Columbia River Project Water Use Plan

MIDDLE COLUMBIA RIVER ECOLOGICAL PRODUCTIVITY MONITORING

Implementation Year 7

Reference: CLBMON–15b

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

Survey Period: 2013

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September 2014

PROGRAM NO. CLBMON-15B

MIDDLE COLUMBIA RIVER ECOLOGICAL PRODUCTIVITY MONITORING, 2007-2013

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CLBMON 15B Status of Objectives Management Questions and Hypotheses After Year 7

Objectives	Management Questions	Management Hypotheses	Year 7 (2014) Status
A key environmental objective of the minimum flow release is to enhance the productivity and diversity of benthic communities. The benthic community of MCR is viewed as a key monitoring component in the Revelstoke Flow Management Program because the productivity and diversity of the benthic community may reflect ecosystem health, and the benthic community supports juvenile and adult life stages of fish populations. Therefore, the objectives of this monitoring program are to 1) provide long term data on the productivity of benthic communities and 2) assess how the recommended minimum flow releases influence benthic productivity as it relates to the availability of food for fishes in the MCR.	Q.1. What is the composition, distribution, abundance and biomass of periphyton and benthic invertebrates in the section of MCR subjected to the influence of minimum flows?	Ho_1: The implementation of the 142 m^3/s minimum flow release does not change the spatial area of productive benthic habitat for periphyton or benthic invertebrates in the MCR.	Ho_1: The hypothesis is rejected, but only under certain operating conditions. Theoretically, the spatial area of habitat should increase with minimum flows. The spatial area of productive habitat is determined by the BC Hydro operating regime and occurred in three typical growth bands that moved across the channel in relation with mean low flows and duration of high daily flows. During certain operating regimes, the total productive area is determined by factors such as high daily average flows, backwatering from Arrow Lakes Reservoir through large portions of habitat between Big Eddy and the Illecillewaet River, and weather conditions. To explicitly determine the spatial area of habitat due to minimum flows, a more complex spatial model is required that considers all aspects of the operating regime due to the strong correlations between submergence and the total area of productive habitat. Developing this more complex spatial model will allow more specific conclusions and will provide useful information for considering alternative operating regimes.
	Q.2. What is the effect of implementing minimum flows on the area of productive benthic habitat?	Ho_2: The implementation of the 142 m^3/s minimum flow release does not change the total biomass accrual rate of periphyton in the MCR.	Ho_2: .Given no other operating constraints, we conclude that minimum flows in combination with daily, weekly, monthly, and annual operating regimes affect the total biomass within the MCR. Peak or total biomass was greatest in permanently wetted areas adjacent to the channel edge at average low flows and in areas directly below average low flows. The overall benefits of minimum flow are greatest under the following conditions: • Periods of low daily flows that exceed 24 hours with high or freezing average daytime temperatures. • Repeated exposure events in excess of 12 hours

CLBMON 15B Status of Objectives Management Questions and Hypotheses After Year 7			
Objectives	Management Questions	Management Hypotheses	Year 7 (2014) Status
	Q3.What is the effect of implementing minimum flows on the accrual rate of periphyton biomass in the MCR? Is there a long term trend in accrual?	Ho_{3A}: There are no changes in accrual rates of periphyton at channel elevations that remain permanently wetted by minimum flow releases.	Ho_{3A}: The hypothesis is accepted. Accrual 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. Peak flows associated with REV 5 or high water events may reduce periphyton accrual and standing crop in permanently submerged habitats.
		Ho_{3B}: There are no changes in accrual rates of periphyton at channel elevations that are periodically dewatered by minimum flow releases.	Ho_{3B}: The hypothesis is accepted, but only under certain conditions. We conclude that minimum flows do not affect areas that are periodically dewatered (i.e., above minimum flow), but they have had an effect in areas that were regularly exposed before the minimum flow operating regime because increased accrual would have occurred as observed in time series sampling in the spring and fall. Daytime submergence, seasonal patterns, algal immigration from Revelstoke Reservoir and operating cycles were also important determinants of periphyton accrual and must also be considered.

CLBMON 15B Status of Objectives Management Questions and Hypotheses After Year 7

Objectives	Management Questions	Management Hypotheses	Year 7 (2014) Status
	Q.4. What is the effect of implementing minimum flows on the total abundance, diversity and biomass of benthic organisms in the section of the MCR subjected to the influence of minimum flows? Is there a long term trend in benthic productivity?	Ho_{4A}: The implementation of the 142 m^3/s minimum flow release does not change the total abundance / biomass / diversity of benthic invertebrates in the MCR.	$H4_{A}$: The hypothesis is rejected, but only under certain operating conditions. Permanently submerged areas were the most productive and diverse, but frequently submerged varial zone areas also had some level of productivity and diversity. The area of productive invertebrate habitat was bounded by average daily low flows and its upper limit was determined by average daily submergence. Specifically determining the benefits of minimum flows is not currently possible because of other confounding factors such as the duration of daily high flows. Without any other operating constraints, minimum flows do affect the total abundance, biomass, and diversity of benthic communities because they establish a minimum area of productive habitat and ensure there are organisms for recolonization in addition to those provided by tributary inflows.
		$Ho_{4B:}$ There are no changes in abundance/biomass/diversity of benthic invertebrates at channel elevations that remain permanently wetted by minimum flow releases.	$Ho_{4B:}$ We conclude that minimum flows have not affected abundance/biomass/diversity in permanently wetted areas and this hypothesis is accepted. However, our data suggest that other aspects of operation, such as high peak flows associated with high water events may also be important determinants of invertebrate production. Thus, consideration of all aspects of flow regulation must occur in conjunction with minimum flows to understand potential effects.
		$Ho_{4C:}$ There are no changes in abundance/biomass/diversity of benthic invertebrates at channel elevations that are periodically dewatered by minimum flow releases.	$Ho_{4C:}$: The hypothesis is accepted, but only under certain conditions. We conclude that minimum flows do not affect areas periodically dewatered (i.e., above minimum flow), but they probably had an effect in areas that were regularly exposed before the minimum flow operating regime because the data suggest that benthic invertebrate abundance, diversity, and biomass are positively associated with submergence or time in the water. Daytime submergence, seasonal patterns, and operating cycles were also important determinants of benthic accrual and must also be considered.

