submerged and lower varial zones were influenced by water temperature. Warmer water temperatures in Spring were correlated with higher productivity (chl-a). For both periphyton and invertebrates, productivity was greatest within the lower varial zone at mid-channel elevations extending from just below the elevation of minimum flow to slightly above it. Like all large rivers, diatoms dominated the periphyton, but diversity was lower than in unregulated rivers of similar size and latitude.

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 overall MCR benthic productivity. Varial zone areas submerged for at least 9 to 12 hours per day (400 to 500 hours over



the deployment period) were typically as productive as areas constantly submerged by minimum flows. However, productivity in the varial zones was dependent upon additional factors such as daytime air temperature and operating regime. Submergence times in excess of 1000 hrs over the deployment period (1056 hours on average) appear to increase productivity compared to less time. Further, the benefits of minimum flows were lessened by backwatering from Arrow Lakes Reservoir when it submerged habitats in the varial zone substrates that would otherwise have desiccated.

Overall benthic community structure was stable at the family taxonomic level across all sites of variable submergence, with similar representation between years. However, there were some taxonomic differences between the three zones. For example, filamentous green algae were more prevalent near the edge of permanently wetted areas (T2), and in the lower varial zone (T3/T4) where stable substrates were present. EPT (Ephemeroptera, Plecoptera and Trichoptera) 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 (Schleppe et al. 2014). These data support the assertion that flow management exerts a powerful influence on the MCR periphyton and invertebrate community.

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

Peak production of either benthic invertebrates or periphyton in the MCR was not achieved within two months from the time of first wetting and may take longer than six months to fully develop if sites experience frequent dewatering, particularly in the spring when growth rates are slow.

Results from previous years showed 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.

Submergence was consistently identified as the single most important determinant of benthic production in the MCR. 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, peak flows exceeding 1800 m³/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 spatial model of productivity was generated for the MCR using a hydrologic model created in Telemac by Northwest Hydraulics; it was used to determine the wetted history of the river. Once the wetted history was known, productivity for a given river segment was determined using growth or accrual curves (periphyton) from this project or as modified using data from the Lower Columbia River (invertebrates). Mortality or death curves from the Lower Columbia River were also used or modified for the spatial model. Using this information, the spatial productivity of the MCR was determined for every hour over the duration of the study period. The results of the model confirmed earlier statistical results,

that the effects of minimum flow on productivity in the river are apparent in Reach 4 during some periods of the year. In Reach 3, the effects of minimum flows are greatest during periods when ALR is not backwatering. The spatial model allowed us to explicitly test and confirm the effects of minimum flows on the MCR. Next year, the spatial productivity model will be used to determine the area of productive habitat within the MCR Reaches.

In the absence of other operating constraints, minimum flows benefit the benthic productivity in the MCR, but alternative operating regimes that have higher average daily flows without permanent minimum flows may also provide habitat conditions that are equally productive.

TABLE OF CONTENTS

ACRONYMS AND ABBREVIATIONS	I
DEFINITIONS II	
ACKNOWLEDGEMENTS	IV
EXECUTIVE SUMMARY	IV
1.0 INTRODUCTION	1
1.1 Objectives, Questions, and Hypotheses	2
2.0 METHODS	7
2.1 Study Area and Sampling Locations.....	7
2.2 Periphyton and Invertebrate Community Sampling Using Artificial Samplers.....	9
2.2.1 Artificial Sampler Design and Deployment	9
2.2.2 Time Series Samplers.....	13
2.2.3 Artificial Sampler Retrieval	14
2.2.4 Post Processing of Periphyton Samples	14
2.2.5 Post Processing of Invertebrate Samples	15
2.3 Variable Descriptions and Analytical Methods	15
2.3.1 Determination of Submergence.....	15
2.3.2 Variables and Statistical Analyses	16
2.3.3 Time Series and Artificial Sampler Assumptions	17
2.4 Spatial Productivity Model	18
2.4.1 River Model.....	18
2.4.2 Productivity Model Notation	19
2.4.3 Growth and Death Curves.....	24
3.0 RESULTS	27
3.1 Biophysical Characteristics of the Middle Columbia River	27
3.1.1 Light and temperature in submerged areas of MCR.....	27
3.1.2 Pattern of Flow in MCR	27
3.2 Periphyton	28
3.2.1 Overview of MCR Periphyton Biofilms.....	28
3.2.2 Periphyton Ash-Free Dry Weight.....	29
3.2.3 Characteristics of MCR Periphyton Algae	29
3.3 Drivers of MCR Periphyton Communities	30
3.3.1 Effects of Reservoir Donation	30
3.3.2 Effects of Flows	30
3.3.3 Effects of Water Depth	32
3.3.4 Effects of Season.....	33
3.3.5 Reach Effects	35
3.3.6 Effects of Backwatering.....	36
3.3.7 Periphyton Spatial Productivity Models	37
3.4 Benthic Invertebrates.....	39
3.4.1 Yearly Comparisons of Benthic Invertebrate Sampling	39
3.4.2 Benthic Invertebrate Production Models.....	40
3.4.3 Benthic Spatial Productivity Models	40
4.0 DISCUSSION	42
4.1 Q.1. What is the composition, distribution, abundance and biomass of periphyton and benthic invertebrates in the section of MCR subjected to the influence of minimum flows?.....	42
4.2 Comparison of MCR to other Large Rivers	43

4.2.1	Permanently Submerged Areas	44
4.2.2	Lower Varial Zone (mid-channel)	45
4.2.3	Upper Varial Zone.....	45
4.2.4	Varial Zone Boundary Conditions.....	46
4.2.5	Benthic Community Determinants and Composition	46
4.2.6	Effects of Flow Ramping	48
4.2.7	Benthic Recovery from Dewatering	48
4.2.8	Seasonal Growth Patterns	49
4.3	Q.2. What is the effect of implementing minimum flows on the area of productive benthic habitat?.....	49
4.4	Q3. What is the effect of implementing minimum flows on the accrual rate of periphyton biomass in the MCR? Is there a long-term trend in accrual?	50
4.5	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?	52
4.6	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?	53
5.0	REFERENCES	54

FIGURES

Figure 2-1:	Map of the study area and sampling locations. Site labels are defined in Table 2-2. R = reach, S = site, T= transect, TSS=Time Series Sampler.....	8
Figure 2-2:	Conceptual drawing of transect positions and periphyton establishment in MCR using data collected from fall 2010 and 2012 in Reach 4	10
Figure 2-3:	Conceptual drawing of periphyton establishment in MCR using data collected from Fall 2010 and 2011 samples in Reach 3.....	11
Figure 2-4:	Schematic drawing of the artificial substrate sampler used in MCR	12
Figure 2-5:	Chl-a growth curve Spring and Fall curves derived from T1 accrual data from 2011 to 2017 and 6 month chl-a samples. Winter and Summer curves derived from Schleppe et al. 2015 with adjusted asymptotes (peak chl-a).	25
Figure 2-6:	Growth curve for invertebrate biomass adjusted from Schleppe et al. 2015.	26
Figure 3-1:	Periphyton productivity by year and season in Reach 3 and Reach 4 in the Thalweg (T1) zone. Spring 2015, Fall 2011 and Fall 2012 had higher flows than average (Table A-1).....	32
Figure 3-2:	Total biovolume of MCR periphyton and chlorophyll-a in spring for 2010 to 2017 by sampler location (T1 deepest in thalweg to T7 shallowest on floodplain). The blue line represents the mean of all years and the red line represents the mean for spring 2017.	33
Figure 3-3:	MCR Periphyton seasonal responses by site, 2011 to 2013 abundance and chl-a are presented in Appendix C.	35
Figure 3-4:	Upper varial zone (T5,T6) periphyton productivity in R3, 2010 – 2017 by year and season. All sampling periods were affected by backwatering except Spring and Fall 2013 (Table A-1).....	37
Figure 3-5:	Comparison of Pre-Post Implementation of minimum flows for periphyton chlorophyll-a. The dotted box represents when R3 is typically backwatered from ALR and the arrows represent the typical range of Spring and Summer deployment periods.....	39
Figure 3-6:	Comparison of Pre-Post Implementation of minimum flows for benthic invertebrate biomass. The dotted box represents when R3 is typically backwatered from ALR and the arrows represent the typical range of Spring and Summer deployment periods.....	41

TABLES

Table 1-1: Key Management Questions and Hypotheses, with Pertinent Components to Address Them	5
Table 2-1: Description of transect depths sampled in Reach 3 and 4	9
Table 2-2: Summary of samples collected from artificial sampler deployment and retrieval in 2017.....	13
Table 3-1: Ash-free dry weight averaged by season (Spring/Fall) and for both seasons in all study years (2007-2017)	29
Table 3-2: Range of periphyton metrics in MCR R4 and R3 (all depths combined) in 2007 – 2017.....	31
Table 3-3: Range of periphyton metrics in MCR (R4 and R3) by season, 2007 – 2017	34
Table 4-1: Summary of average MCR periphyton metrics from spring and fall 2010 – 2017 deployments, with comparison to oligotrophic, typical, and productive large rivers	44

APPENDICES

Appendix A – Supplemental Results

Figure A-1:	The pattern of daily water temperature in MCR by reach during the spring study period. The blue line represents the mean from 2011 to 2017 (Spring) and red represents the mean water temperature in 2017 from all submerged samplers. The green line represents the average temperature of exposed sites in Spring 2017. Data were pooled for spring periods between 2011 – 2017 (\pm SD in grey).	61
Figure A-2:	Spring daily pattern of light intensity (lux) while samplers were submerged in the MCR at varying depths, where T1 is the deepest and T6 is the shallowest for samplers. The blue line represents the mean from 2011 to 2017 (\pm SD in grey) and red represents the mean 2017 spring data from all submerged samplers. The x-axis is time in hours of the day (0:00 to 24:00).	62
Figure A-3:	Spring daily pattern of light intensity (lux) in the MCR when samplers were exposed (out of the water). T3 is the deepest and T6 is the shallowest for samplers. Noting T1 and T2 were continuously submerged so are not included in the above figure. The blue line represents the mean from 2011 to 2017 (\pm SD in grey) and red represents the mean spring 2017 data from all exposed samplers. The x-axis is time in hours of the day (0:00 to 24:00).	63
Figure A-4:	The pattern of daily flow in the MCR during the spring study periods in pre (2007-2010) and post implementation (2011-2017) of minimum flows. Average hourly flows from 2017 (Spring) are shown in red, while the average of all data pooled (2010-2017) is shown in blue. The standard deviation of average hourly flow across all years pooled is shown in grey. The minimum flows are shown as a black dotted line.	64
Figure A-5:	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.	65
Table A-1:	Flow summary table for each deployment period, summary statistics are calculated from mean daily flows.	66
Figure A-6:	Periphyton total abundance compared by season and site 2011-2013.	68
Figure A-7:	Periphyton chl-a compared by season and site 2011-2013.	68
Table A-2:	Summary of fish food index models with a Δ AIC <3.	69
Figure A-8:	Standardized Residual plot for R3 periphyton chl-a model without interaction term.	70
Figure A-9:	Standardized Residual plot for R4 periphyton chl-a model without interaction term.	70
Figure A-10:	Standardized Residual plot for R3 benthic invertebrate biomass model without interaction term.	71
Figure A-11:	Standardized Residual plot for R4 benthic invertebrate biomass model without interaction term.	71

Appendix B – Digital Data

The digital appendix contains summary statistics of data in Excel.

Appendix C – Supplemental Methods and Results



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 backwatering from Arrow Lakes Reservoir (ALR), and tributary inflows. In 2007, introduction of the Columbia River Water Use Plan (WUP) supported implementation of a year-round minimum flow from REV of 142 m³/s to mitigate the effects of variable flow releases. In December 2010, BC Hydro (BCH) added a fifth generating unit (REV 5), that increased the maximum possible flow discharge of REV from 1699 to 2124 m³/s.

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

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

In the study years prior to the implementation of minimum flows, water releases from Revelstoke Dam varied from 8.5 m³/s to 1700 m³/s, depending on power demands, and could result in sudden water fluctuations between 3 to 5 vertical meters. With the initiation of REV 5 and the minimum flows operating regime (2011-present), flows have ranged from 142 m³/s to 2124 m³/s. These variable water releases and backwatering from the downstream Arrow Lakes Reservoir (ALR) largely determine the extent of submergence of river substrates in the MCR.

The results from the Ecological Productivity Monitoring will be integrated with other BC Hydro monitoring programs, including Physical Habitat Monitoring (CLBMON15a), Fish Population Indexing Surveys (CLBMON16), Juvenile Habitat Use (CLBMON17) and Adult Habitat Use (CLBMON18). The findings from these monitoring programs will be used collectively to evaluate 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. Specifically, the data collected in CLBMON15b 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 11 of the monitoring program, and focuses on Spring 2017 (Year 11) sampling session. At this time, the project is proposed to transition from understanding the specific effects of submergence due to minimum flows and important environmental factors (e.g., velocity, light, and depth), to understanding the spatial effects of the operating regime on productivity.



1.1 Objectives, Questions, and Hypotheses

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

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

The first objective was satisfied by the basic study design developed by Perrin et al. (2004). A conceptual model was developed (Figure 1-1) to address the second and third objectives, and to understand the potential interactions of the complex factors affected by changes in flow. With each study session, our understanding of the relative importance and role of each parameter increases. This model highlights the many variables and complex interactions that can influence benthic productivity and ultimately food for fish. Species specific life histories, such as diurnal timing and habitat selection for egg laying insects versus hydropeaking frequency, are also an important consideration (Kennedy et al. 2016), and this has not been fully explored because it would add further, complex interactions. Greyed boxes with bolded text indicate the parameters under assessment in this study to address BC Hydro's management questions. At the forefront of the model are BC Hydro operations that determine quantity and duration of water release. Flows directly influence factors including velocity, turbulence, depth, submergence, scour, etc. and therefore have a direct effect on benthic productivity.

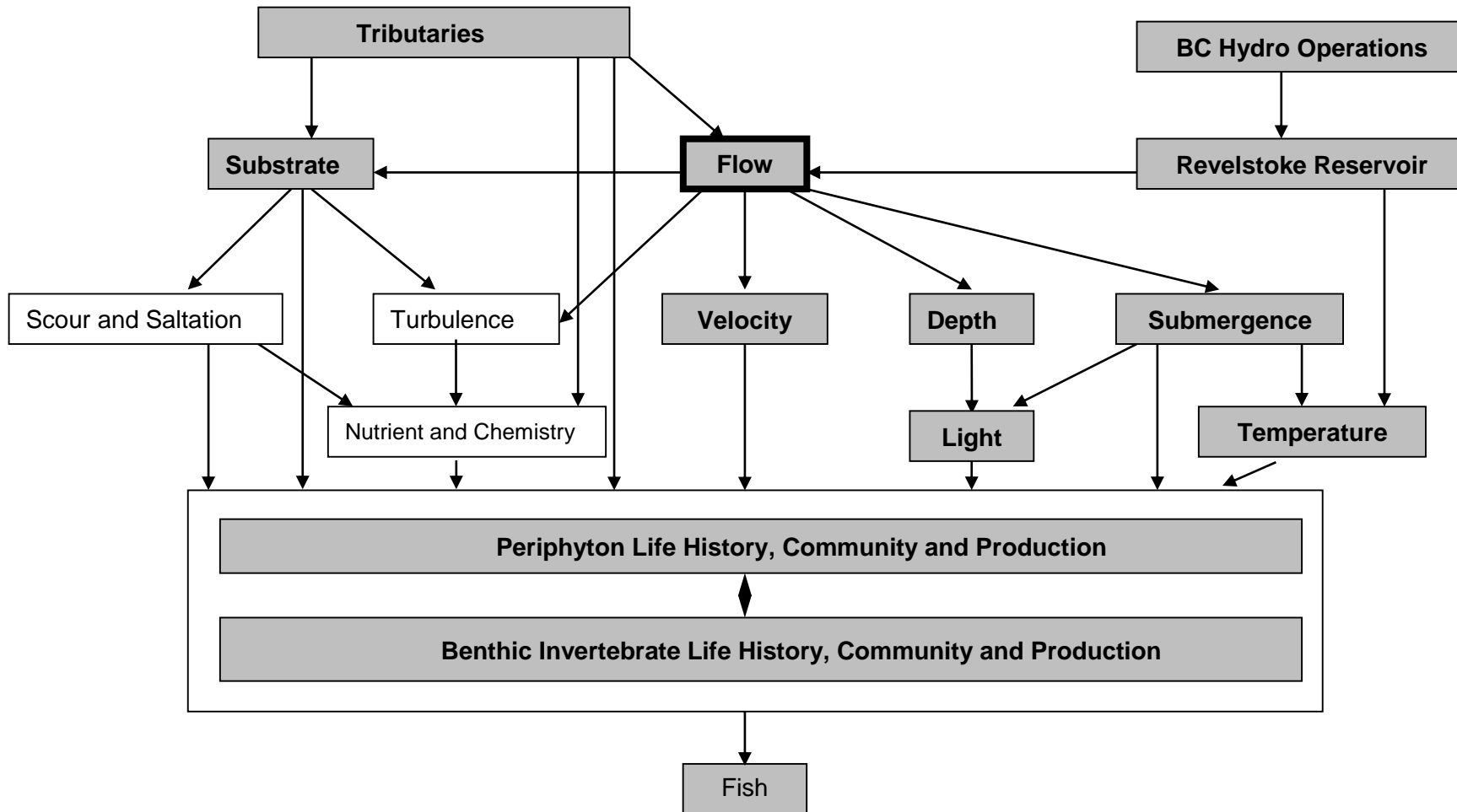


Figure 1-1: Conceptual interactions model of habitat variables and benthic production as they relate to food for fish in MCR. Parameters shaded in grey, with bolded text represent parameters under assessment in this study.



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

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 directly influenced by flows including area of wetted habitat, and frequency and duration of submergence. From this, we were able to infer the effects of the operating regime including minimum flows. This approach is advantageous because it allows consideration of alternative operating regimes that may be as, or more, beneficial than minimum flow from both a productivity and a financial perspective. The 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 the MCR under a minimum flow or alternative operating regime. The ultimate goal is to identify and describe what habitat attributes are most influential and to identify how implementation of different operational regimes may affect benthic productivity in MCR including both a minimum flow and a REV 5 operating regime.