CLBMON 15B Status of Objectives Management Questions and Hypotheses After Year 7

Objectives	Management Questions	Management Hypotheses	Year 7 (2014) Status
	Q5. If changes in the benthic community associated with minimum flow releases are detected, what effect can be inferred on juvenile or adult life stages of fishes?	Ho_5: The implementation of the 142 m^3/s minimum flow release does not change the availability of fish food organisms in the Middle Columbia.	Ho_5: This hypothesis is rejected, but only under certain operating conditions. Food for fish was assessed using a Fish Food Index (FFI). The index consisted of three parameters for each benthic taxon, 1) invertebrate abundance, 2) relative invertebrate biomass, and 3) fish food preference for a given benthic taxon. The overall benefits of minimum flow are greatest under the following conditions: • Periods of low daily flows that exceed 24 hours with freezing or high average daytime temperatures. • Repeated exposure events in excess of 12 hours Substrates submerged for 450 to 500 hours (10 to 11 hours per day) during daytime hours had the greatest availability of preferred fish food items. Both periphyton and invertebrates showed similar responses, suggesting that overall productivity and food for fish is directly affected by the BC Hydro operating regime. 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.

ACRONYMS AND ABBREVIATIONS

AFDW	Ash-Free Dry Weight
ALR	Arrow Lakes Reservoir
ANOSIM	analysis of similarity
ANOVA	analysis of variance
BC Hydro	British Columbia Hydro and Power Authority
BW	backwater
BE	Big Eddy
BR	bedrock
CFU	Colony forming units (bacteria culture)
chl-a	chlorophyll-a
CLBMON 15-b	Middle Columbia River Ecological Productivity Monitoring (this study)
Cultus Lake	Department of Fisheries and Oceans Cultus Lake Laboratory
d.f.	degrees of freedom
EPT	Ephemeroptera (mayflies), Plecoptera (stoneflies) & Trichoptera (caddis flies)
F	F-Statistic
HBI	Hilsenhoff Index
HTPC	Heterotrophic plate count (non-photosynthetic bacteria)
IL	Illecillewaet River
JR	Jordan River
MCR	Middle Columbia River
m	metre
min	minimum
max	maximum
MW	megawatts
NMDS	Non metric multi-dimensional scaling
REV 5	Revelstoke 5
SD	standard deviation
WUP CC	Columbia River Water Use Plan Consultative Committee
WW	whitewater
FFG	functional feeding group
ALR	Arrow Lakes Reservoir

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	Capable of photosynthesis
Autotrophic Index	Autotrophic index is the proportion of an organic matrix which is viable algae, and is calculated as (AFDM / chl-a) The inverse is known as AP or autotrophic potential
Benthic	Organisms that dwell in or are associated with the sediments
Benthic production	The production within the benthos originating from both periphyton and benthic invertebrates
Bioaccumulation	Removal of metal from solution by organisms via adsorption, metabolism
Bioavailable	Available for use or uptake by plants or animals
Catastrophic flow or event	Flow events that have population level consequences of >50% mortality in areas affected by the operational flow changes, either through exposure related mortality or stress-induced mortality after exposure.
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
Flow	The instantaneous volume of water flowing at any given time (e.g.1200 m^3/s)
Functional Feeding group	(FFG) Benthic invertebrates can be classified by mechanism by which they forage, referred to as functional feeding or foraging groups
Heteroscedasticity	Random variables from sub-populations that have different variability from others
Invertebrate Production	Benthic invertebrate biomass, abundances, and measures of diversity
Large river	A fluvial system of sufficient scale to intimidate researchers (Hynes 1989).
Light attenuation	Reduction of sunlight strength during transmission through water
Limnoplankton	Algae that can only function while suspended in a stationary water column
Microflora	The sum of algae, bacteria, fungi, Actinomycetes, etc., in water or biofilms
Minimum flow	The current operating regime that maintains a minimum flow of 142 m^3/s in MCR, which does not refer to increased potential flows with the addition of the REV 5 turbine,
Myxotrophic	Organisms that can be photosynthetic or can absorb organic materials directly from the environment as needed
Nano plankton	Minute algae that are less than 5 microns in their largest dimension
Operations / operating regime	the day to day changes in flow associated with on- demand power generation
Pico plankton	Minute algae that are less than 2 microns in their largest dimension
Peak biomass	The highest density, biovolume or chl-a attained in a set time on a substrate
Periphyton	Microflora that are attached to aquatic plants or solid substrates
Periphyton production	Periphyton productivity measures include chl-a, biovolume, and abundance
Phytoplankton	Algae that float, drift or swim in water columns of reservoirs, lakes and slow-moving rivers
REV 5 flow	REV 5 is the newest turbine added to the Revelstoke Dam. It added 500 MW generating capacity, and increased potential peak discharge to 2124 m^3/s
Riparian	The interface between land and a stream or lake
Saltation	The movement of hard particles such as sand over an uneven surface in turbulent flows
Varial Zone	The zone between maximum and minimum water elevations over a specific period of time.
Zooplankton	Minute animals that graze algae, bacteria and detritus in water bodies

EXECUTIVE SUMMARY

Aquatic habitats in the Middle Columbia River (MCR) are heavily influenced by variable flow releases from Revelstoke Reservoir. To lessen the effect of these variable flow releases, the Columbia River Water Use Plan supported implementation of a year-round minimum flow of 142 m^3/s from Revelstoke Dam to the MCR. The key objective of the 142 m^3/s minimum flow strategy is to enhance the productivity and diversity of benthic communities in the MCR by increasing the permanently wetted area by an estimated 32–37% (Golder 2012). The goal of this project, the ecological productivity monitoring program CLBMON-15b, is to provide long-term data on benthic productivity of MCR using artificial substrate samplers that assess how minimum flow influences benthic communities and availability of food for fish. This summary report presents data from years 1 through 7 of the study period (2007 to 2010 (pre) and 2011 to 2013 (post)). following the implementation of minimum flow in 2011 and full in service operation of a fifth unit at REV in December 2010.

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

Distinguishing between the benefits of minimum flows and variation in the operating regimes observed over the study period was difficult. Daytime submergence and high average daily flows were key factors in determining benthic productivity because varial zone areas submerged for at least 9 hours per day were typically as productive as those in areas submerged by minimum flows. Further, the benefits of minimum flows were lessened by other factors, most notably backwatering from Arrow Lakes Reservoir that submerged habitats in the varial zone substrates which would otherwise have desiccated. In the absence of other operating constraints, minimum flows will benefit benthic productivity in MCR, but alternative operating regimes that have higher average daily flows without minimum flows may also create habitat conditions that are equally productive.

Overall benthic community structure was stable at the family group across all sites of variable submergence, with similar representation between years. However, when MCR periphyton data were examined at the genera or species level, distinctions between years, seasons, and flow changes emerged. For example, the 2013 fall data showed that a much higher than normal proportion of the periphyton was derived from species exported by Revelstoke Reservoir.

Benthic invertebrates were more sensitive to exposure than periphyton. Exposure events of as little as 24 hours during high daytime temperatures caused substantial stresses and die-off in the benthic community, such as those observed in the spring of 2011. For periphyton, exposures exceeding 48 hours were required before similar effects were observed.

Peak production in MCR was not achieved within two months from the time of first wetting and may take longer than six months to establish if sites experience frequent dewatering, particularly in the spring when growth rates were slow.

Submergence was identified as the single most important determinant of benthic production in MCR. Minimum flows benefit productivity most during periods when average daytime flows over the preceding 30 to 70 days are lower (e.g., 400 to 600 m^3/s versus 1200 to 1600 m^3/s). Thus, a small shift in water releases would increase the area of productive habitat, and could occur under an operating regime that included brief excursions to <10 m^3/s flow, provided that flows of 400 to 600 m^3/s occurred every day for at least 9 daytime hours. However, many factors affect the total area of productive habitat and need to be considered in conjunction with the effects of minimum flows. Factors such as Arrow Lakes Reservoir backwatering, operational flow patterns, high peak flows (exceeding 1800 m^3/s), seasonal cycles and species tolerances were all important determinants of benthic productivity and should be considered when reviewing future operational flow regime guidelines. Future analyses of this data should allow the development of a spatial model to determine the total area and quantity of production in MCR using results from habitat modelling.

Keywords:

Middle Columbia River, Ecological Productivity, Minimum Flows Management

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1.0 INTRODUCTION

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

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

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

In the study years prior to implementation of a minimum flow (2007 – 2010), the water release from the Revelstoke Dam varied from 8.5 m^3/s to 1700 m^3/s, depending on power demands, and could result in sudden water fluctuations between 3 to 5 vertical meters. Since Rev 5 and minimum flows were initiated (2011-2013), flows have ranged from 142 m^3/s to 2124 m^3/s. The extent of submergence of river substrates was therefore determined by the variable water releases, in combination with backwatering from the downstream Arrow Lakes Reservoir (ALR) into portions of MCR as far as just upstream of Big Eddy, a large deep pool near Revelstoke.

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

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

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

This report summarizes years 1 through 7 of the monitoring program, and focuses on the 2013 (Year 7) sampling season.

1.2 Objectives, Questions, and Hypotheses

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

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

The first objective was satisfied by the basic study design developed by Perrin et al. (2004). We developed a conceptual model, presented in Figure 1-1, to address the second and third objectives, and to understand the potential interactions of the complex factors affected by changes in flow. Although the relative importance and role of each parameter have yet to be fully clarified, this model identifies the many variables that can influence benthic productivity and ultimately food for fish. Further, it highlights areas for which data is being collected to address the management questions. At the forefront of the model are BC Hydro operations that determine quantity and duration of water release. Altered flows directly influence several factors such as velocity, turbulence, depth, submergence, scour, etc. and therefore have a direct effect on benthic productivity.