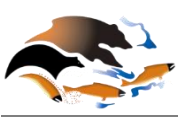
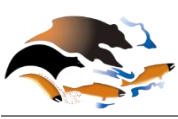


Table 1-1: Key Management Questions and Hypotheses, with Pertinent Components to Address Them

Key Management Questions	Management Hypotheses:	Study Components to Address Management Questions/Hypotheses
<p>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?</p> <p>Q2. What is the effect of implementing minimum flows on the area of productive benthic habitat?</p>	<p>Ho₁. The implementation of the 142 m³/s minimum flow release does not change the composition, distribution, abundance, biomass, or spatial area of productive benthic habitat for periphyton or benthic invertebrates in MCR.</p>	<p>Artificial sampler arrays are deployed across the range of flows/elevations of the MCR. Data collection includes:</p> <ul style="list-style-type: none"> • Abundance –periphyton & invertebrates • Diversity – taxonomy indices for periphyton and invertebrates • Production/Biomass – chlorophyll-a (chl-a), ash-free dry weight (AFDW)/dry weight (DW), biovolume, benthic invertebrate biomass • Natural substrate comparisons <p>Productive habitat area is considered using the analogous measure submergence as a surrogate for minimum flow. Spatial productivity models were used to model periphyton chl-a and invertebrate biomass based on hourly submergence and exposure. The submergence and exposure were determined using a hydrological model. Daily productivity estimates from the models were compared before and after the implementation of minimum flows for Reach 3 and 4.</p>
<p>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?</p>	<p>Ho₂. The implementation of the 142 m³/s minimum flow release does not change the total biomass accrual rate of periphyton in MCR.</p> <p>Ho_{2A}. There are no changes in accrual rates of periphyton at channel elevations that remain permanently wetted by minimum flow releases.</p> <p>Ho_{2B}. There are no changes in accrual rates of periphyton at channel elevations that are periodically dewatered by minimum flow releases.</p>	<p>Artificial samplers and time series samplers are deployed across the range of submerged habitat areas on the MCR. Data collection includes:</p> <ul style="list-style-type: none"> • Abundance • Diversity – taxonomy indices for periphyton and invertebrates • Production/Biomass – chl-a, AFDW/DW, biovolume • Nano-flora heterotrophic plate counts (HTPC) <p>Periphyton production (both accrual and peak biomass) are assessed using a variety of different measures of productivity. Periphyton productivity is considered using the analogous measure submergence as a surrogate for minimum flows because this data is easier to use in models. Periphyton models are developed to test the effects of submergence on periphyton peak biomass. 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.</p>
<p>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?</p>	<p>Ho₃. The implementation of the 142 m³/s minimum flow release does not change the total abundance/biomass/diversity of benthic invertebrates in MCR.</p> <p>Ho_{3A}. There are no changes in abundance/biomass/diversity of benthic invertebrates at channel elevations that remain permanently wetted by minimum flow releases.</p> <p>Ho_{3B}. There are no changes in abundance/biomass/diversity of benthic invertebrates at channel</p>	<p>Artificial samplers are deployed across the range of submerged habitat areas on the MCR. Data collection includes:</p> <ul style="list-style-type: none"> • Abundance • Diversity – taxonomy indices for periphyton and invertebrates • Production/Biomass – biomass <p>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</p>



elevations that are periodically dewatered by minimum flow releases.

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?

Ho₄.

The implementation of the 142 m³/s minimum flow release does not change the availability of fish food organisms in the Middle Columbia.

Potential effects of minimum flow on food for fish are considered using an index of fish food availability. The Fish Food Index (FFI) consists of three parameters, Relative Abundance, Relative Biomass, and Fish Food Preference for each different benthic taxon. Higher index values indicate a higher prevalence of preferred benthic species available as food for fish. This index is useful because it considers availability (abundance), biomass, and fish preference of benthic invertebrates as food. The fish food index is used in statistical models where a variety of measures of submergence (analogous to minimum flow) are used to test fish food availability.



2.0 METHODS

2.1 Study Area and Sampling Locations

The MCR is a section of the Upper Columbia River adjacent to the town of Revelstoke, British Columbia, encompassing approximately 38.5 km of river between the Revelstoke Dam and the Upper Arrow Lake Reservoir (ALR) near Galena Bay. The MCR is sectioned into four Reaches, and this study focused on Reaches 4 and 3, that have 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 1 to 5 m depending on flows. Reach 4 encompasses large areas of stable substrate consisting predominantly of larger gravels, cobble and boulder, and lesser amounts of sands, pebbles and smaller gravels that occur beneath and within the interstitial spaces of the cobble-armoured surface. The bankfull width in Reach 4 ranges from 147 – 223 m (Perrin and Chapman 2010a). Big Eddy occurs at the interface of Reaches 4 and 3, immediately downstream of the Jordan River. It consists of a large, 250 m wide, deep eddy bounded along the right bank by a vertical rock face. This habitat unit provides > 6 m deep water refuge during periods of lower flow and could be considered its own reach due to the unique habitat it provides.

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

The main tributaries that influence the MCR are the Jordan and Illecillewaet Rivers. 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.



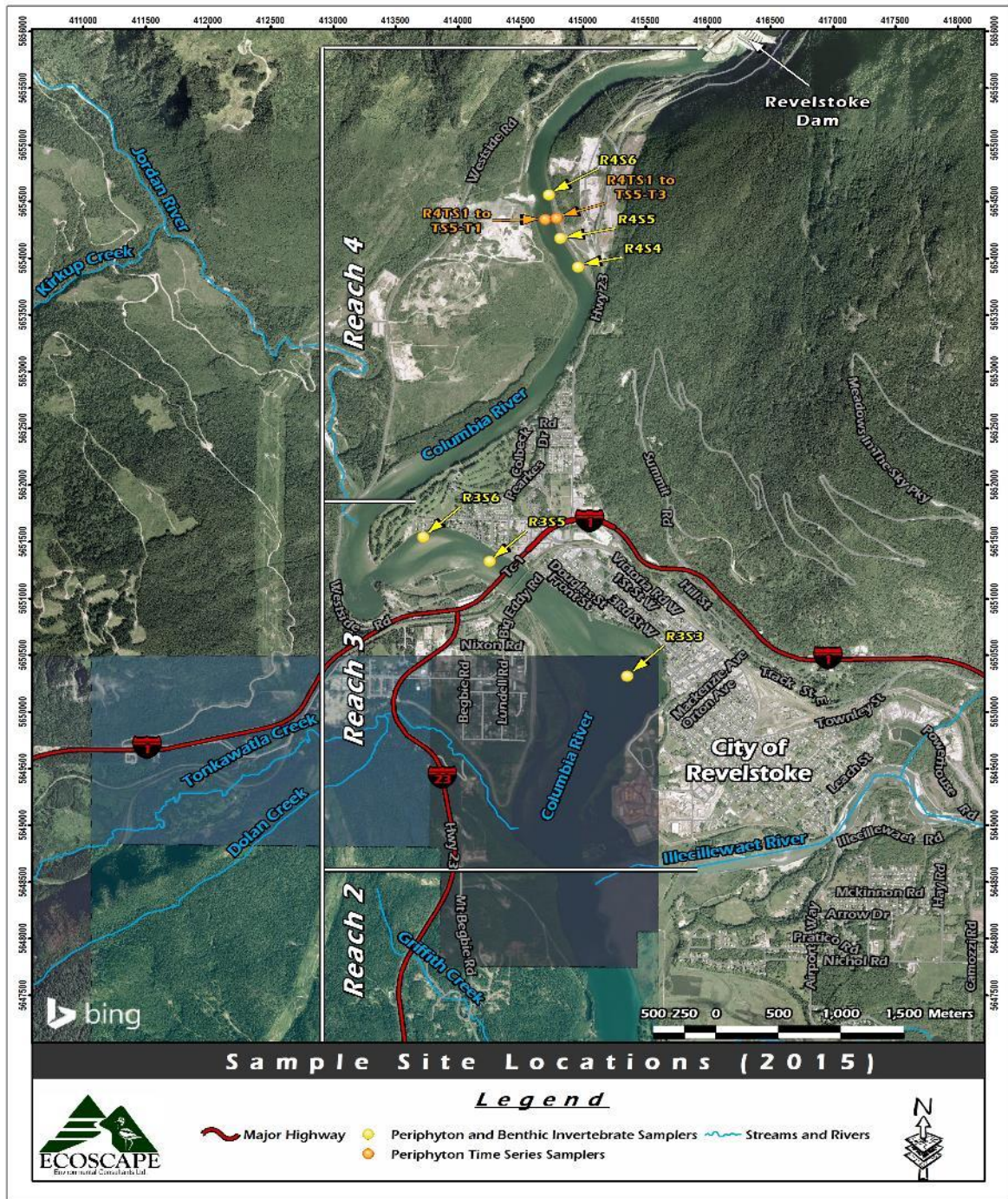


Figure 2-1: Map of the study area and sampling locations. Site labels are defined in Table 2-2. R = reach, S = site, T= transect, TSS=Time Series Sampler.





2.2 Periphyton and Invertebrate Community Sampling Using Artificial Samplers

2.2.1 Artificial Sampler Design and Deployment

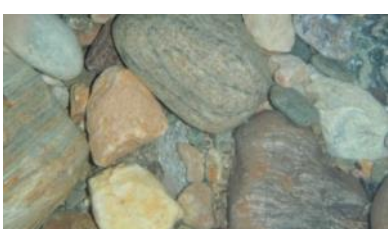
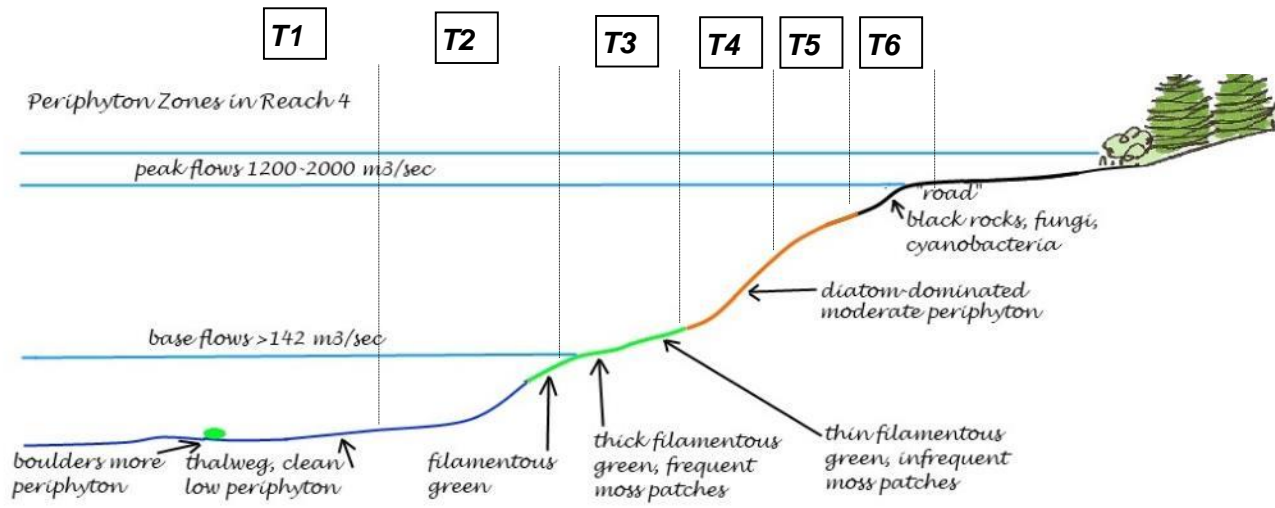
Year 11 of the CLBMON 15-b study involved a spring (2017) sampling session, where artificial samplers were placed in the river and left for a minimum of 44 days (Table 2-1). Data for earlier years are available in previous CLBMON15b reports, however the sample sites used in 2017 were consistent with previous years, and the same naming system was used to reference sampling sites. Site references include Reach, Site, and Transect. Samplers were deployed in Reach 3 (R3) at S3, S5, and S6. Reach 4 (R4) samplers were deployed at sites S4, S5, and S6.

Sampling sites at transect depths T1 through T6 were deployed in Reaches 3 and 4 as shown in Figures 2-2 and 2-3. Transect position refers to the position of the sampler within the river cross-section, as explained in Table 2-1. During the fall 2010 sampling session, a T7 position in the infrequently wetted floodplain was also used. This sampler elevation was subsequently deleted, and new sampling sites in Reach 4 at the bedrock (BR) location were studied instead. However, in spring 2017 Big Eddy (BE), bedrock (BR), Backwater areas (BW) sites were not sampled.

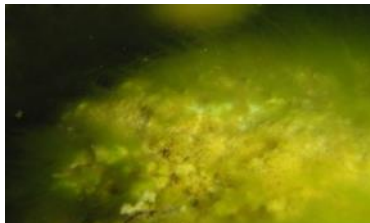
Table 2-1: Description of transect depths sampled in Reach 3 and 4.

Reach	Sampler	Relative depth/zone	Submergence	Years Sampled
3 and 4	T1	Mid channel / thalweg	Permanently submerged by minimum flows	2010-2017
	T2			2010-2017
	T3	Mid channel / lower varial zone	Submerged by flows from 200 to 800 cm/s	2010-2017
	T4			2010-2017
	T5	Upper varial zone	Submerged by flows > 1000 cm/s	2010-2017
	T6			2010-2017
	T7			Infrequently wetted floodplain

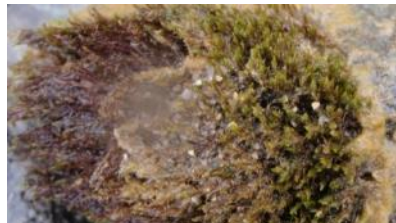




thalweg
(low periphyton)



filamentous green zone



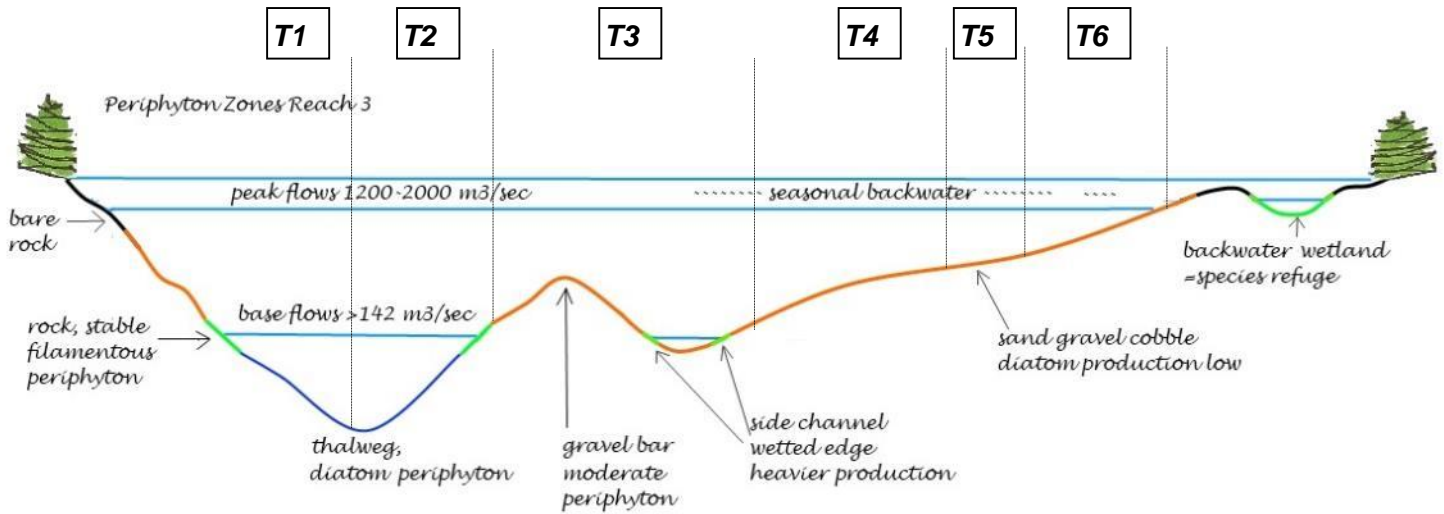
filamentous green + moss
zone



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 deployed April 10-11, 2017 (Table 2-2). 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.

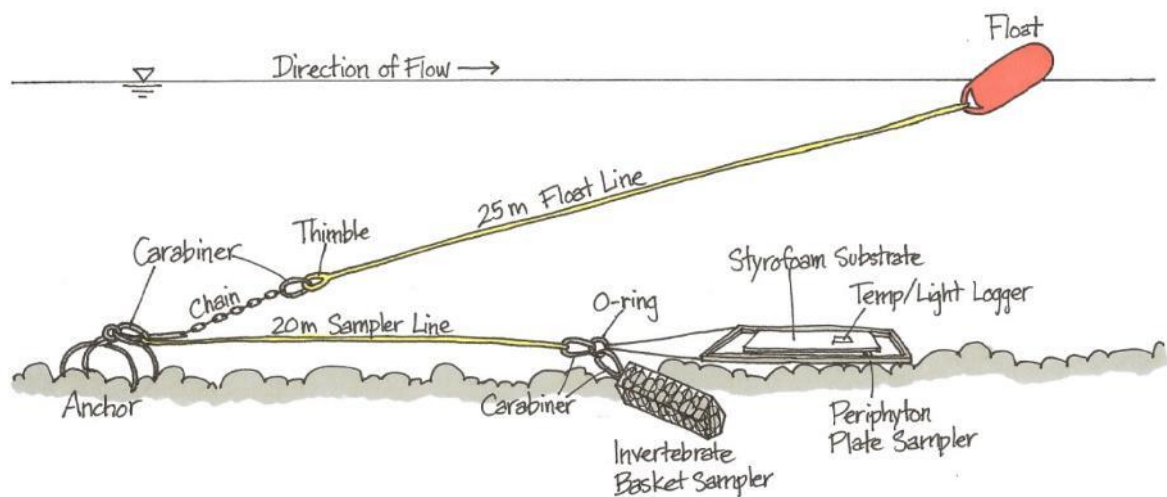


Figure 2-4: Schematic drawing of the artificial substrate sampler used in MCR





Table 2-2: Summary of samples collected from artificial sampler deployment and retrieval in 2017

Season	Reach	Site	Periphyton Samplers		Invertebrate Basket Samplers		
Spring (April 10– May 24 2017)	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)	
	Reach 3 (R3)	Site 6 (S6)	6	6 (100)	6	6 (100)	
		Site 5 (S5)	6	4 (67)	6	4 (67)	
		Site 3 (S3)	6	6 (100)	6	6 (100)	
	2017 Totals			60	34 (94.5)	60	34 (94.5)

Notes: ¹The 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. In Spring 2017, five time-series samplers were deployed in Reach 4 in both T1 and T3/T4 transect positions.