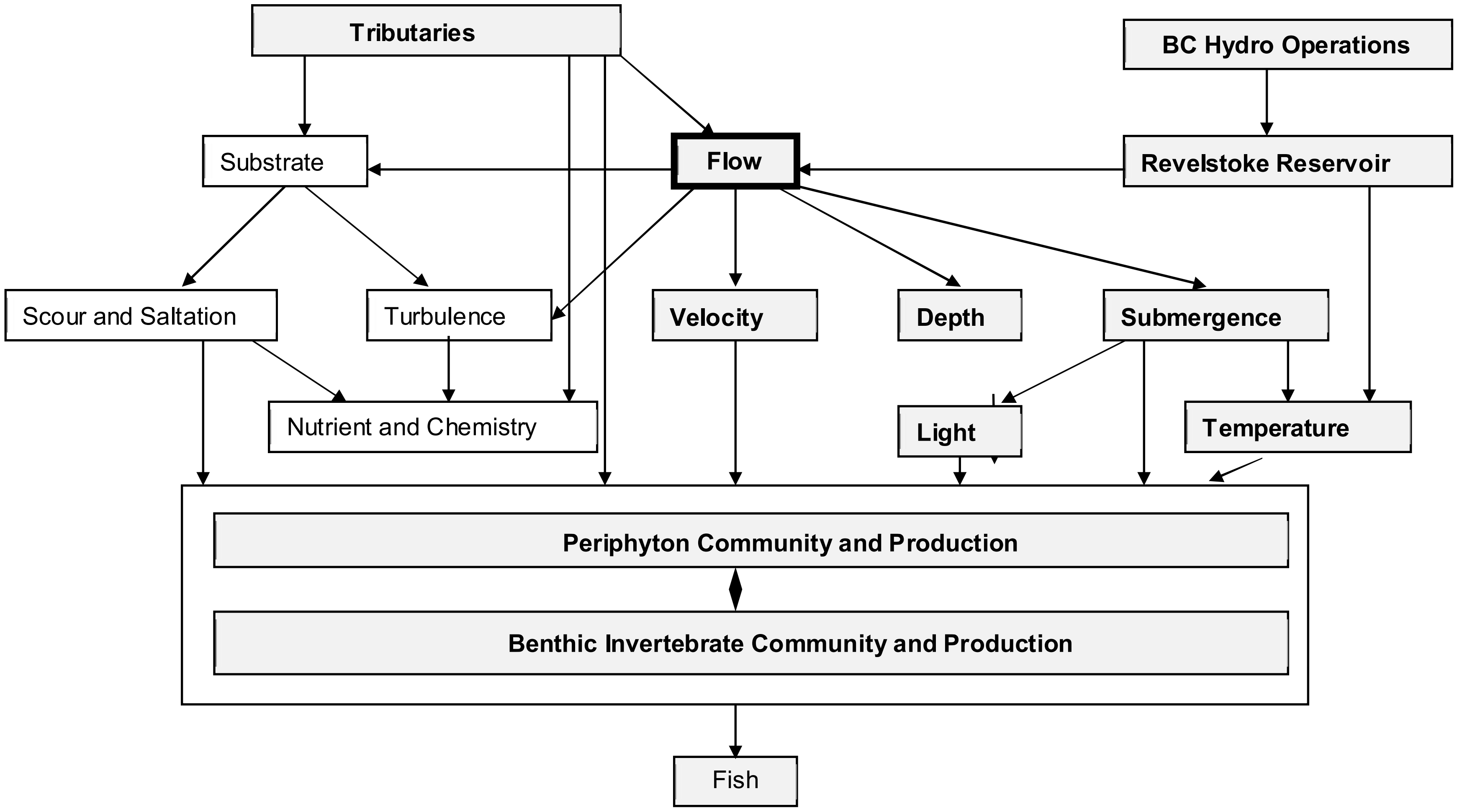


Figure 1-1: Conceptual interactions model of habitat variables and benthic production as they relate to food for fish in MCR. Parameters shaded in grey, with bolded text represent parameters being assessed in this study.

To comprehensively address the three main objectives, five management questions with related hypotheses were developed. Table 1.1 lists each of the management questions/hypotheses (BC Hydro 2010), and relevant components of our 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.

We used simple statistical models to understand the physical responses of periphyton and benthic productivity to flows. In a complex system like MCR, we could not test the effects of minimum flows and REV 5 flows in isolation from each other and the larger flow regime. In lieu of this approach, we identified relationships between benthic production and spatial features that are directly influenced by flows including area of wetted habitat, and frequency and duration of submergence. From this, the effects of the operating regime, including minimum flow, is inferred. Using 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 financial aspect. The intent of the data collection is to facilitate the extrapolation of benthic and periphyton productivity in the river as a whole and to enable estimation of the spatial area of productive habitat in MCR under a minimum flow or alternative operating regime. The ultimate goal is to identify and describe what habitat attributes are most influential and to identify how implementation of different operational regimes may affect benthic productivity in MCR including both a minimum flow and REV 5 operating regime.