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

Time series samplers were retrieved once per week following deployment. During each weekly sample, the light/temp loggers were wiped clean with a paper towel so light measurements were accurate during time series sampling. Every week, two periphyton punches were randomly collected from the Styrofoam and were immediately packed on ice





and placed in the dark until they could be delivered to Caro Labs Kelowna for chlorophyll-a analysis. Taxonomy of time series samples has not been conducted since 2013.

2.2.3 Artificial Sampler Retrieval

Artificial samplers remained in the river for a total of 43-44 consecutive days in Spring 2017. This deployment period matches earlier MCR deployments and is within the incubation period required for attainment of peak biomass defined by Perrin et al. (2004). Spring samplers were retrieved either by boat, wading or by foot on May 23-24, 2017.

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

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

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

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

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

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

2.2.4 Post Processing of Periphyton Samples

Four Styrofoam punches were obtained from each artificial substrate. One 6.6 cm² 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 cm² 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 cm² punches were used for taxonomic identification that was completed





by H. Larratt, with QA/QC and initial taxonomic verifications provided by Dr. J. Stockner. Fresh, chilled samples were examined within 48-hrs for protozoa and other microflora that are difficult to identify from preserved samples. The final punch was preserved using Lugol's solution and was stored until taxonomic identification and biovolume measurements could be taken. Species cell density and total biovolume were recorded for each sample. A photograph archive was compiled from MCR samples. Detailed protocols on periphyton laboratory processing are available from Larratt Aquatic.

2.2.5 Post Processing of Invertebrate Samples

Following retrieval, fixed benthic invertebrate samples were transported to Cordillera Consulting in Summerland, BC. Samples were sorted and identified to the genus-species level where possible. Benthic invertebrate identification and biomass calculations followed standard procedures. Briefly, field samples had organic portions removed and rough estimates of invertebrate density were calculated to determine if sub-sampling was required. After samples were sorted, all macro invertebrates were identified to species and all micro portions were identified following The Standard Taxonomic Effort lists compiled by the Xerces Society for Invertebrate Conservation for the Pacific Northwest (Richards and Rogers 2011). A reference sample was kept for each unique taxon found. A sampling efficiency of 95% was used for benthic invertebrate identification and was determined through independent sampling. Numerous identification keys were referenced in the identification of benthic invertebrate taxa and a partial list of references is provided in Schleppe et al. (2012). Species abundance and biomass were determined for each sample. Biomass estimates were completed using standard regression from Benke et al. (1999) for invertebrates and Smock (1980) for Oligochaetes. If samples were large, subsamples were processed following similar methods. Detailed protocols on invertebrate laboratory processing are available from Cordillera Consulting.

2.3 Variable Descriptions and Analytical Methods

2.3.1 Determination of Submergence

Water and air temperature data obtained from the HOBO light/temperature loggers was the primary dataset used to determine how long 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 $\pm 0.5^{\circ}\text{C}$ 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 $\pm 0.5^{\circ}\text{C}$. 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°C of each other (Schleppe et al. 2010).

To ensure that the determination of submergence was accurate, the entire database was reviewed for each session and professional judgment and field experience were used to assess whether a plate was submerged or exposed. During this review, the following criteria were used 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 submerged 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

The focus of the 2017 analysis was to run the spatial productivity model for periphyton chl-a and benthic invertebrate biomass. Other analyses were attempted to explore possible trends that have not been explored yet. All statistical tests were conducted using R (R Development Core Team 2017) and model averaging was completed using the R package “MuMIn” (Barton 2016).

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

The relationship between periphyton productivity metrics and benthic fish food index was explored using linear mixed effects models. Only samples that had a total number of hours submerged over 500 were included in the models. Separate models were run using each periphyton productivity metric (abundance, biovolume, and chl-a) as the fixed effect (predictor). Transect and site were used as random effects. The fish food index and the periphyton production metrics were log₁₀ transformed.

The relative support for the effects of the explanatory variables was evaluated using an all model combinations approach. Model uncertainty was assessed using AICc and multi-model averaging (Burnham and Anderson 2002; Anderson 2008). We used the MuMIn package in R (Barton 2016) to compare 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) 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 R² 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).

The fish food index models are not presented in the results section because the periphyton production metrics explained very little variation (Pseudo R²<0.05) and there were not





enough models with $\Delta AICc$ below 3 to calculate confidence intervals. Model results are in Appendix C.

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, Styrofoam damage over the deployment occasionally necessitated collecting a sample near the edge.

The effects of foraging invertebrates were assumed to be randomly distributed over the artificial substrate within and between all sites. It is acknowledged that invertebrates may spend more time foraging along the edges of substrata and therefore disproportionately affect productivity along the perimeter of artificial samplers. Therefore, we avoided collecting samples from substrate edges unless no other viable alternative was available. Foraging intensity on MCR samples is still considered to be a small effect, reducing any potential data-skewing. Further, it is probable that invertebrate distributions around plates were clumped, reducing the potential for effects across multiple replicates. Finally, the populations of invertebrates in the MCR were low relative to other large rivers, and we did not do a power analysis to determine if the sample size is adequate.

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

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

2.4 Spatial Productivity Model

This section outlines and defines the various component formulae of the growth and death phase functions in the predictive spatial models describing total production across a section of river or within a river polygon in a given time period. The first component of the model is a river elevation model, which was used to define the wetted perimeter of the river. Then, the second component of the model used wetted history to determine riverine production. To determine riverine production, we first define exactly 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.

This year spatial productivity models were implemented to calculate daily productivity for chl-a and invertebrate biomass for 2007-2017. These model results were used to test the effect of minimum flows on benthic productivity. The two components of the spatial productivity model are: (1) a hydrologic model that determines water depth on an hourly basis and, (2) a productivity model that uses growth and death curves for chl-a and invertebrate biomass. Both of these components were refined this year.

2.4.1 River Model

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

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

Ecoscape compared the Full MCR Model and the Upper MCR Model for use in the study area. The study area is limited to a stretch covering approximately 10 kilometers below the Revelstoke Dam (Reaches 3 and 4). After running simulations of the two models, Ecoscape determined that the Upper MCR Model was superior in its representation of the physical and hydraulic characteristic of the study area when compared to the Full MCR Model. Due to the increased complexity and magnitude of the Upper MCR Model runtimes were substantially increased but judged necessary to achieve maximum resolution.





The Upper MCR Model was run for Reaches 3 and 4 using hourly discharge data from BC Hydro covering January 1, 2007 to December 31, 2017. The 11 years of data were divided up into monthly runs and programmed into the Telemac-2D simulations. The last simulated data from any given month was extracted and used as a seed file for the next monthly computation to ensure seamless transitions and accurate flow results between time blocks. This was done to manage both database size and runtime.

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

A full resolution intersection is currently not feasible within R due to the size of the databases. To accommodate this limitation Ecoscape created a polygon mesh covering the maximum potential water level within reaches 3 and 4. This was done by drawing a polyline from the thalweg of the river and offsetting it to both sides by 1 meter. This process was repeated until the full breadth of the maximum inundation potential of the river was covered. The linear polygons were then cut in 20 meter lengths perpendicular to the thalweg polyline essentially dividing the river into 1 meter by 20 meter polygons oriented with the flow of the river. A point file was generated from the centroids of each polygon and the area of each polygon was added as an attribute to the database.

All hourly depth data was imported into a PostgreSQL database using RPostgreSQL package version 0.6-2 (Conway et al. 2017). A separate database was generated for Reach 3 (R3) and Reach 4 (R4). Each point had a polygon associated with it. The areal productivity of each polygon was calculated hourly using growth or death curves that were developed based upon the time spent either exposed or submerged. The growth and death functions were derived as part of the BRX productivity work (Schleppe et al. 2015), then coded in C++ by Sean Anderson and subsequently modified slightly by Ecoscape to address transitions between different seasons and the specific growth or death function that was used for each metric.

2.4.2 Productivity Model Notation

The following 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 dependent responses (units/m²), the derivation of formulae is identical between responses with only the coefficient values differing among them. For periphyton, we considered Chl-a and for benthic invertebrates we considered benthic biomass, each 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:

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

2.4.2.1 Model for Individual Polygon

In a regulated flow regime, two distinct processes are most 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. The Telemac model was used to determine the state of submergence for any given river polygon at any given time period on an hourly basis.

2.4.2.1.1 Growth Phase

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:

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

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

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

2.4.2.1.2 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}





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

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

$$(5) \quad c_i(t) = \frac{asym}{1 + \exp\left(\frac{(xmid - h(t))}{scal}\right)} \cdot S_i \quad \text{if } t_a \leq t < t_b$$

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

2.4.2.1.3 Death Phase for an Individual Polygon

Death or loss within any given time period will occur between time $t = t_a \dots t_b$, 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:

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

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

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

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

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

in which case

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





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

2.4.2.1.4 Exponential Decay

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

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

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:

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

2.4.2.2 Full Production Model for All Polygons

At any given time there are river polygons which are both growing denoted with i , polygons which are saturated at peak biomass denoted with j , and polygons which are dying denoted with k . 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 $t = t_a$:

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

2.4.2.3 Model Assumptions and Limitations

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

1. Several assumptions are required for starting response values $c_i(t_a)$. For 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 have no direct effect on any other given river cell. This means that factors such as invertebrate drift due to natural migration or effects 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 yet well understood. Other specific parameters that might be important include velocity, substrate, weather, and substrate stability. Both the peak biomass and the rate of growth to peak biomass have been observed to vary between years on the MCR.
6. Production is greater than zero upon the first hour of growth and is equal to the minimum predicted growth at hour 1 in logistic regressions for each season. This is necessary for logistic growth curves to be predicted as values cannot start outside of the range of production predicted by the model.
7. In cases where the previous production value is higher than the maximum predicted growth for a given season, production will exponentially decrease until it reaches the maximum predicted growth for that season. Currently, the same exponential decay death function for exposure is being used to transition between seasons, which is likely more abrupt than what would occur naturally. Realistically, this process is governed by processes of natural slough, and we do not currently have any data to this transition. This process could be easily added to the spatial model to further develop seasonal transitions. Since seasonal transitions occurred on the first of the month, data was not analyzed spanning any month.
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 (CPC). The data collected in these assessments has been integrated into one data set and relies upon the full suite of work completed by CPC and BC Hydro. This dataset is primarily based on data from the LCR. The LCR has higher periphyton and benthic productivity than the MCR and also different periphyton and benthic community compositions. From this data set, predictive growth and death functions have been developed that are directly linked to submergence times. The





predictive growth curves have been adjusted to better represent the productivity in MCR. However, no data has been collected in the summer and winter in the MCR. As a result, professional judgement has been used to adjust the summer and winter curves. It is acknowledged that productivity estimates in these seasons have large uncertainties. 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.

2.4.3 Growth and Death Curves

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

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

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

For chl-a separate growth curves were calculated for each season (Figure 2-5). Seasonal transitions were defined as March 1st, June 1st, September 1st, and December 1st. MCR accrual data from 2011-2017 for T1 samples were used to generate Spring and Fall growth curves for chl-a. The chl-a growth curves were forced to a logistic curve by using chl-a samples that were incubated for six months as the horizontal asymptote. Winter and Summer chl-a growth curves used growth curves from LCR because no accrual data is available for MCR. The horizontal asymptote of the Winter and Summer chl-a curves were adjusted to account for differences of productivity in LCR and MCR. The formula for each of the growth curves were as follows:

Chl-a

a.	$Chla = \frac{1.171}{1 + e^{\frac{(1001 - hrs.in)}{259.4}}}$	Spring
b.	$Chla = \frac{0.8}{1 + e^{\frac{(579.939 - hrs.in)}{257.53}}}$	Summer
c.	$Chla = \frac{2.671}{1 + e^{\frac{(995.338 - hrs.in)}{301.129}}}$	Fall





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

Winter

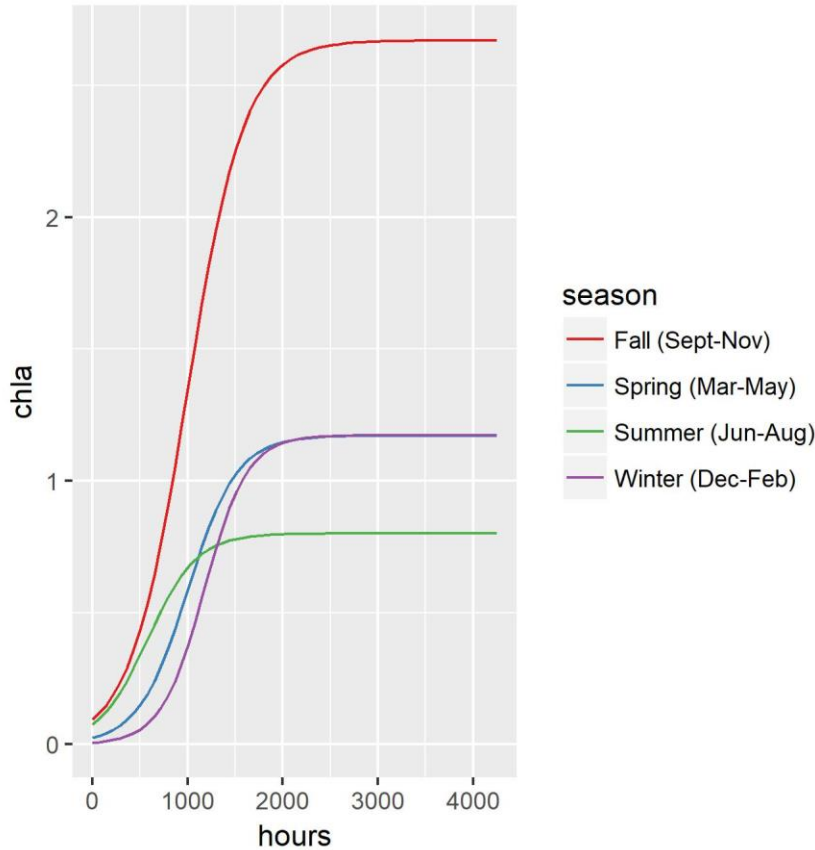


Figure 2-5: Chl-a growth curve Spring and Fall curves derived from T1 accrual data from 2011 to 2017 and 6 month chl-a samples. Winter and Summer curves derived from Schleppe et al. 2015 with adjusted asymptotes (peak chl-a).

For the invertebrate biomass growth curve the growth curve was adjusted from Schleppe et al. 2015 and used the same growth curve in all seasons (Figure 2-6). A different asymptote was used for the biomass growth curve; this asymptote was based on the mean invertebrate biomass of permanently submerged sites. The MCR invertebrate biomass data (2007-2017) was used to calculate the mean biomass for all T1 sites; Big Eddy (BE) sites were not included in this calculation. The formula for the invertebrate biomass growth curve was as follows:

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



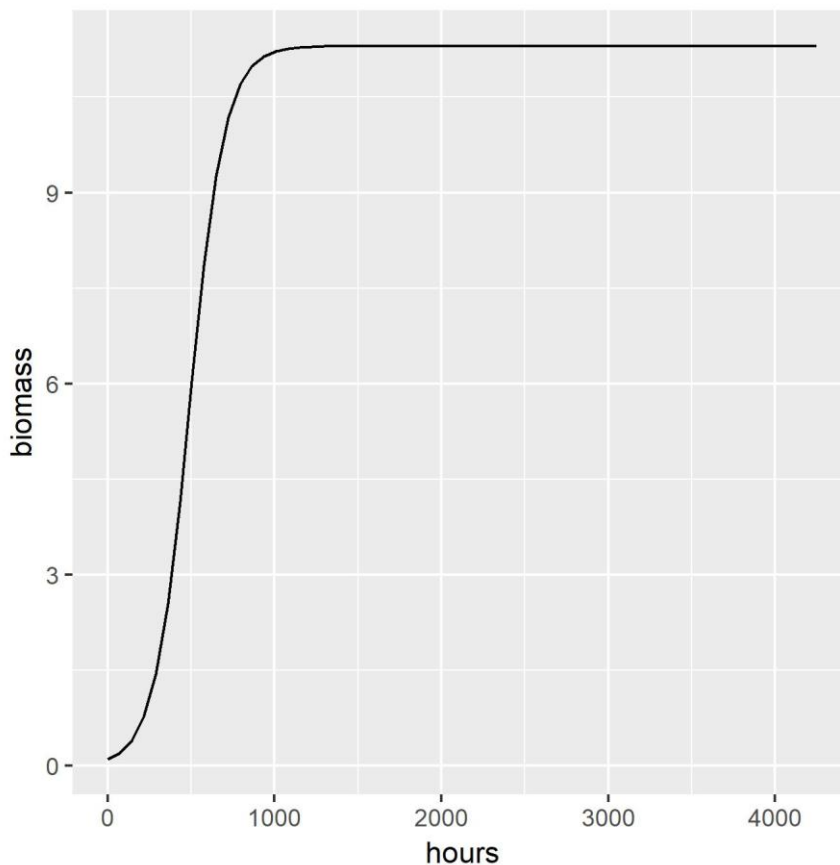


Figure 2-6: Growth curve for invertebrate biomass adjusted from Schleppe et al. 2015.

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

The daily productivity (chl-a or invertebrate biomass) of each MCR reach was estimated from taking the modelled productivity at 12 o'clock noon each day. The total productivity of each reach was determined by summing all polygons at this time period.

Daily productivity estimates for each reach were compared before the implementation of minimum flows (2007-2010) and after implementation of minimum flows (2011-2017) using linear mixed effects models. Separate linear mixed effects models were used for Reach 3 and 4. Before and after implementation of minimum flows and month as well as their interaction were used as fixed effects in the model. The random effect was date nested within before and after implementation of minimum flows. The mixed effects models were implemented in R package nlme version 3.1-131 (Pinheiro et al. 2017).

For both Reach 3 and 4 models of periphyton chl-a, chl-a was log₁₀ transformed to better meet linear mixed effects models assumptions. However, all four chl-a models violated the





assumption of homoscedasticity (see Appendix C). Benthic invertebrate biomass models for Reach 3 and 4 also violated the assumption of homoscedasticity.

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 Spring 2017 were consistently lower than temperatures collected in 2010 through 2016 (Figure A-1). Fewer spikes in temperature were observed compared to previous years. Reservoir conditions upstream and the temperature/flow of tributaries are the most probable factors affecting the daily variation in observed temperature (Larratt et al. 2013; Olson-Russello et al. 2015). During the spring deployment, initial river temperatures were cooler and ranged from 2 to 3°C.

Temperatures of exposed plates in the spring usually exceeded water temperatures (Figure A-1). On the LCR, winter river temperatures were more dependent upon the temperature of the upstream reservoir, while during the fall riverine temperatures were more dependent upon air temperature due to seasonal patterns (Olson-Russello et al. 2015). If similar trends exist on the MCR, it is probable that springtime water temperatures are more dependent on reservoir temperature, whereas fall water temperatures are more dependent on air temperature, recognizing that summer weather determines the upstream reservoir temperature.

Light intensity during Spring 2017 followed a similar pattern to 2010 – 2016, although the light lux decreased earlier in the day in 2017 compared to the 2010-2016 average at all locations (Figure A-2). In accordance with the physics of light transmission through moving water with low suspended solids, light intensity on submerged samplers increased from deep sites at T1 locations to shallow sites at T6 locations in the spring. When samplers were in shallow water, they received more energy to support periphyton production, but these sites were also more likely to be exposed during the variable daily operating regime. Peak light intensities occur around noon, a period when flows are usually high. Light intensities were much greater when samplers were exposed, and were highest at the T6 locations where exposure was the most frequent (Figure A-2).

Figure A-3 presents the spring light logger data when samplers were exposed. It shows the expected reception of far more light than during water-covered periods. The differences between the results at the various transect positions reflects a combination of aspect, riverbank shading and periphyton growth on the sensors.

3.1.2 Pattern of Flow in MCR

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

- Minimum flows of 142 m³/s were maintained from 2011 onwards (refer to 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 higher discharge from REV 5. Small morphological and biological channel changes were observed. For instance, in 2010 there was a noticeable fungal/bacterial black coloration on substrates in Reach 4, and this was less apparent following the high water years.
- Very high flows exceeding 2000 m³/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 in 2011, 2013, 2014, 2015 and 2016.
- Flows followed a similar pattern between years, with low flows occurring during evening periods after midnight and high flows occurring during daytime periods from 10:00 until 19:00. At all other times, flows were either ramping up or down from high or low flow periods. An exception to this trend was seen in 2017 when peak flows occurred from 15:00 to 21:00. (Figure A-4).
- 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 2017, with the exception that daily high flows were consistently higher (<250 m³/sec difference) than what had been observed in 2007 – 2012 pre-implementation years (Figure A-6). This resulted in slightly deeper average depths of 5 – 8 m at T1 locations and 2 to 3 m at T6 locations.
- The Arrow Lakes Reservoir (ALR) elevation can result in extensive back watering of Reach 3 from early June through October, and can extend into Reach 4 during the summer months (Figure A-5). Backwatering effects have been considered through the submergence variables but these variables do not distinguish between submergence due to backwatering and submergence due to flows in the model analyses. During Spring 2017, back watering occurred in Reach 3 in the last couple of weeks of the spring deployment period.

The 2017 spring flows were similar to previous years (both pre and post implementation of minimum flows). As REV is a hydropeaking facility, it is hard to generalize flow patterns for daily or weekly comparisons, making summaries of flow trends difficult.

3.2 Periphyton

Periphyton samples have been collected during the fall (backwatering probable) in 2010 to 2014 for five sample sessions, and spring (minimal backwatering) in 2011 to 2017 for six sample sessions. The results to date are presented here, with emphasis on the parameters that inform the spatial model of periphyton productivity.

3.2.1 Overview of MCR Periphyton Biofilms

Periphyton consists of two broad groups of micro-organisms, photosynthetic algae and bacteria, and non-photosynthetic (heterotrophic) bacteria and fungi. Algal periphyton production only grows while substrates are submerged and exposed to sunlight, while the bacterial biofilm component can grow in the dark (Lear et al. 2008). For both components,





growth in the MCR slowed dramatically and mortality progressively increased during periods of desiccation. Drift of viable phytoplankton cells originating from the upstream Revelstoke Reservoir, and to a lesser extent, from Arrow Lakes Reservoir during back-watering also contribute to the periphyton population.

3.2.2 Periphyton Ash-Free Dry Weight

Collection of ash-free dry weight (AFDW or volatile solids) commenced in 2010. AFDW provides an estimate of all organic components of the biofilm plus detritus. Average MCR ash-free dry weight samples remained in the typical range for large rivers but with considerable variation from year to year. AFDW has averaged about 0.60 mg/cm² in both seasons, but with wider variation in the fall than in the spring. With both seasons and all years combined, AFDW remained consistent in the permanently submerged substrates from T1 through T4, and peaked at T5 in the lower varial zone before declining at T6 in the upper varial zone / floodplain (Table 3-1). T5 appears to be a zone of organic accumulation or decomposition. Variable results from year to year are likely flow-driven and they highlight the volatility of conditions in MCR. Field observations of reduced black banding since 2011 suggest a decline in heterotrophic members of the biofilm in years with longer inundation of the flood plain areas (T5, T6). They are displaced by algae during periods of increased substrate submergence.

Table 3-1: Ash-free dry weight averaged by season (Spring/Fall) and for both seasons in all study years (2007-2017).

Season	T1	T2	T3	T4	T5	T6
Spring	0.58 ±0.51 mg/cm ²	0.57±0.49 mg/cm ²	0.58±0.49 mg/cm ²	0.54±0.34 mg/cm ²	0.59±0.82 mg/cm ²	0.57±0.44 mg/cm ²
Fall	0.66 ± 0.66 mg/cm ²	0.53 ± 0.34 mg/cm ²	0.48 ± 0.22 mg/cm ²	0.48 ± 0.35 mg/cm ²	1.0 ± 3.66 mg/cm ²	0.37 ± 0.43 mg/cm ²
Spring & Fall all years	0.56 ± 0.45 mg/cm ²	0.56 ± 0.45 mg/cm ²	0.56 ± 0.45 mg/cm ²	0.56 ± 0.45 mg/cm ²	0.78 ± 2.54 mg/cm ²	0.48 ± 0.44 mg/cm ²

3.2.3 Characteristics of MCR Periphyton Algae

Like most large rivers, MCR species were dominated by diatoms representing up to 100% of the biovolume in all sample sites on both natural and artificial substrates (Schleppe et al. 2013). When all years of study to date are considered, diatoms accounted for 90 ± 15% of the fall biovolume and 92 ± 17% of the spring biovolume. 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. Green algae accounted for 8 ± 15% in the fall with large filamentous species, and only 3 ± 11% in the spring samples where rigorous conditions including freeze-dry events eliminated all but the single-celled





green types. The relative biomass contributions of flagellates ranged from $1.8 \pm 4.7\%$ in the fall to $3.2 \pm 9.1\%$ in the spring. Although cyanobacteria were functionally and numerically important, they only accounted for $0.006 \pm 1.6\%$ of total biovolume in the fall and increased to $1.7 \pm 6.8\%$ under spring conditions that favour species with rapid reproduction rates.

The taxonomic structure of all river periphyton communities tends to be predominated by a small number of taxa. The MCR had 5 - 52 species per sample, with all microflora taxa included. Among the true algae, mean taxa richness was 18 ± 6 in the spring and 20 ± 6 taxa in the fall (Digital Appendix B, 3-4). These results suggest that species richness in the MCR was lower than is typical for unregulated large rivers of similar latitude.

The range of river habitats investigated was expanded to include backwater, Big Eddy and bedrock in 2011, but still found many of the same species that occurred at mainstem sites. Over the years of study on the MCR habitats, ten dominant taxa accounted for 9 – 93% of abundance (71 - 99% of total biovolume) in the fall and 18 – 97% of abundance (73 - 99% of biovolume) in the spring (Figure 3-2).

3.3 Drivers of MCR Periphyton Communities

3.3.1 Effects of Reservoir Donation

The donation of Revelstoke Reservoir diatoms to MCR periphyton was highly variable from year to year, and relates to production dynamics within the reservoir versus the timing of releases. These diatoms accounted for 0 - 76% of biovolume in fall samples and 0 - 69% of biovolume in spring samples to date. Most of the limnoplanktonic types were only found in mainstem samples and not in the backwater and Big Eddy samples. This may be due to greater exposure of drifting algae along the mainstem. Similarly, R4 samples had 30 - 45% more planktonic drift taxa than R3 samples because the reservoir algae cells progressively settle out.

3.3.2 Effects of Flows

Year-round implementation of 142 m³/s minimum flows and full in-service operation of REV 5 were initiated on December 20, 2010. Fall samples collected before and after REV 5 are compared in Table 3-2. While species diversity was unchanged, periphyton growth metrics were lower after the flow regime change, with 2012 having the lowest periphyton metrics and the highest flows to date. Both abundance and biovolume decreased significantly, while chl-a did not, implying that a shift to fast-growing photosynthetic bacteria occurred. Bacterial components of the biofilm can be utilized incidentally when invertebrates are foraging.





Table 3-2: Range of periphyton metrics in MCR R4 and R3 (all depths combined) in 2007 – 2017

Fall	abundance	biovolume	chl-a	n
	cells/cm ²	um ³ /cm ²	ug/cm ²	
Pre REV 5	6.55±4.57x10 ⁵	3.78±3.09x10 ^{8*}	1.04±0.75	105
Post REV 5	5.10±3.14x10 ⁵	2.98±2.87x10 ⁸	1.05±0.96	187
% difference	-22%	-21%	0.7%	
Spring				
Post REV 5	3.44±2.38x10 ⁵	1.65±1.64x10 ⁸	0.45±0.40	262

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

An increase in filamentous green algae has been observed in R4 and R3 in the fall since the implementation of the new flow regime. These slow-growing algae can form visible mats in the summer where shear is low under stable, lower flows, but during high flows their mats are dislodged and they are intolerant of desiccation. The area remaining wetted by minimum flows should retain short growths that could re-populate dewatered substrates. Filamentous growth in the Reach 4 T2-T4 zone may continue to gradually increase over the years since minimum flows were implemented. Filamentous green algae were also prevalent in the spring 2012 samples but were uncommon during subsequent spring sampling sessions. This review of filamentous green algae distributions supports the assumption that flow management exerts a powerful influence on the MCR periphyton community.

Under the new flow regime, high flows can generate water velocities in the thalweg greater than 2 m/sec (Schleppe et al. 2013). Since Fall 2012 was the highest flow sampling session studied to date, the growth metrics at T1 positions in 2012 were compared to other years (Figure 3-2). As expected with higher 2012 flows, thalweg T1 periphyton metrics dropped significantly in both reaches during the fall and the spring compared to years with a lower range of flows. In the fall thalweg data, R4 showed a greater difference than R3 between 2012 and typical flow years, possibly because water velocities would have been higher in the narrower Reach 4 channel.

In the spring, the difference between reaches was smaller and reversed, so that the difference between 2012 and typical flow years was greater at R3 than R4. The short spring days may have increased the influence of available light, where greater water depth during high flows lowers light penetration to the substrates. Year by year, productivity in R3 and R4 show the same patterns in all growth metrics, however in both the spring and fall samples, R4 showed greater reactions to flows and growing conditions, while R3 reactions were more subdued.



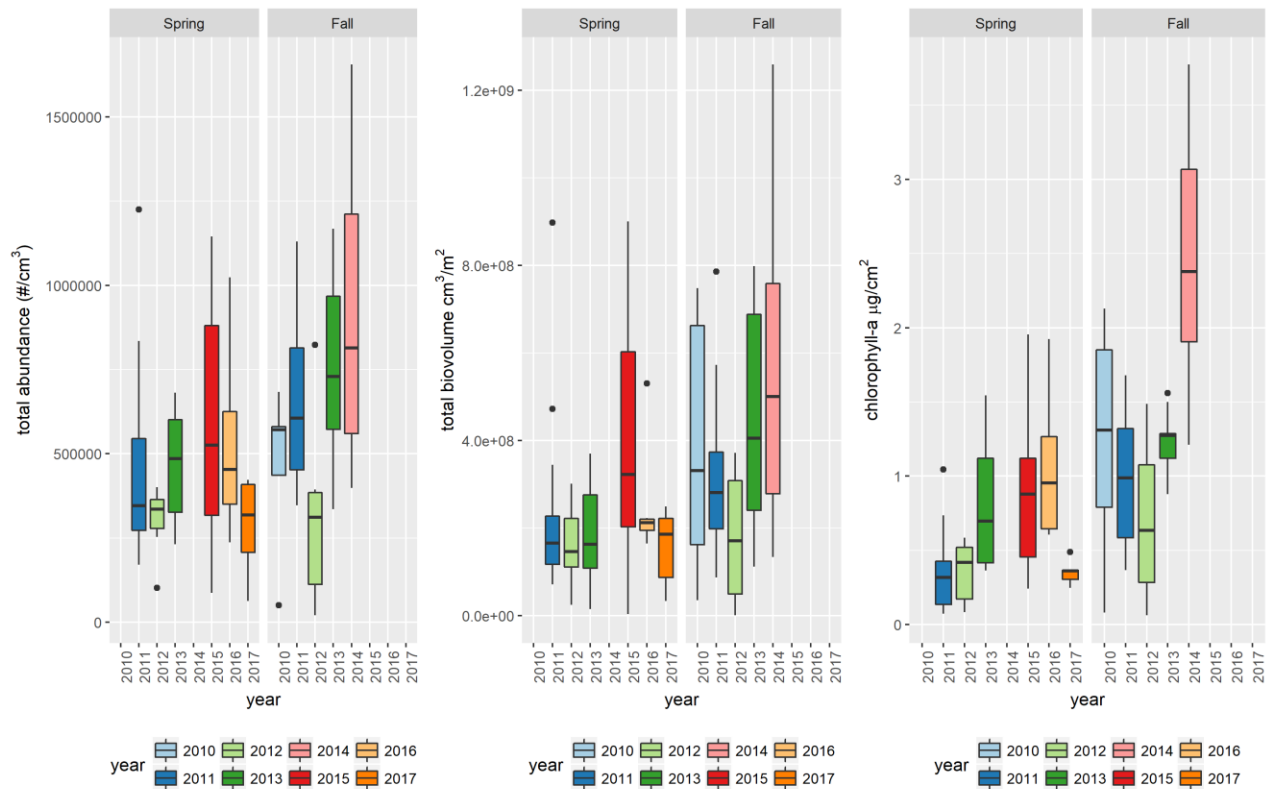


Figure 3-1: Periphyton productivity by year and season in Reach 3 and Reach 4 in the Thalweg (T1) zone. Spring 2015, Fall 2011 and Fall 2012 had higher flows than average (Table A-1).

3.3.3 Effects of Water Depth

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

When all biovolume measurements were compared to chlorophyll-a (chl-a) results, similar curves emerged (Figure 3-3). Average periphyton productivity decreased with increasing exposure from T1/T2 through T5/T6. For the transect depths that were consistently covered by minimum flows (T1/T2), or adjacent to the wetted edge (T3), algae cell biovolume was stable. The frequently dewatered T6 and T7 locations had the lowest biovolume and chl-a, particularly in 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 greater than 9 hours per day experienced rapid periphyton growth (Schleppe et al. 2012).

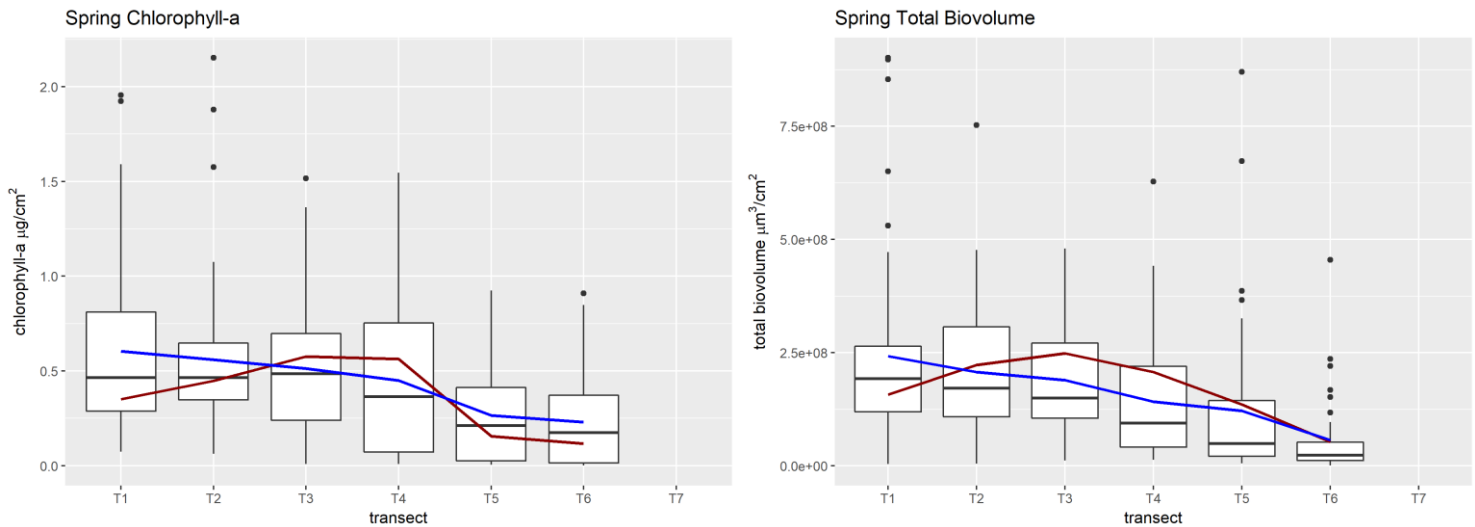


Figure 3-2: Total biovolume of MCR periphyton and chlorophyll-a in spring for 2010 to 2017 by sampler location (T1 deepest in thalweg to T7 shallowest on floodplain). The blue line represents the mean of all years and the red line represents the mean for spring 2017.

Available light for photosynthesis (PAR) is directly affected by water depth. For example, light data from spring 2015 was lower than spring 2011 or 2012, indicating greater water depth on MCR substrates in that year.

3.3.4 Effects of Season

There were subtle seasonal shifts in the dominant periphyton taxa in the MCR, likely in response to flows, water temperature and freezing conditions. In all spring samples, the same diatoms dominated the periphyton, along with large concentrations of rapidly reproducing single-celled algae. In fall samples, similar diatoms dominated and there was a greater contribution made by filamentous green algae. Spring samples had lower average species richness of 13 (T6) to 19 (T2) species/sample compared to fall samples at 15 (T6) to 23 (T2) species/sample.