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

Key Management Questions	Management Hypotheses:	Study Components to Address Management Questions/Hypotheses
Q1. What is the composition, distribution, abundance and biomass of periphyton and benthic invertebrates in the section of MCR subjected to the influence of minimum flows? Q2. What is the effect of implementing minimum flows on the area of productive benthic habitat?	Ho_1. The implementation of the 142 m3/s minimum flow release does not change the composition, distribution, abundance, biomass, or spatial area of productive benthic habitat for periphyton or benthic invertebrates in MCR.	Artificial sampler arrays deployed across the spectrum of flows/elevations of the MCR. Data collection includes: • Abundance –periphyton & invertebrates • Diversity – taxonomy indices for periphyton and invertebrates • Production/Biomass – chl-a, AFDW/DW, biovolume, benthic invertebrate biomass • Natural Substrate Comparisons Productive habitat area is considered using the analogous measure submergence as a surrogate for minimum flow. Statistical models using a variety of parameters describing submergence are tested for the different measures of production. Future data analysis will attempt to directly link submergence time to the total spatial area of productive benthic habitats
Q3. What is the effect of implementing minimum flows on the accrual rate of periphyton biomass in MCR? Is there a long term trend in accrual?	Ho_3. The implementation of the 142 m3/s minimum flow release does not change the total biomass accrual rate of periphyton in MCR. Ho_{3A}. There are no changes in accrual rates of periphyton at channel elevations that remain permanently wetted by minimum flow releases. Ho_{3B}. There are no changes in accrual rates of periphyton at channel elevations that are periodically dewatered by minimum flow releases.	Artificial Samplers and time series samplers are deployed across the spectrum of submerged habitat areas on the MCR. Data collection includes: • Abundance • Diversity – taxonomy indices for periphyton and invertebrates • Production/Biomass – chl-a, AFDW/DW, biovolume • Nano-flora HTPC plate counts Periphyton production (both accrual and peak biomass) are assessed using a variety of different measures of productivity. Periphyton productivity is considered using the analogous measure submergence as a surrogate for minimum flows because this data is easier to use in models. Periphyton models are developed that test the effects of submergence on periphyton peak biomass. Future data analysis will attempt to directly link submergence time to the periphyton productivity in three areas of the river, those permanently submerged, those in varial zone areas, and those in floodplain areas of MCR.
Q4. What is the effect of implementing minimum flows on the total abundance, diversity and biomass of benthic organisms in the section of MCR subjected to the influence of minimum flows? Is there a long term trend in benthic productivity?	Ho_4. The implementation of the 142 m3/s minimum flow release does not change the total abundance/biomass/diversity of benthic invertebrates in MCR. Ho_{4A}. There are no changes in abundance/biomass/diversity of benthic invertebrates at channel elevations that remain permanently wetted by minimum flow releases. Ho_{4B}. There are no changes in abundance/biomass/diversity of benthic invertebrates at channel elevations that are periodically dewatered by minimum flow releases.	Artificial Samplers are deployed across the spectrum of submerged habitat areas on the MCR. Data collection includes: • Abundance • Diversity – taxonomy indices for periphyton and invertebrates • Production/Biomass – biomass Invertebrate production is assessed using a variety of different measures of productivity. Benthic productivity is considered using the analogous measure submergence as a surrogate for minimum flows because this data is easier to use in models. Invertebrate models are developed that test the effects of submergence on invertebrate biomass, abundance, and diversity. Future data analysis will attempt to directly link submergence time to the invertebrate productivity in three areas of the river, those permanently submerged, those in varial zone areas, and those in floodplain areas of MCR.
Q5. If changes in the benthic community associated with minimum flow releases are detected, what effect can be inferred on juvenile or adult life stages of fishes?	Ho_5. 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.

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

2.0 METHODS

2.1 Study Area

The MCR consists of Reaches 4 through 1 of the upper Columbia River adjacent to the town of Revelstoke, encompassing approximately 38.5 km between the Revelstoke Dam and the Upper Arrow Lake Reservoir (ALR) near Galena Bay. This study focused on Reaches 4 and 3, which exhibit more riverine-like conditions than Reaches 2 and 1. Reach 4 extends approximately 5 km from the Revelstoke Dam to the confluence of the Jordan River. Reach 3 starts at the confluence of the Jordan River and extends approximately 3.5 km downstream to the confluence with the Illecillewaet River (Figure 2-1).