Summary statistics are provided for all five spring sample periods in Appendix B Table A3-4. Spring periphyton growth metrics were stable and low, ranging from $2.54 - 4.76 \times 10^5$ cells/cm². Chlorophyll-a ranged from 0.16 – 0.19 ug/cm² chl-a in the first three years, but increased to 0.55 ug/cm² in 2013 and to 0.75 ug/cm² in spring 2015, 0.70 ug/cm² in spring 2016 and was 0.37 ug/cm² in 2017. The cause of this increased spring periphyton growth is not known but occurred despite moderate to high flows in those years and is presumed to be attributed to early warm spring weather. In all spring sample periods, average species diversity metrics were stable at 0.71 – 0.81 Simpson's index and at 13 – 21 taxa. Productive





spring seasons tended to have low contributions of reservoir algae to the periphyton mat. Overall, spring means and spring maxima among growth metrics were usually significantly lower than fall samples from the same year (Figure 3-4). Fall periphyton total abundance, chl-a, and total biovolume were significantly higher than spring periphyton productivity metrics in paired T-tests ($p < 0.001$, Appendix C).

Periphyton summary statistics are provided for all eight fall sample periods in digital Appendix B. The fall sampling sessions demonstrated a range of mean abundance from 2.73 to 12.5×10^5 cells/cm², a range of mean biovolume of 0.98 – 6.05×10^8 microns³/cm² and a range of mean chl-a of 0.49 to 1.76 ug/cm². For all growth metrics, the lowest year was 2012, the highest flow year to date. In all fall samples, the same diatoms were dominant, but with a significant filamentous green component.

There was minimal nuisance algae *Didymo* (<0.01%) in spring 2017 biovolume samples compared to spring 2016 samples that had 8% *Didymo*.

Table 3-3: Range of periphyton metrics in MCR (R4 and R3) by season, 2007 – 2017

Fall (all depths)	abundance cells/cm²	biovolume um³/cm²	chl-a ug/cm²	AFDW mg/cm²	species richness	Simpson's Index
2007 – 2010	7.10×10^5	3.78×10^8	1.01	0.499	17.2	0.695
2012	2.76×10^5	1.11×10^8	0.47	0.400	21.6	0.704
2011 – 2014	5.10×10^5	3.45×10^8	1.03	0.581	22.3	0.703
Spring (all depths)	abundance cells/cm²	biovolume um³/cm²	chl-a ug/cm²	AFDW mg/cm²	species richness	Simpson's Index
2011 – 2017	3.44×10^5	1.65×10^8	0.45	0.57	17.6	0.77



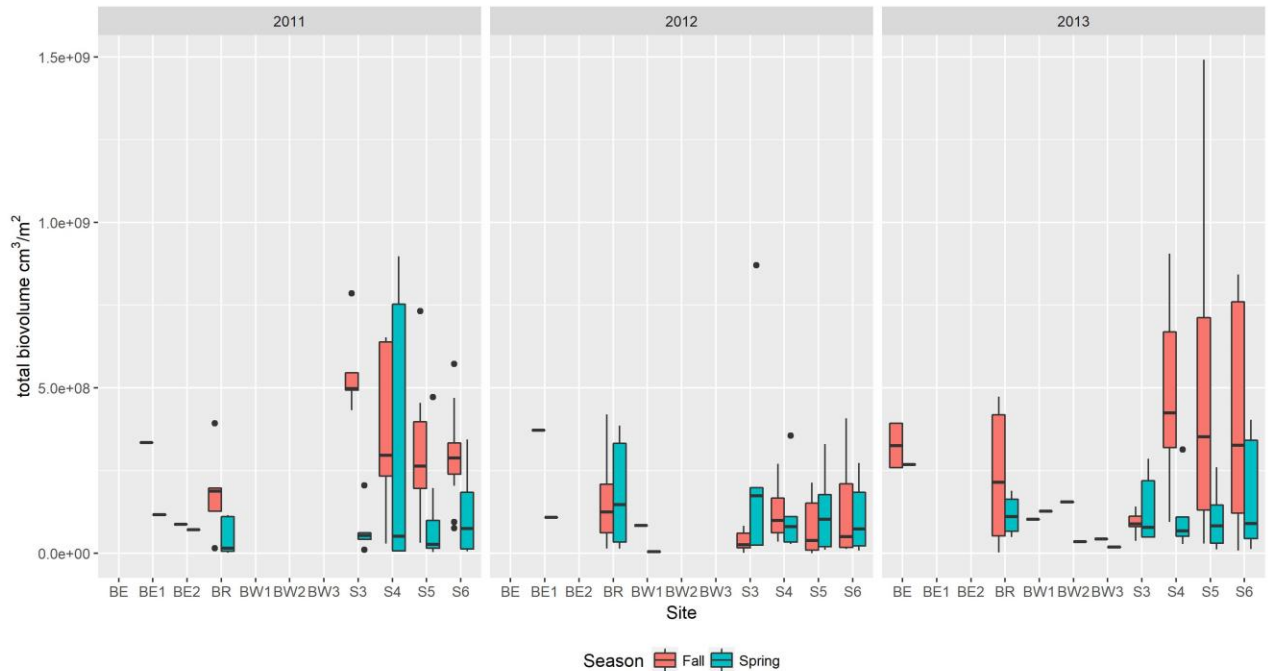


Figure 3-3: MCR Periphyton seasonal responses by site, 2011 to 2013 abundance and chl-a are presented in Appendix C.

Throughout the MCR, conditions including weather, flows, light and water temperature all contribute to the observed seasonal periphyton growth patterns.

3.3.5 Reach Effects

Many growth metrics were higher in Reach 3 than Reach 4 over the years of study, depending factors including flows, back-watering and weather. When Spring sample sessions are compared by reach, R3 had 18% higher cell abundance, 7% more biomass and 116% higher chl-a than R4 averages. When all fall samples to date are compared, R3 had the same abundance and biovolume as R4, but with 36% higher chl-a than R4. The large reach difference in Spring chl-a is often driven by the occurrence of filamentous green algae in R3 samples but not R4 samples. Thus, spring was the season with the greatest difference between R3 and R4 periphyton productivity.

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





Although species composition changed between reaches, there was no observable difference in the Simpson's index (0.79) and only a negligible 5% difference in species diversity (19.7 – 18.8) between reaches, and this finding was confirmed by statistical modelling (see section 3.3.1.). There are numerous mechanisms that account for similarities in species distribution in large rivers such as the 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 and continuously received drifting algae from Revelstoke Reservoir, can function as a source of organisms to re-colonize exposed habitat areas with the same suite of taxa after catastrophic flow events.

3.3.6 Effects of Backwatering

A final aspect of MCR flow regime affected by both BC Hydro releases and by watershed hydrology is back-watering by Arrow Lakes Reservoir (ALR). This seasonal water cover reduces desiccation on substrates that would otherwise be exposed by low flow releases, particularly in the fall. It should also increase the opportunity for limnoplankton suspended in the ALR water column to settle onto MCR periphyton. In most years, sampler deployments in spring occurred at the lowest Arrow Lakes Reservoir levels and ended when backwatering was just starting in R3, while fall deployments commenced as backwatering declined in R3 and R4. Both seasonal deployments can be affected by backwatering with R3 receiving the greatest effect. Since the hydrologic regime in the preceding week is always of greater importance to periphyton production than events that occurred further in the past (Schleppe et al. 2013), fall data should provide the best insight into the effects of backwatering on R3 productivity because of the recent loss of backwatering cover on the substrates (declining limb of hydrograph). The data summarized in Figure 3-4 illustrates the benefits of backwatering on periphyton, and this was confirmed by statistical modelling.

The Reach 3 upper varial zone is the most variable region for periphyton productivity in the MCR. With continuous backwatering, it can exceed the productivity of deeper areas but in seasons without backwatering, it can have minimal productivity. For example, without backwatering, upper varial zone abundance dropped by about 30% and biovolume by 70% in fall 2013, while in fall 2014, the upper varial zone was continuously covered by backwatering, resulting in far greater periphyton growth throughout the R3 upper varial zone (Figure 3-4).

Another important influence on the R3 upper varial zone is high flows. Very high flows without backwatering (2012) apparently curtailed productivity, while high flows with backwatering into R3 (2015) allowed moderate productivity. These effects of backwatering are accounted for in the statistical models because they consider duration and timing of submergence.



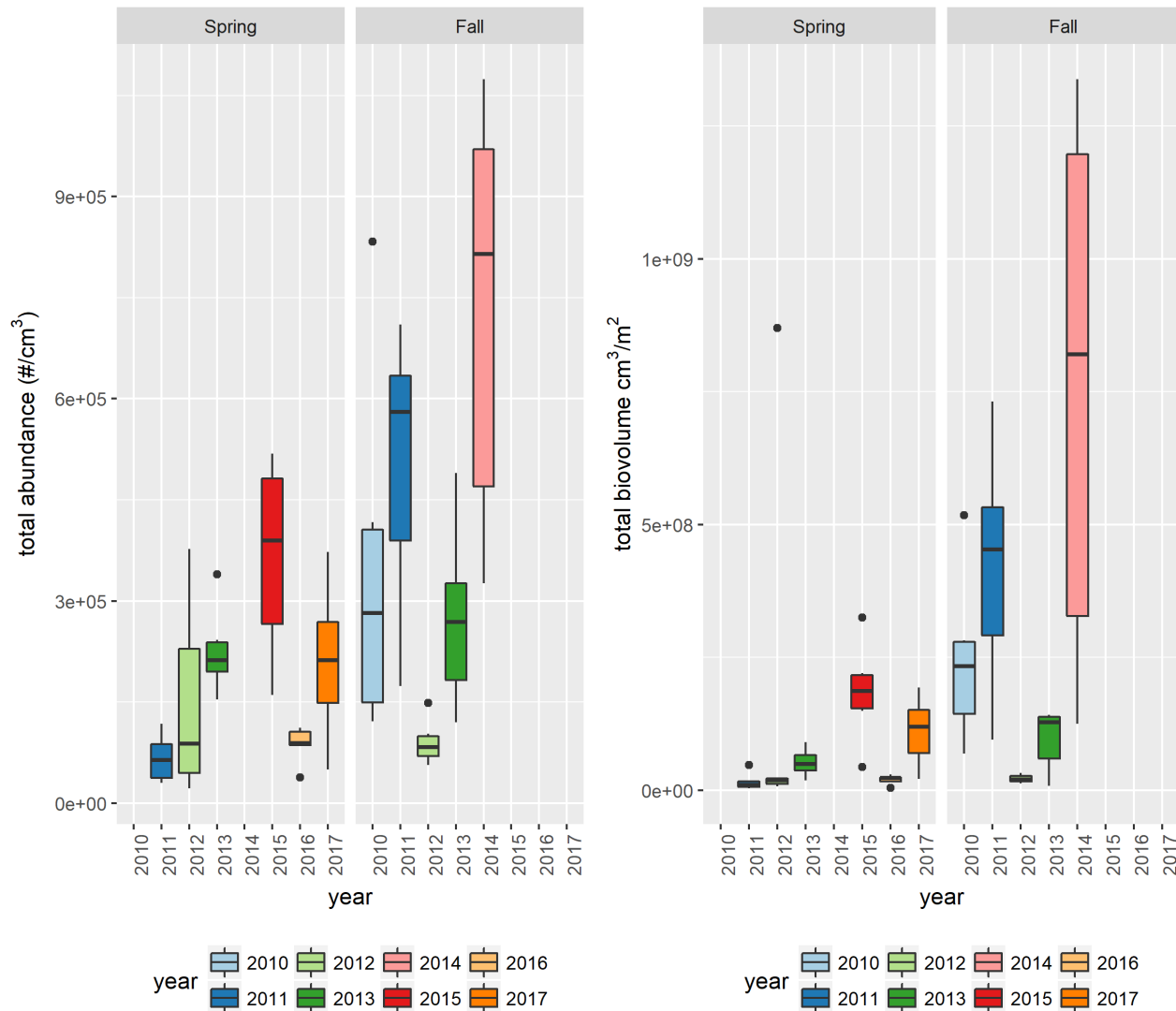


Figure 3-4: Upper varial zone (T5,T6) periphyton productivity in R3, 2010 – 2017 by year and season. All sampling periods were affected by backwatering except Spring and Fall 2013 (Table A-1).

3.3.7 Periphyton Spatial Productivity Models

A hydrologic model determined the wetted history of Reaches 3 and 4 and the spatial productivity model estimated periphyton chl-a as a function of growth and death, as determined by patterns of submergence. Daily periphyton chl-a estimates for 2007-2017 of Reaches 3 and 4 were compared used linear mixed effects models (Figure 3-5). The effect of minimum flows was first tested by comparing daily productivity without considering monthly differences. The second linear mixed effects model considered the effect of month and its interaction with the implementation of minimum flows. The effects of minimum flows





on periphyton chl-a in Reach 3 and Reach 4 were significant in both statistical models. When month was not included in the model, the effect of minimum flows on periphyton chl-a in Reach 3 was significant but small ($m=-0.005$, $p<0.001$). The effect of minimum flows in Reach 3 was stronger when month was added as a fixed effect with an interaction ($m=-0.030$, $p<0.001$). Month and its interaction with the implementation of minimum flows were also significant.

The periphyton chl-a model indicated that implementation of minimum flows had a stronger effect on Reach 4 chl-a than Reach 3 chl-a. After the implementation of minimum flows daily productivity was higher in February and March in both R3 and R4. The mean daily productivity of R4 was higher in October and November after the implementation of minimum flows. This agrees with the greater effects of back-watering in R3 than R4 observed in the periphyton metrics.

Implementation of minimum flows had a significant effect on both statistical models in Reach 4. Similar to Reach 3, the effect of implementation of minimum flows on periphyton chl-a was stronger when month was included as an interaction term in Reach 4. The slope of the implementation of minimum flows was -0.024 ($p<0.001$) for the model without the interaction term, whereas the model with the interaction term had a slope of -0.029 , $p<0.001$.

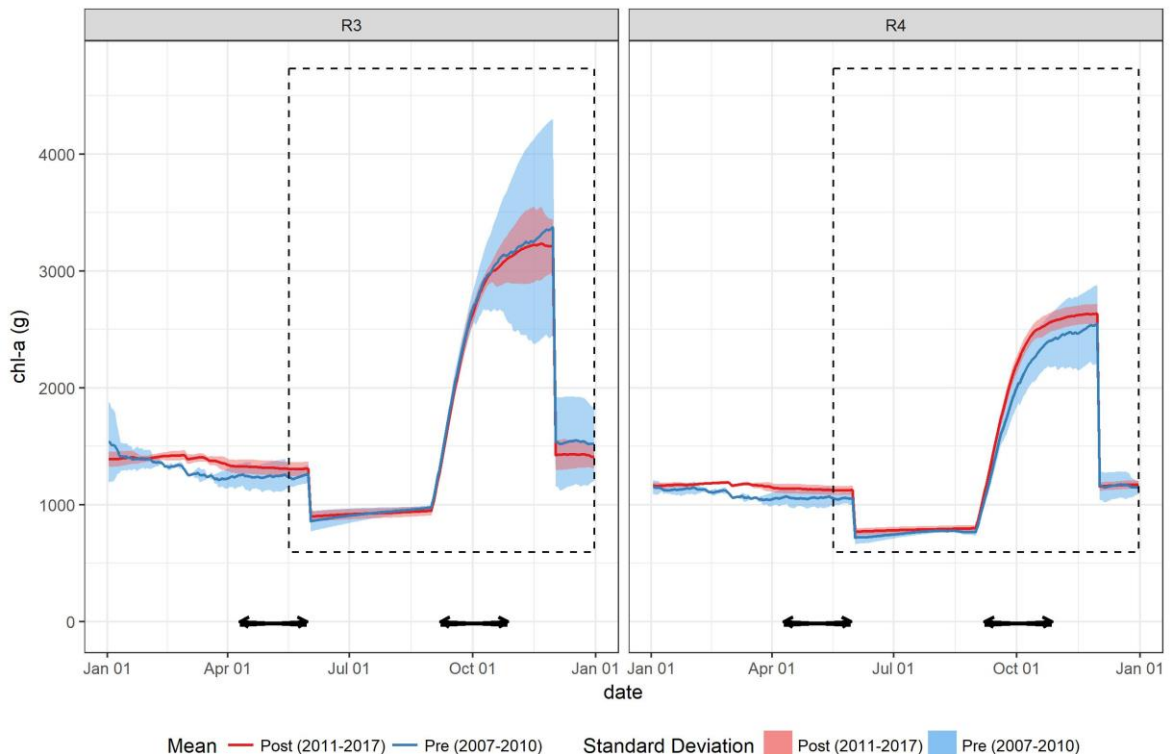




Figure 3-5: Comparison of Pre-Post Implementation of minimum flows for periphyton chlorophyll-a. The dotted box represents when R3 is typically backwatered from ALR and the arrows represent the typical range of Spring and Summer deployment periods.

3.4 Benthic Invertebrates

The results from previous NMDS analyses based on 2007-2015 data suggest that annual differences and pre- and post-implementation of minimum flows explained some community variation (Schleppe and Larratt 2016). However, it was not possible to separate natural annual variability from differences in operation or effects associated with implementation of minimum flow. Analyses for community groupings of benthics were not analyzed in 2016 or 2017 because past years results summarize key findings and additional data is not likely to yield better interpretation of community structure resulting exclusively from the effects of minimum flow.

Analyses in previous years used benthic production models to understand the underlying processes that may affect invertebrate production. In 2017, benthic production models were not run because the focus was shifted to the spatial productivity model. The primary variable found to influence invertebrate production (abundance, biomass, EPT+D) was increasing submergence (Schleppe and Larratt 2015). Other variables, such as water temperature and substrate score, were also identified as the top predictors in different iterations of the model, but submergence in either the day or night is still considered the most important factor affecting food for fish.

In 2016, only invertebrate abundance and biomass models were run to determine influential predictors independent of submergence (Larratt et al. 2017). Substrate score was the top predictor of fall and spring biomass, and spring abundance. However, regression analysis indicated substrate score explained a limited amount of variation in biomass and abundance ($R^2 < 0.10$), most likely because there are multiple confounding factors that make determining the actual effect size very challenging. Further, the consistent patterns of daytime peak flows, and nighttime low flows, contribute to a complex interaction between benthic productivity and flow, resulting in a bias where not all conditions exist to sample (i.e., there are few, if any, sites with both high light and high submergence). Water temperature was the top predictor for fall abundance and explained some variation in regression analysis ($R^2 = 0.24$, $p < 0.001$).

3.4.1 Yearly Comparisons of Benthic Invertebrate Sampling

Relative biomass and relative abundance of benthic invertebrates varied between years at the lowest taxonomic levels of identification (family to genus). 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, percent EPT measured as relative abundance was consistent across years. However, percent EPT measured as relative biomass increased each year and peaked in 2017 due to a marked increase in Ephemeroptera biomass. In other words, the size of EPT increased in recent years, although they had the same percent contribution to the community (Appendix B). These trends were consistently observed in both spring and fall





data. In most samples, 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, with standard deviations within a given year/season consistently higher than the mean. Invertebrate species richness also varied among years with the lowest values in fall months occurring in 2010, and highest in sampling periods of 2014, 2016 and 2017. Species richness also appeared to be slightly greater in R3 than R4 in all years and spring 2015, 2016 and 2017 had higher species richness than other spring sampling periods (Appendix B). In contrast, while some variability was observed in percent EPT, Simpson's Index, and Hilsenhoff index, these metrics were much more consistent among years and seasons than invertebrate biomass and abundance. Percent Chironomidae and Diptera were higher in spring 2017 compared to previous spring samplings. Benthic invertebrates were usually more abundant in the fall than in spring, however effects of flow, season, or year were not apparent. The fall and spring sample pairs for benthic invertebrate abundance and biomass confirmed productivity is significantly higher in the fall compared to the spring ($p < 0.01$). Chironomidae were much more prevalent than EPT taxa, and accounted for 29-100% 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 was associated with increased submergence of substrates within varial zones. Although the Jordan River was not sampled in 2017, it is likely an important source of invertebrates for areas within Reach 3 and may partially explain the increased diversity and richness observed in R3 sites, similar to the results of Kennedy et al. (2016).

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 (T4-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.

3.4.2 Benthic Invertebrate Production Models

Previous years of this study have used benthic production models to understand the underlying processes that affect benthic invertebrate production. The most important driver of invertebrate production in Spring and Fall was hours of submergence. The longer a sampler was submerged the more productive it was, and this relationship does not appear to be linear. Thus, a minimum period of submergence is generally required for sites to be considered aquatic in nature, and this minimum period likely varies with year, season, and other factors that influence death rates of invertebrates or periphyton.

3.4.3 Benthic Spatial Productivity Models

The implementation of minimum flows in Reach 3 did not yield a significant difference between invertebrate biomass ($m=64.2$, $p=0.26$). However, when month and its interaction with the implementation of minimum flows was included, benthic invertebrate biomass in R3 had a significant difference before and after the implementation of minimum flows ($m=-988$,





$p < 0.001$). Month and the interaction between month and implementation of flows were also significant ($p < 0.001$). The significance of the interaction term means the effect of minimum flows in Reach 3 varies according to month, where productivity in Reach 3 tended to be greater during the late winter and early spring when ALR elevations were low. During the summer and fall periods, when ALR tends to be higher, the effects of minimum flows were not as apparent, either because of operational differences or the backwatering effects resulting from high ALR elevations (Figure 3-6).

For Reach 4, both statistical models showed a significant difference for invertebrate biomass. Benthic invertebrate biomass had a negative slope with the implementation of flow, meaning invertebrate biomass was lower pre-implementation of minimum flows. However, the interaction term of month and the implementation of minimum flows was also significant ($m=49$, $p < 0.001$) and month was also significant ($m=19$, $p < 0.001$). The effects of ALR backwater are not apparent in Reach 4, because the reservoir elevations do not typically result in backwater, which partially explains the observed differences between reaches.

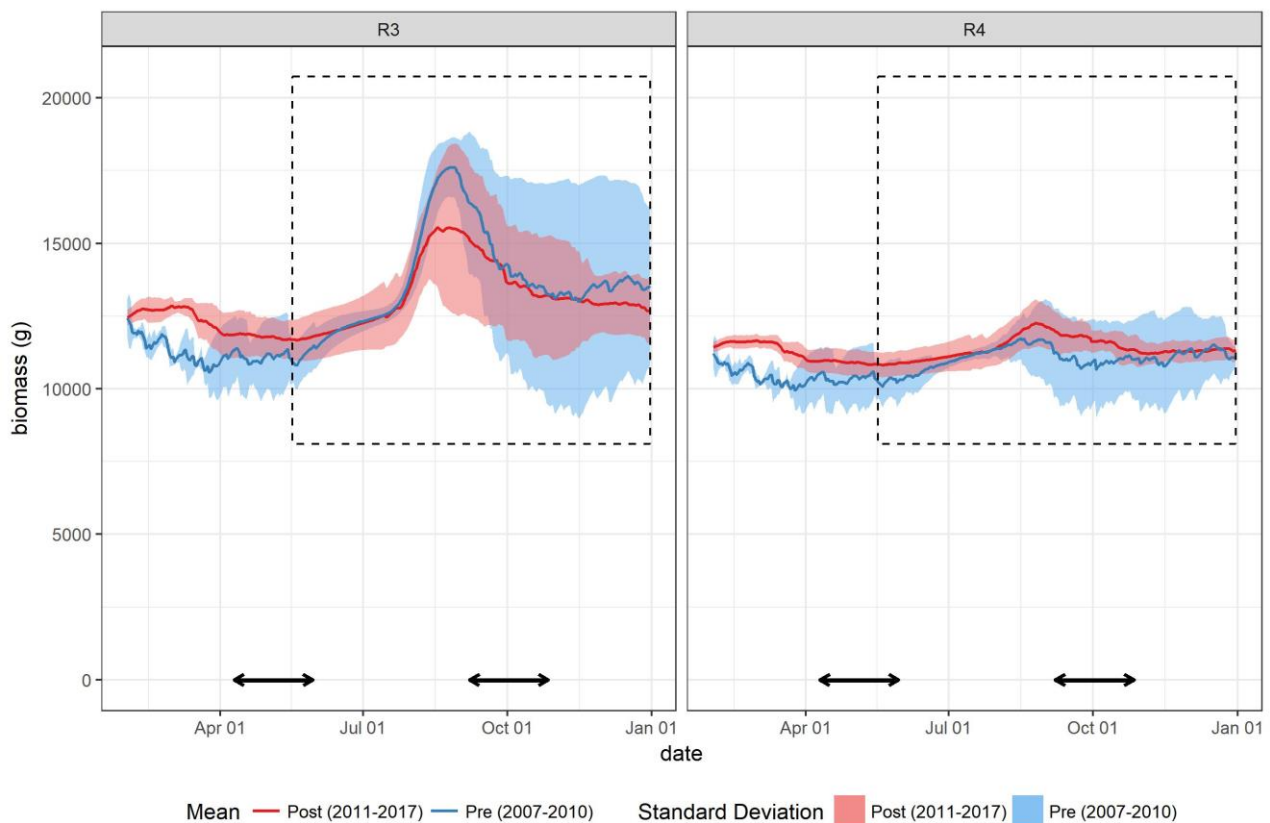


Figure 3-6: Comparison of Pre-Post Implementation of minimum flows for benthic invertebrate biomass. The dotted box represents when R3 is typically backwatered from ALR and the arrows represent the typical range of Spring and Summer deployment periods.





4.0 DISCUSSION

As in all regulated rivers, periphyton and benthic invertebrate components of the MCR benthic communities are sensitive to changes in habitat conditions and are good indicators of hydrologic disturbance (Biggs and Close 1989; Blinn et al. 1995). A long-term monitoring program of MCR periphyton and benthic invertebrates is underway in the MCR to determine the effects of minimum flows and REV 5 flows. The main objective of the 142 m³/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 2017 field surveys and subsequent analyses.

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

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

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

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

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 in BC. 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 the 2012 freshet. Extreme events (flows in excess of 1800 m³/s, or minimum flows of 142 m³/s that extend beyond 48 hours) occur regularly and can create habitat conditions that affect community structure and productivity, even to the point of large-scale die-off of benthic communities. 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 area of productive habitat within the MCR.





The study data demonstrate that minimum flows did not affect periphyton accrual rates in the permanently wetted areas but flows did affect accrual in the varial zones. Similarly, the area permanently wetted by minimum flows supported the most productive and diverse benthic invertebrate communities. None the less, increasing EPT taxa were associated with increased substrate submergence within the varial zones and at times, frequently wetted substrates were as productive as those that were permanently wetted. These findings are discussed in detail in the following sections.

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 its size. However, the open-celled Styrofoam used in these trials may exaggerate production from 20% (Perrin et al. 2004) to as much as 400% (median = 200%) based on 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 indicate 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 unregulated 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 – 2017 deployments, with comparison to oligotrophic, typical, and productive large rivers

Metric	Oligotrophic or stressed	Typical large rivers	Eutrophic or productive	MCR Seasonal Averages -50-day deployment (values bolded in bracket = 6 month samples)
Number of taxa (live & dead)	<20 – 40	25 – 60	Variable	5 - 52 (39-50)
Chlorophyll-a ug/cm ²	<2	2 – 5	>5 – 10 (30+)	0.41 – 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 – 13.1x10⁶)
Algae biovolume cm ³ /m ²	<0.5	0.5 – 5	20 - 80	1.54 – 3.12 (0.6 - 5.9)
Diatom density frustules/cm ²	<0.15 x10 ⁶	1 - 2 x10 ⁶	>20 x10 ⁶	0.32 – 0.51 x10 ⁶ (0.2-1.0 x10⁶)
Biomass –AFDW mg/cm ²	<0.5	0.5 – 2	>3	0.56 – 0.80 (0.35-3.5)
Biomass –dry wt mg/cm ²	<1	1 – 5	>10	26 (6-99)
Organic matter (% of dry wt)		4 – 7		3.9 – 6.1 (2 - 7)
Bacteria count, HTPC CFU/cm ²	<4 -10 x10 ⁶	0.4 – 50 x10 ⁶	>50x10 ⁶ - >10 ¹⁰	0.2 – 5 x10 ⁶
Fungal count CFU/cm ²	<50	50 – 200	>200	<250 – 6000
Accrual chl-a ug/cm ² /d	<0.1	0.1 – 0.6	>0.6	0.062 - 1.6 shallow; 0.89 – 2.0 deep

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

Throughout the 2007 – 2017 study period, periphyton communities in MCR occurred in three large zones created by the operating regime over the preceding 30 to 70 days as it interacted with the physical habitat. These zones are: 1) substrates that are permanently submerged, 2) substrates in the lower varial zone, and 3) substrates in the upper varial zone. Despite the establishment of these three distinct benthic communities with variable dominant species, both periphyton and invertebrate communities were relatively stable when viewed at the family taxonomic level. These zones are discussed in detail in the following sections.

4.2.1 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 (Schleppe and Larratt 2016). Peak production occurred near the edge of the permanently wetted channel at T2 locations where shear stress was less, light penetration was greater, substrates were stable, and the effects of scour and saltation were not as pronounced as they were near the thalweg at T1 locations. 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).

Normal operational patterns involve high daytime flows and low nighttime flows and this flow pattern prevented sampling substrates in very high light and low velocity. This could bias the results.

4.2.2 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 m³/s), and they occurred more frequently than higher flow events. The heterotrophic components of the biofilm can continue growing in damp substrates in the dark, while the photosynthetic components cannot, resulting in greater heterotrophic contributions to overall production in this zone. The invertebrate community underwent periods of growth and decline depending on how the recent operating regime coincided with their life cycles. The variable hydrologic conditions of MCR tended to select for rapid colonizers and rapid reproducers.

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

4.2.3 Upper Varial Zone

The frequently de-watered upper varial zone was typified by T5 and T6 locations, and included some samples from T7 located in the floodplain. It was less productive than the lower varial zone because these substrates experience regular daytime fluctuations between submergence and exposure. These conditions resulted in a benthic community that underwent brief periods of growth and frequent collapses determined by the timing and duration of exposures and how they intersected benthic invertebrate life cycles. Although





the upper varial zone periphyton community had a similar structure to deeper zones, reduced species diversity and accrual rates indicated stress, particularly to the photosynthetic microflora. Periphyton production commenced and rapid growth occurred after the substrates were wetted during daylight hours for periods in excess of 9 hours (Schleppe et al. 2012). Periphyton production halted when the substrates were dewatered during the day because normal cell processes could not proceed and desiccation stress reduced survival in both invertebrates and periphyton. The upper varial zone became more heterotrophic as the frequency or duration of drying events increased. This finding is also supported by modelling data for the periphyton autotrophic index in previous years that identified the frequency of 12-hour submergence events and total incubation time in the water and light, as important factors (Schleppe et al. 2013).

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. The floodplain did donate terrestrial detritus during flows exceeding 1700 m³/s, but these floodplain benefits occurred infrequently and were mostly associated with allochthonous nutrient input rather than production originating from benthic community development. Infrequent floodplain contributions to river productivity are typical of larger rivers (Doi 2009).

4.2.4 Varial Zone Boundary Conditions

The boundaries between the productivity zones in MCR were dynamic, and depended upon the average flow regime during the preceding 30-70 days, based on MCR and LCR time series data (Olson-Russello et al. 2015). Growth within these zones occurred rapidly during a 6-month period, when appropriate conditions for benthic community development occurred. The width of the productive lower varial zone expanded during stable flows in the 400 to 800 m³/s range.

4.2.5 Benthic Community Determinants and Composition

Statistical modelling results previously identified submergence as the top predictor of benthic production and diversity (Schleppe and Larratt 2016). In previous years, benthic invertebrate diversity models explained limited variation. This could be a result of diversity being fairly uniform among sites and transects. The effect of hydropeaking on diversity has not been well studied. However, there is one study that found benthic diversity was less variable below a dam (Hasting 2014). Other physical parameters including substrate type and velocity were identified as key factors determining periphyton and invertebrate community establishment (Schleppe and Larratt 2016). These physical parameters were more important determinants of community in permanently submerged habitat areas (Schleppe et al. 2014). Other physical factors that may also be important to benthic abundance and diversity that have not been investigated include frequency and magnitude of flow events. During hydropeaking operations, complete dewatering of river-edge substrates used exclusively by some Ephemeroptera and Trichoptera egg-layers, can cause their extirpation (Kennedy et al. 2016). 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). Overall, MCR benthic invertebrate productivity indicates that MCR has signs of stress when compared to other river systems of similar size (Table 4-2).

Table 4-2: Comparison of benthic invertebrate communities in different river systems.

River	Average Annual Discharge (m ³ /s)	Mean # of Invertebrates/m ² (±SE)	Total # of Taxa	Diversity (Simpson's Index)	Most Abundant Taxa (percent abundance)
MCR (Revelstoke)	955	3167(±6283)	33	0.58	Orthocladius complex (28) Hydra sp. (24) Orthoclaadiinae (10) (9.4) Eukiefferiella sp. (6.6)
LCR (Castlegar)- Winter	1,997	42502(±54789)	43	0.7	Simulium spp. (29) Simuliidae (25) Orthocladius Complex (13) Orthoclaadiinae (9)
LCR (Castlegar)- Summer	1,997	68760(±72944)	51	0.78	Hydropsychidae (33) Hydropsyche (19) Tvetenia spp. (8) Simulium spp. (6)
LCR (Castlegar)- Fall	1,997	58824(±59714)	41	0.77	Hydropsyche (26) Tvetenia spp.(12) Tvetenia discoloripes group (9) Parachironomus (7)
Fraser River (Agassiz)	3,620	829 (±301)	55	0.84	Orthoclaadiinae (62.7) Baetis spp. (7.2) Ephemerella spp. (5.4)
Thompson River (Spence's Bridge)	781	2108 (±1040.8)	48	0.44	Orthoclaadiinae (62.7) Baetis spp. (7.2) Ephemerella spp. (5.4)
Cheakamus River		1252 (±1149)	6		Ephemeroptera Plecoptera Diptera w/o chironomids

Data sources include Plewes *et al.* 2017, Reece & Richardson 2000, Triton Environmental Consultants Ltd. 2008 and this report.

Like most large rivers, MCR periphyton communities were dominated by diatoms representing between 82 and 98% of the biovolume at all sample sites. Other taxa, 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 producer to consumer organisms, as indicated by the Autotrophic Index at T5/T6 locations. AFDW (volatile solids) results have oscillated over the years and seasons indicating continual adjustments in the balance of producers and consumers, probably in response to habitat drivers, such as flows.

Benthic invertebrate communities were also dominated by taxa that are more tolerant of disturbance, such as chironomids (Tonkin et al. 2009). These taxa are often over-represented in flow-managed rivers (Bunn and Arthington 2002). EPT taxa and chironomids 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 (Schleppe et al. 2014).

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

4.2.6 Effects of Flow Ramping

For many reasons, the rates of de-watering (ramping) influence the mode of periphyton and benthic invertebrate recovery and interact with the life history of different taxa. In large rivers, rapid water loss such as ramping down hydro releases restricts or prevents in-situ recovery by reproduction and causes benthic recovery to be driven by recolonization (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 the MCR, similar to other studies conducted on other regulated rivers (Kennedy et al. 2016). However, since the full suite of environmental data, including detailed submergence predictor variables, is not available prior to Rev 5 flows, a full model to test the importance of ramping is not possible.

4.2.7 Benthic Recovery from Dewatering

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 >24 to 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 in warm or freezing weather (Stanley et al. 2004). Periphyton species that do not have strategies capable of allowing them to withstand repeated exposure would presumably become eliminated from the varial zones of the MCR, resulting in the observed homogeneity of the periphyton community structure throughout the varial zone. Invertebrate





recovery after a catastrophic event could take several weeks or more (if at all, may become extirpated) and was dependent upon the life-stage of the invertebrates at the time of the event (Kennedy et al. 2016). Species with specific riverside, substrate-dependent egg-laying strategies such as EPT species are more vulnerable to the effects of hydro-peaking than species that use a different strategy such as Dipterans (Kennedy et al. 2016). Such pressures on the invertebrate and periphyton communities are common to all large rivers, however, BC Hydro operations create a larger, more dynamic varial zone in the MCR than would otherwise be expected, and these operations can have a subsequently greater effect on populations than those observed in a natural system.

The rates at which recovery occurs is also variable among organisms present in the benthic communities of the MCR. Periphyton biofilm recovery is dependent on the reproduction rates of its constituent species. 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 Steveninck 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 also vary by species, with some laying eggs multiple times per season, whereas others may only emerge once during any given year and each taxa uses a different reproductive strategy that may further affect colonization rates (Kennedy et al. 2016). In summary, the effects of desiccation on either periphyton or invertebrates are function of species-specific desiccation tolerance, and how life history and reproductive strategies intersect with the timing and duration of dewatering. For this reason, species specific responses are both expected, and likely present, where responses are dependent upon key life history strategies of the species in question.