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

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

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

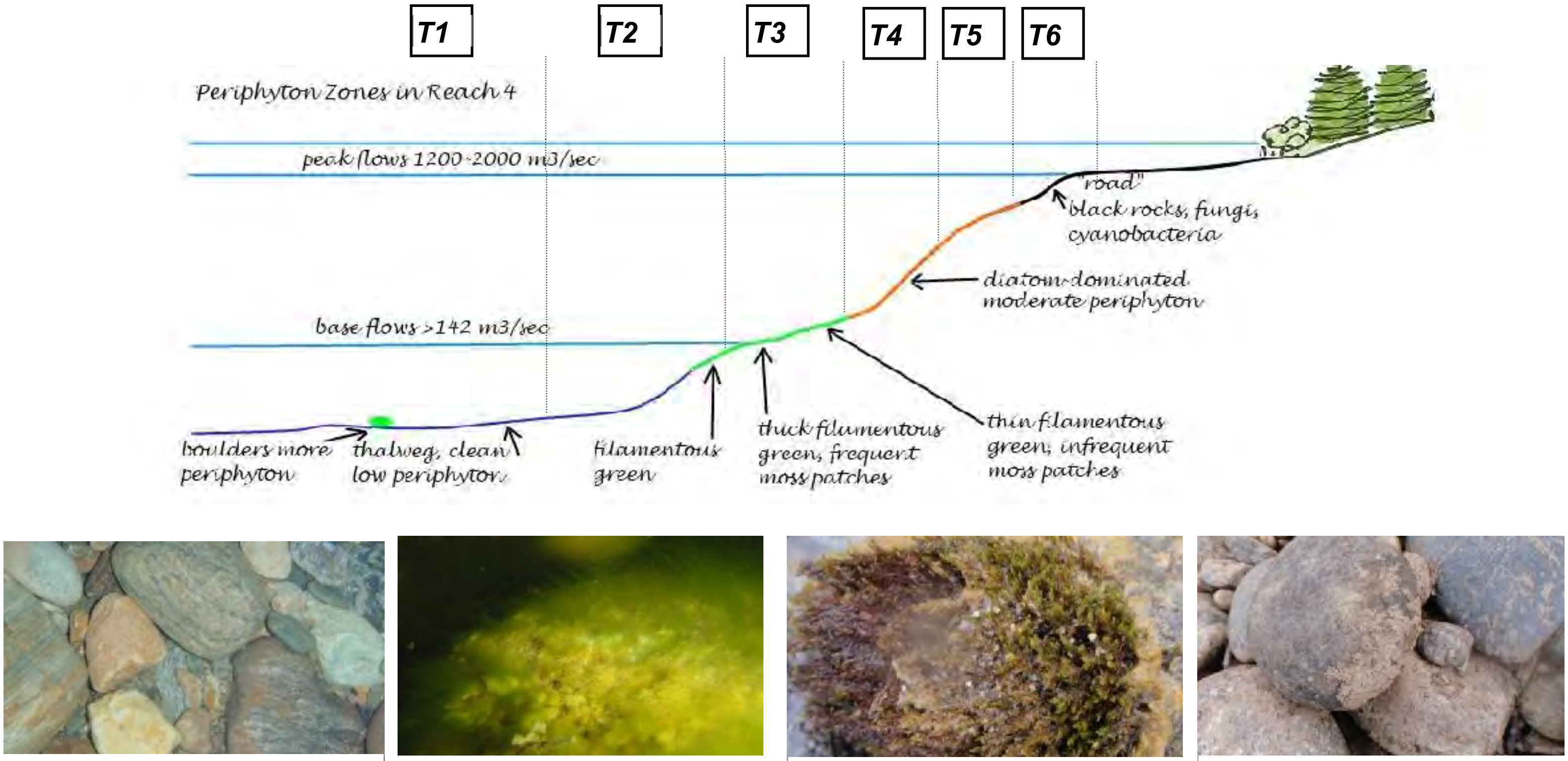
Figure 2-1: Map of the study area and sampling locations. Site names are fully defined in Table 2-1

2.2 Periphyton and Invertebrate Community Sampling Using Artificial Samplers

2.2.1 Artificial Sampler Design and Deployment

Years 6 and 7 of the CLBMON 15-b study included both spring and fall sampling sessions, where artificial samplers were placed in the river and left for a minimum of 46 days for each session (Table 2-1). Data for previous years are available in previous CLBMON15b reports, however the sample sites used in 2013 were consistent with previous years. The same naming system was used to reference sampling sites. Site references include Reach, Site, and Transect. Samplers were deployed in Reach 3 (R3) at S3, S5, and S6. Reach 4 (R4) samplers were sampled at sites S4, S5, and S6. Finally, sites at Big Eddy (BE), bedrock (BR), and Backwater areas (BW) were also sampled.

Sampling sites at transects T1 through T6 were deployed in Reach 4 as shown in Figures 2-2 and 2-3. Transect position refers to the position of the sampler within the river cross-section. T1 samplers were positioned mid-channel, within or near the thalweg. T2 samplers were placed in slightly shallower areas than T1. Both T1 and T2 were typically permanently wetted at minimum flows. T3 through T4 were placed in the mid-channel and were wetted during moderate flow levels (e.g., 200 to 800 m^3/s). T3 and some T4 positions sampled the lower varial zone. T5 and T6 samplers were placed within the upper varial zone and were only wetted during higher flows from 1000 to 1600 m^3/s. During the fall 2010 sampling session, a T7 position in the floodplain was also used. This sampler was subsequently deleted, and new sampling sites in Reach 4 at the bedrock (BR) location were studied instead.