4.2.8 Seasonal Growth Patterns

Benthic communities 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 in the spring exposed both the upper and lower varial zone substrates to freezing temperatures, and because low water temperatures reduce enzymatic activity and slow growth even in the rapidly reproducing bacterial biofilm (Wetzel 2001). The MCR benthic community structure is stable but is still subject to seasonal variation.

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

The intent of implementing minimum flows is to increase the spatial area of wetted habitat and subsequently improve benthic community function at these locations. Minimum flows will increase the area of productive habitat because they maintain a minimum area of wetted perimeter. All MCR data indicate that productive benthic habitat was highly influenced by submergence parameters, including duration and timing of flow events. In fact, submergence (or metrics of it) appears to be the most important determinant of benthic





communities in the MCR, most notably abundance, biomass, and food for fish. For this reason, the spatial model of production derived for the MCR used submergence as the primary factor to determine overall growth. Deriving the spatial model in this fashion ensured it included production generated within the highly productive areas that occur at T2 through T3/T4 in areas (between the wetted edge of minimum flows to slightly above in the varial zone). The spatial model predicted productivity on an hourly basis. Hourly productivity estimates ensure the effects of operations and river bed topography are both considered.

The effect of minimum flows on benthic invertebrate biomass and periphyton chl-a was stronger in Reach 4 compared to Reach 3, likely because of ALR backwatering. There was no observed effect of minimum flows on benthic invertebrate biomass in Reach 3 annually. However, when monthly differences were considered minimum flows benefited benthic invertebrate production in months where ALR backwatering does not occur. In Reach 4, where minimal backwatering occurs, minimum flows provided an increase in benthic invertebrate biomass. The strength of the effect of minimum flows on benthic invertebrate biomass was variable across different months. The effect of minimum flows on daily productivity of benthic invertebrates was the strongest in February and March. The implementation of minimum flows caused an increase in periphyton chl-a in Reaches 3 and 4 of the MCR. However, the effect of minimum flows was stronger across months when ALR backwatering does not occur.

In summary, the operating regimes on the MCR directly affect the benthic community abundance and diversity in areas subjected to minimum flows because they create the wetted history in any given stretch of river, which is the most important determinant of overall benthic productivity. However, other parameters such as duration of daytime submergence were also important, but more challenging to model spatially. A key finding of the spatial model was that the elevation of the ALR plays an important role, because when it is higher the benefit of minimum flows on the spatial area of productivity are lessened by the effects of backwatering throughout Reach 3 and to a lesser extent Reach 4. In the 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 and is likely greatest in Reach 4, or in all stretches of river during periods when ALR is not backwatering riverine areas. Despite difficulties in determining the exact benefits of minimum flows to spatial area of productive habitats, we can conclude that minimum flow increased the spatial area of productive habitat for at least portions of the year because it provided a minimum wetted habitat area that is more productive than pre-minimum flows. Next year, the focus will be to explicitly determine the productive area of habitat in the MCR reaches.

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

The 2007 through 2017 data demonstrate that the accrual rate of biomass was not significantly altered following the introduction of minimum flows, and this finding is explored below. However, it is important to acknowledge that minimum flows do safeguard the thalweg areas from desiccation.





Historically, BC Hydro avoided daytime dewatering prior to the establishment of 142 m³/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 Questions 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 occurred most often 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 m³/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. Extended minimum flow events in excess of one week would cause extensive periphyton losses in the lower varial zone and would require a recovery period of several weeks with consistent submergence by flows greater than the 142 m³/s minimum. 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 °C were all beneficial to periphyton viability on exposed substrates (Stanley et al. 2004). Conversely, dry weather with air temperatures below 0 °C (spring) or exceeding 15 °C to 20 °C (fall) reduced periphyton viability on 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.

Establishment and accrual of periphyton communities in the 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 (Schleppe and Larratt 2016). Therefore, incubation periods of greater than 46 days are required to achieve peak periphyton biomass in MCR and may require more than 6 months for full development (Wu et al. 2009; Biggs 1989). Further, the daily, weekly, and annual patterns of operation, ALR 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 enable Reach 3 periphyton to recover faster after catastrophic flow events. Many of these areas may also act as impoundments to fish, resulting in mortalities, inferring that trade-offs are probable and should be considered in any flow management decisions.

Patterns of periphyton accrual and recovery in the MCR are further complicated by drifting limnoplankton exported by flows from Revelstoke Reservoir. Phytoplankton that becomes trapped in the periphyton matrix (Middleton 2010) can subsidize the population for many kilometers below a dam (Doi et al. 2008; Larratt et al. 2013). In the MCR, this subsidy is important to standing crop and accrual rates. Contributions of phytoplankton to MCR periphyton may also occur from the ALR to Reach 3 during backwatering, but the results of plankton hauls suggested the ALR phytoplankton was impoverished, likely by turbidity (Schleppe et al. 2012). Species contributed by Revelstoke Reservoir appeared to account for a significant proportion of the MCR periphyton, particularly in the fall and at R4. This means phytoplankton events occurring in Revelstoke Reservoir and the timing and depth of reservoir releases exerted an influence on MCR periphyton accrual and recovery rates, as well as community structure.

In summary, the study data to date indicate that 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, an important explanatory variable in our modelling data.

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

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





Further, invertebrates are more sensitive to desiccation than periphyton (Schleppe et al. 2012; Golder 2012) and were probably more heavily influenced by daytime exposure because of this, and some species may also have become extirpated due to timing of hydropeaking (Kennedy et al. 2016). The spatial area of the lower varial zone available to invertebrates was probably smaller than that available to periphyton. For these reasons, determining the effectiveness of minimum flows on improving benthic conditions for invertebrates is difficult, but data indicate 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 in MCR.

4.6 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?

The area of productive MCR habitat is directly correlated with submergence. Our data from previous years suggest that the abundance, biomass, and overall availability of fish food (using the Fish Food Index in 2013 or the EPT+Diptera responses in 2014-2016) were directly dependent upon submergence. Fish food varies depending upon the fish 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, an increase in wetted productive habitat should cause a subsequent increase in fish food availability, provided there are 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, we conclude minimum flows increased fish food availability, but other key influences on productivity such as frequency and duration of daytime submergence events, and timing of insect life history events (e.g., egg-laying) must also be considered. Substrates submerged for 450 – 500 hours (10 – 11 hours/day during the sampling duration) during daytime hours had the greatest availability of preferred fish food items. Similarly, EPT+D biomass was greatest in areas submerged for at least 500 – 1000 hours over >46 days.

EPT taxa were most commonly observed in areas of boulder or cobble substrate, whereas overall benthic abundance was greatest at sites with finer substrates. Areas of larger substrates should provide more food for the fish that forage on invertebrates. 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 and also timing of hydropeaking events. This will be considered in future years by considering the abundance and biomass of invertebrates in a spatial context over the study area.

Since the density of invertebrates is directly related to submergence, productivity, and ultimately food for fish, it is hoped that we can understand the specific effects of minimum flow on invertebrate abundance and biomass, and subsequently infer the effects on food for fish.





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APPENDIX A DATA TABLES AND FIGURES

Light and Temperature Figures

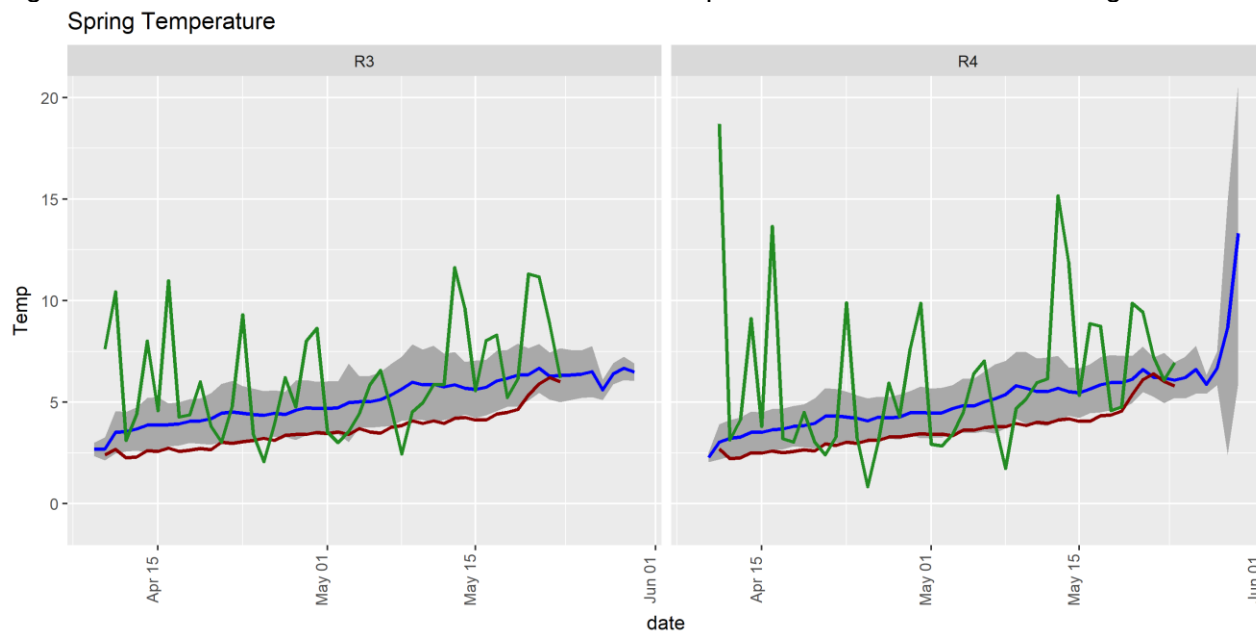


Figure A-1: The pattern of daily water temperature in MCR by reach during the spring study period. The blue line represents the mean from 2011 to 2017 (Spring) and red represents the mean water temperature in 2017 from all submerged samplers. The green line represents the average temperature of exposed sites in Spring 2017. Data were pooled for spring periods between 2011 – 2017 (\pm SD in grey).



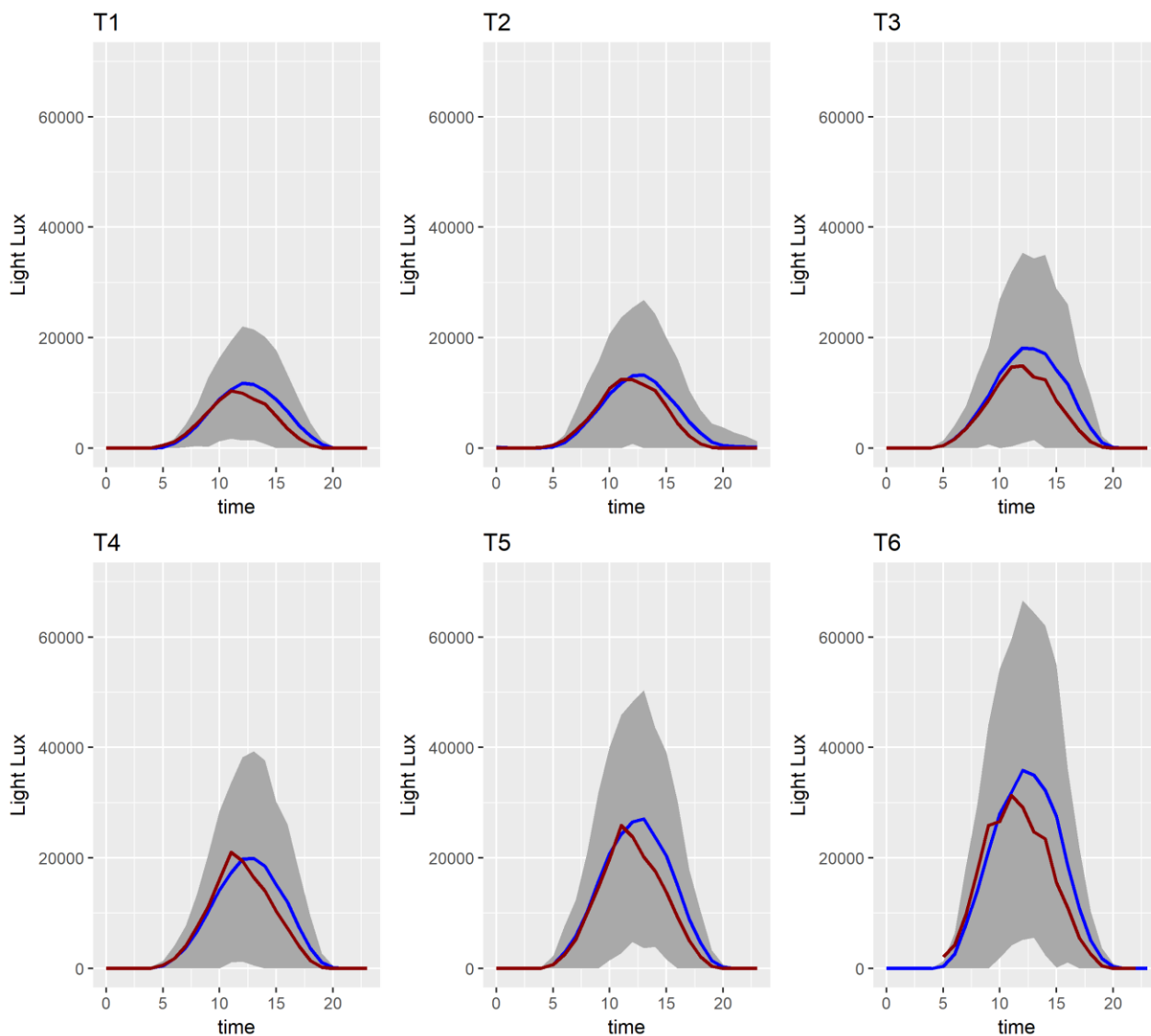


Figure A-2: Spring daily pattern of light intensity (lux) while samplers were submerged in the MCR at varying depths, where T1 is the deepest and T6 is the shallowest for samplers. The blue line represents the mean from 2011 to 2017 (\pm SD in grey) and red represents the mean 2017 spring data from all submerged samplers. The x-axis is time in hours of the day (0:00 to 24:00).



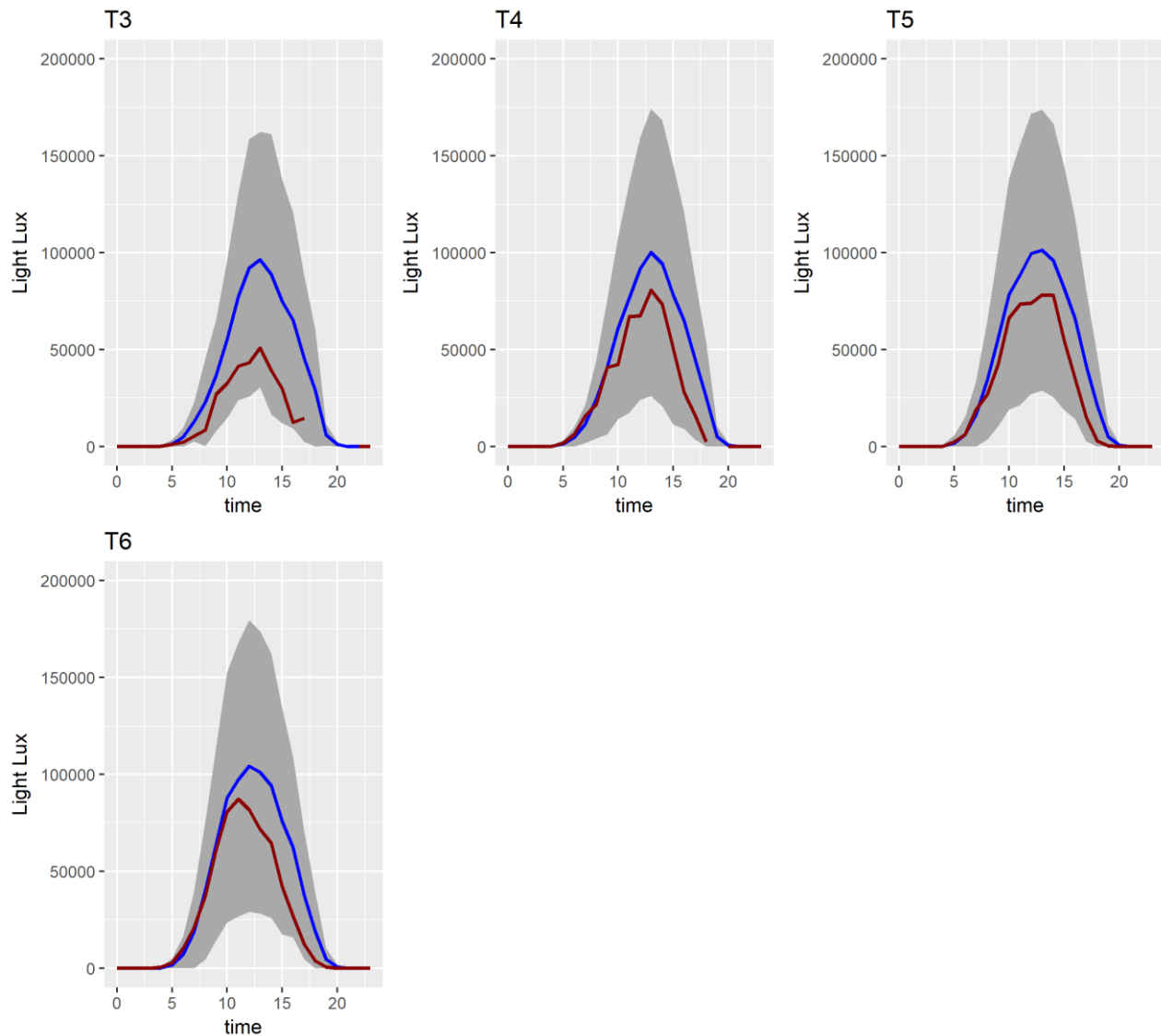


Figure A-3: Spring daily pattern of light intensity (lux) in the MCR when samplers were exposed (out of the water). T3 is the deepest and T6 is the shallowest for samplers. Noting T1 and T2 were continuously submerged so are not included in the above figure. The blue line represents the mean from 2011 to 2017 (\pm SD in grey) and red represents the mean spring 2017 data from all exposed samplers. The x-axis is time in hours of the day (0:00 to 24:00).



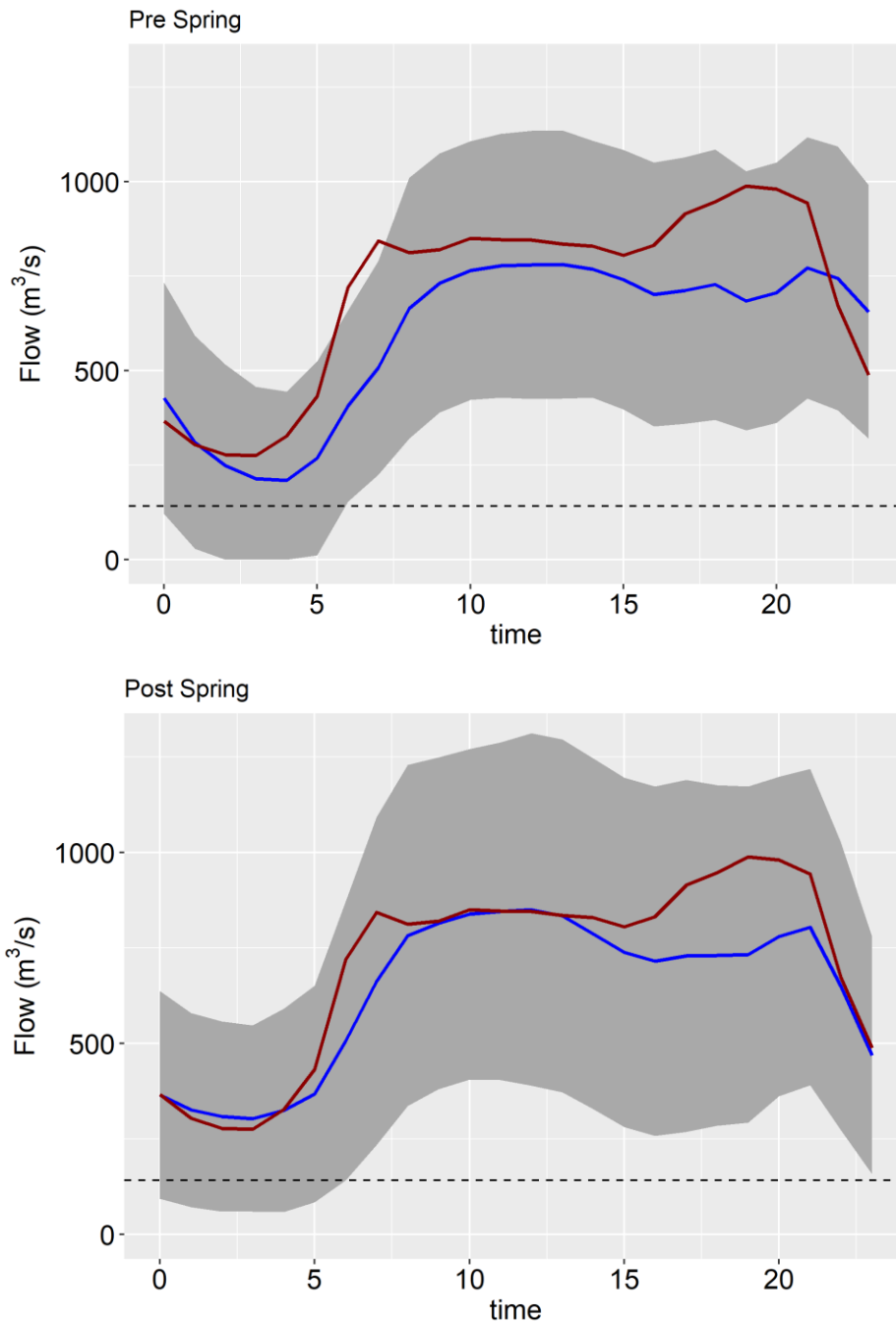


Figure A-4: The pattern of daily flow in the MCR during the spring study periods in pre (2007-2010) and post implementation (2011-2017) of minimum flows. Average hourly flows from 2017 (Spring) are shown in red, while the average of all data pooled (2010-2017) is shown in blue. The standard deviation of





average hourly flow across all years pooled is shown in grey. The minimum flows are shown as a black dotted line.

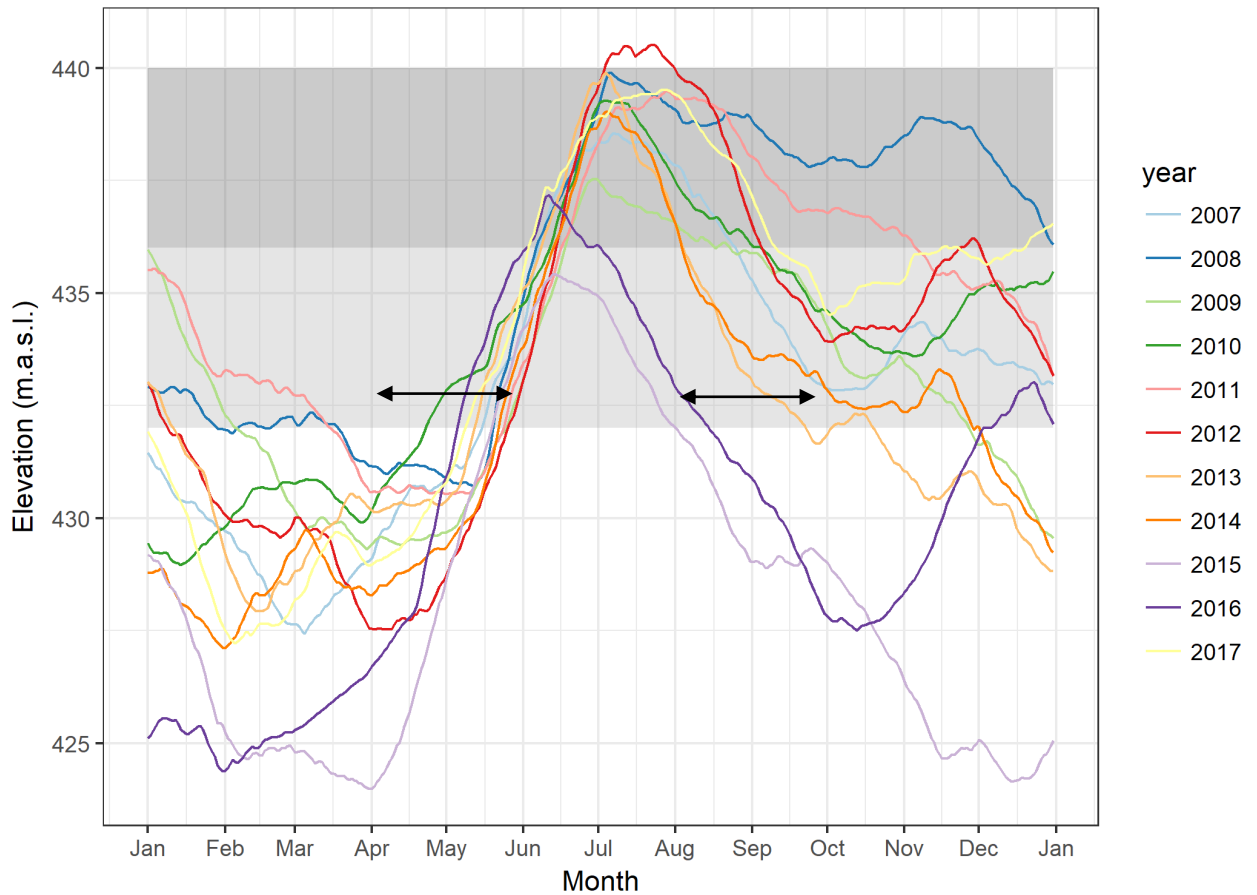


Figure A-5: Backwatering of Arrow Lakes Reservoir (ALR) into MCR Reach 3 and Reach 4 with typical spring and fall deployment periods occurring between the arrows. The vertical axis shows elevations in the normal operating range of ALR. Light grey shading denotes R3 was backwatered; dark grey shading denotes R3 and R4 were backwatered.





Table A-1: Flow summary table for each deployment period, summary statistics are calculated from mean daily flows.

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



APPENDIX B DIGITAL DATA TABLES AND FIGURES





APPENDIX C SUPPLEMENTAL METHODS AND RESULTS

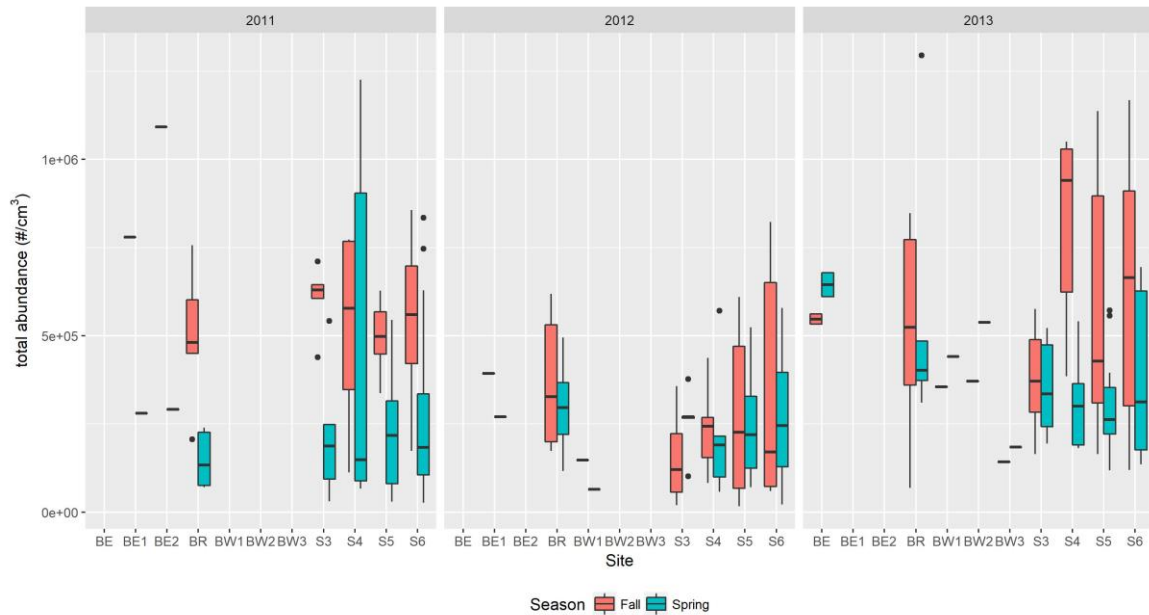


Figure A-6: Periphyton total abundance compared by season and site 2011-2013.

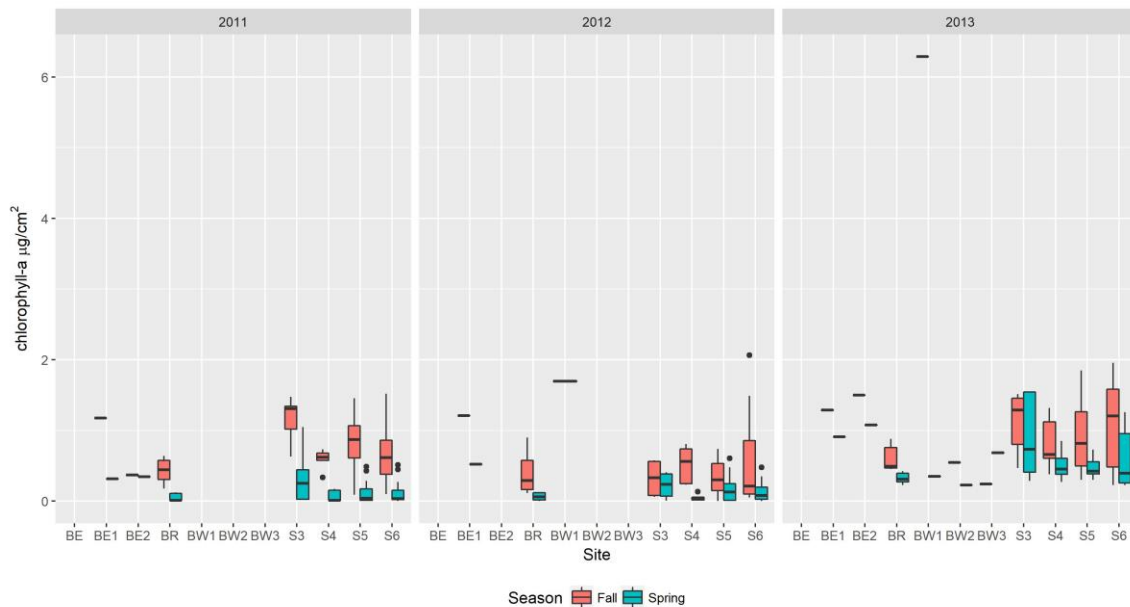


Figure A-7: Periphyton chl-a compared by season and site 2011-2013.





Table A-2: Summary of fish food index models with a $\Delta AIC < 3$.

Predictor	Model Number	X Intercept	Standardized Predictor Value	R2	df	logLik	AICc
Log Total Abundance	2	-1.48	1.73	0.02	5.00	1036.41	2085.80
Log Total Abundance	1	-1.48	NA	0.01	4.00	1039.41	2088.26
Log Total Biovolume	1	-1.48	NA	0.01	4.00	1039.41	2088.26
Log Total Biovolume	2	-1.45	0.74	0.01	5.00	1038.29	2089.55
Log chla	2	-1.49	2.76	0.11	5.00	1023.89	2062.41



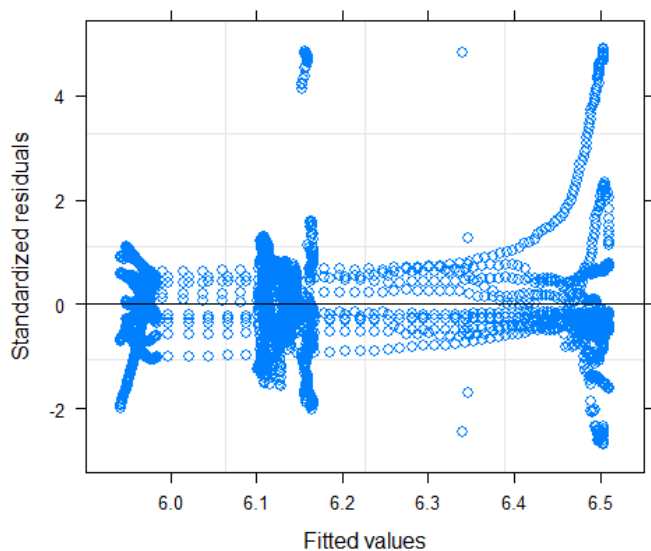


Figure A-8: Standardized Residual plot for R3 periphyton chl-a model without interaction term.

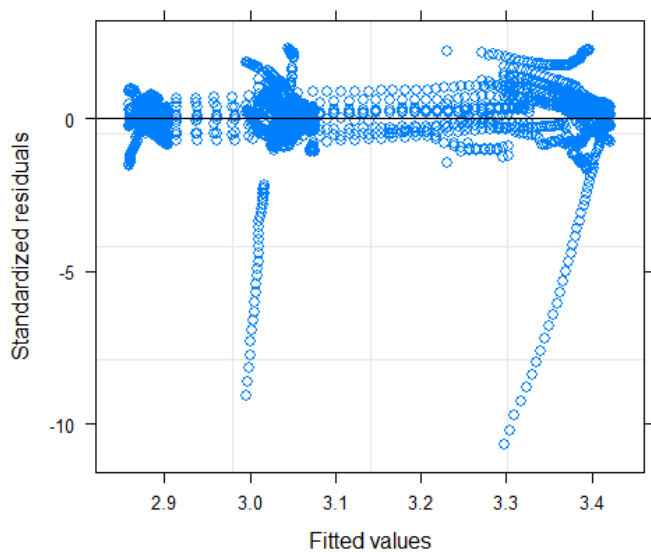


Figure A-9: Standardized Residual plot for R4 periphyton chl-a model without interaction term.



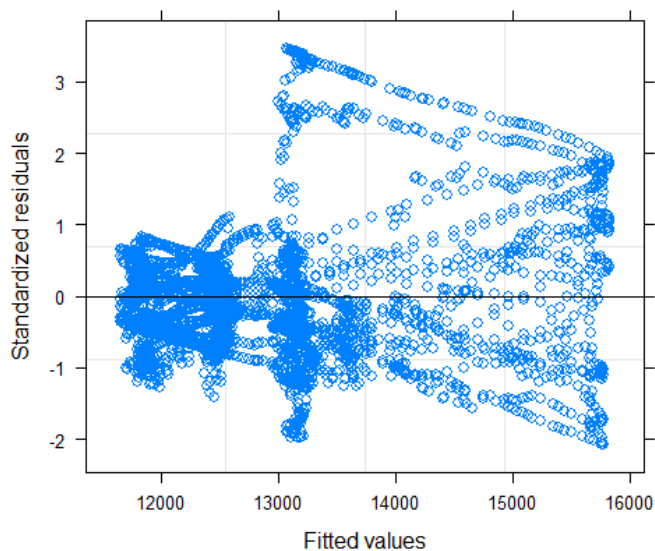


Figure A-10: Standardized Residual plot for R3 benthic invertebrate biomass model without interaction term.

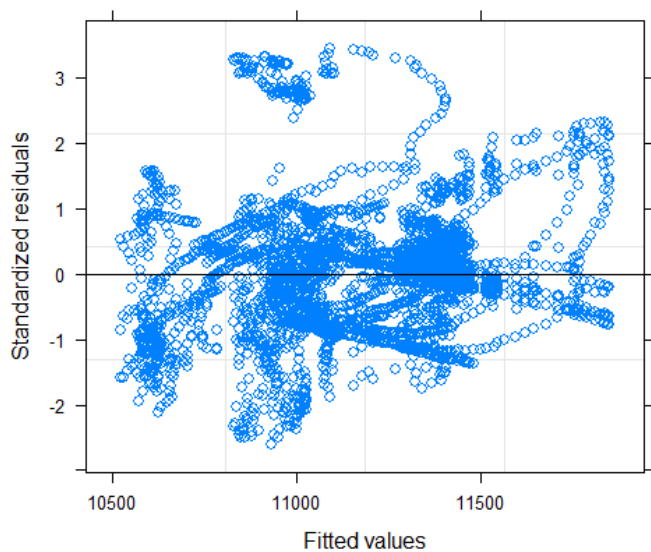


Figure A-11: Standardized Residual plot for R4 benthic invertebrate biomass model without interaction term.