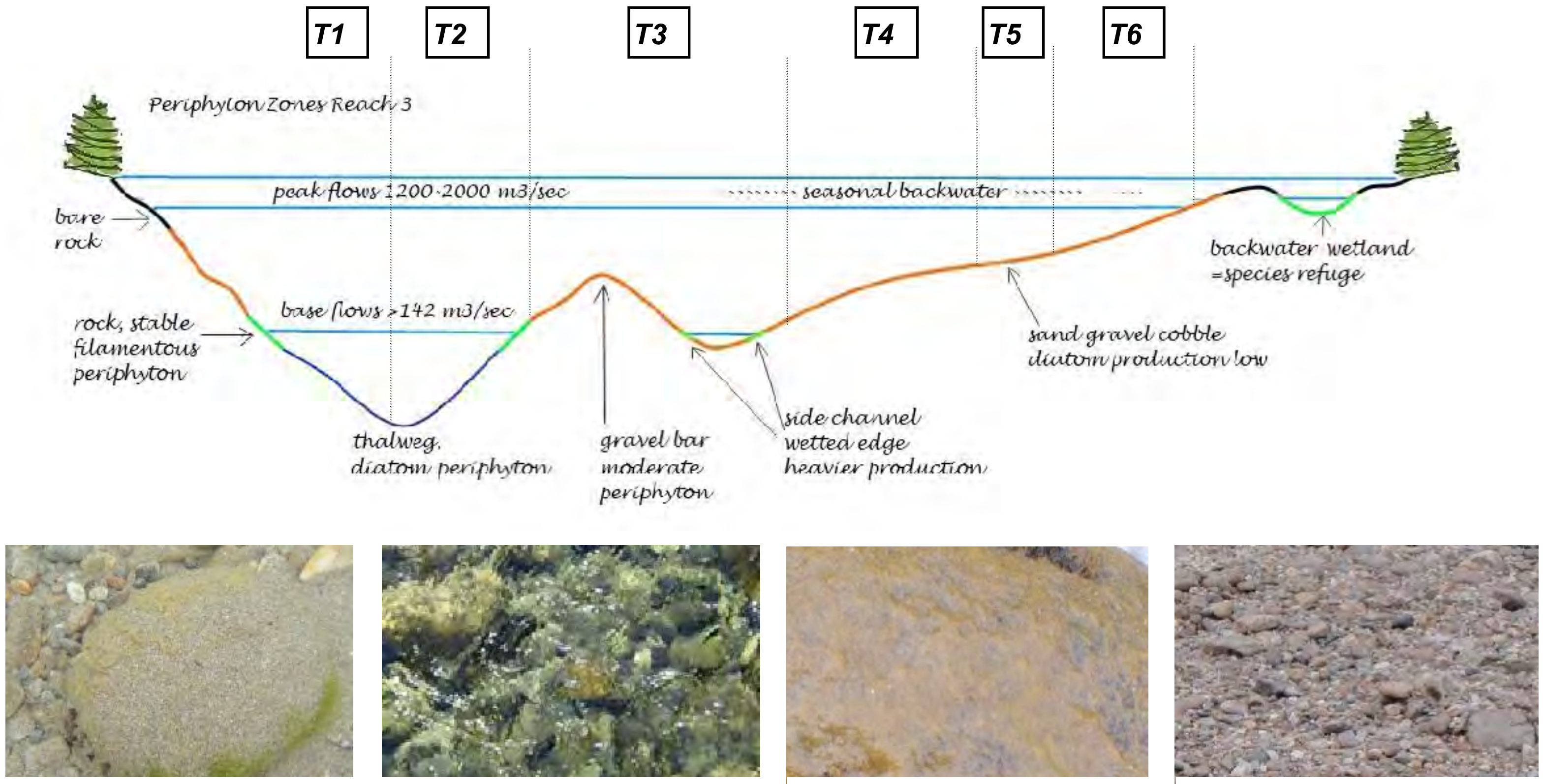
thalweg
(low periphyton

filamentous green zone

filamentous green + moss zone

diatom dominated zone

Figure 2-2: Conceptual drawing of transect positions and periphyton establishment in MCR using data collected from fall 2010 and 2012 in Reach 4



filamentous green+, sand thalweg, diatom periphyton wetted edge heavy diatom zone low diatom, bacteria zone

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

Samplers and associated rigging were assembled and deployed in the spring during April 10 -12, and in the fall during September 9 - 11, 2013. 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.

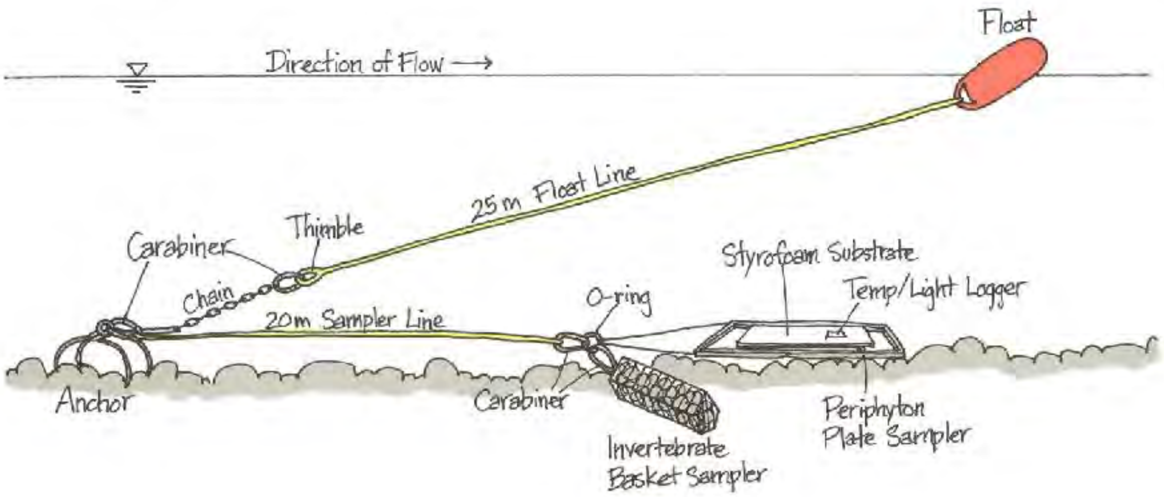


Figure 2-4: Schematic drawing of a standard artificial substrate sampler

Table 2-1: Artificial sampler deployment and retrieval in 2013

Season	Reach	Site/Habitat Type	Periphyton Samplers		Invertebrate Basket Samplers	
			# Deployed	# Retrieved (% Recovery)	# Deployed	# Retrieved (% Recovery)
Spring (Apr 10th - May 29th)	4	Site 6 (S6)	6	5 (83)	6	5 (83)
		Site 5 (S5)	6	6 (100)	6	6 (100)
		Site 4 (S4)	6	6 (100)	6	6 (100)
		Bedrock (BR)	6	6 (100)	6	6 (100)
		Time Series (TS)[1]	10	10 (100)	10	10 (100)
	3	Big Eddie (BE)	4	4 (100)	4	4 (100)
		Site 6 (S6)	6	6 (100)	6	6 (100)
		Site 5 (S5)	6	6 (100)	6	6 (100)
		Backwater (BW)	3	3 (100)	3	2 (67)
		Site 3 (S3)	6	6 (100)	6	6 (100)
Spring Totals			**59**	**58 (98)**	**59**	**57 (97)**
Fall (Sept 9th - Oct 30th)	4	Site 6 (S6)	6	6 (100)	6	6 (100)
		Site 5 (S5)	6	6 (100)	6	6 (100)
		Site 4 (S4)	6	6 (100)	6	6 (100)
		Bedrock (BR)	6	6 (100)	6	6 (100)
		Time Series (TS)	10	10 (100)	10	10 (100)
	3	Big Eddie (BE)	2	2 (100)	2	2 (100)
		Site 6 (S6)	6	6 (100)	6	6 (100)
		Site 5 (S5)	6	5 (83)	6	4 (67)
		Backwater (BW)	3	3 (100)	3	3 (100)
		Site 3 (S3)	6	6 (100)	6	6 (100)
Fall Totals			**57**	**56 (98)**	**57**	**55 (96)**
2013 Totals			**116**	**114 (98)**	**116**	**112 (96.5)**

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

2.2.2 Time Series Samplers

In addition to regular samplers, 10 time series periphyton samplers were deployed in both spring and fall sessions to investigate periphyton accrual rates using the same methodology as 2012 and 2013, with effort focussed in two key areas for better statistical strength: the deep area permanently wetted by minimum flows (T1) and the lower varial zone (T3/T4), located above the permanently wetted edge. Five time series samplers were deployed in Reach 4 in both transects positions. Time series samplers were retrieved once per week following deployment. During each weekly sampling, the light/temp loggers were wiped clean with a paper towel, so light measurements from time series periphyton samplers could be compared with undisturbed loggers left in place for the entire study duration. Although we knew that light attenuation would occur as periphyton growth covered the sensor, this simple methodology facilitated our understanding of the degree and rate of light attenuation across the study period on sensors that were not cleaned weekly versus those that were cleaned weekly.

Every week, two periphyton punches were randomly collected from the Styrofoam and were immediately packed and placed in the dark, on ice until they could be delivered to Caro Labs Kelowna for chl-a analysis. Taxonomy of time series samples was not conducted in 2013.

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, 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. To help understand the effects of minimum flow, samplers were subsequently deployed at T1 and T3/T4 locations from 2011 onwards, simulating permanently submerged areas, and those that were just exposed at minimum flow. Varial zone time series samplers are considered to representative of conditions between T3 and T4 locations because they cannot be accurately placed, retrieved, and re-deployed at the same location/depth during sample collections. Time series samples collected within the varial zone areas are therefore considered to be representative of accrual in the varial zone rather than a discrete sampling location such as T3.

2.2.3 Artificial Sampler Retrieval

Artificial samplers remained in the river for a total of 48-51 consecutive days for each season. This deployment period matches earlier MCR deployments and is within the incubation period required for attainment of peak biomass defined by Perrin (2004). Spring and fall samplers were retrieved either by boat, wading or by foot on May 29 - 30 and Oct 28 – 29 2013, respectively.

Four Styrofoam punches were randomly sampled from each sampler in order to assess the following metrics: 1) Chlorophyll-a to give an estimate of only live autotrophic biomass; 2) Ash-Free Dry Weight (volatile solids) / total dry weight to give an estimate of the carbon component (Stockner and Armstrong, 1971); 3) taxa and biovolume to give an accurate estimate of live and dead standing crop (Wetzel and Likens, 1991); and 4) a second sample was frozen in case a sample was damaged. At the time of collection, Styrofoam punches were placed in pre-labeled containers and stored on ice in the dark until further processing.

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

Benthic invertebrate baskets were retrieved similar to previous years following guidelines developed by Perrin et al. (2004). A 250 μm mesh net was placed beneath baskets while still in the water column to collect any invertebrates that could have been lost as baskets were lifted from the water. The net was inverted and any contents were rinsed into a labeled bucket with pre-filtered river water. The retrieved baskets were also placed in the labeled buckets until further field processing.

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

2.2.4 Post Processing of Periphyton Samples

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

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. A reference sample was kept for each unique taxon found. A sampling efficiency of 95% was used for benthic invertebrate identification and was determined through independent sampling. Numerous keys were referenced in the identification of benthic invertebrate taxa and a partial list of references is provided in Schleppe *et al*. (2012). Species abundance and biomass were determined for each sample. Biomass estimates were completed using standard regression from Benke (1999) for invertebrates and Smock (1980) for Oligochaetes. If samples were large, subsamples were processed following similar methods. Detailed protocols on invertebrate laboratory processing are available from Cordillera Consulting.

2.3 Variable Descriptions and Analytical Methods

2.3.1 Determination of Submergence

Water and air temperature data obtained from the HOBO light/temperature loggers was the primary dataset used to determine whether an artificial sampler (either invertebrate or periphyton) was submerged. Four HOBO light/temperature loggers were placed in the upland areas above the high water level within Reaches 4 and 3 to measure air temperature. Similar to Schleppe et al. (2011), a script that considered a temperature difference of ± 0.5ºC was used to compare samplers from permanently submerged locations with samplers across a transect. A sampler was considered exposed to air when the logger temperature differed from the permanently submerged logger by more than ±0.5ºC. However, this analysis of submergence was only partially reliable as there were times during the deployment when the air and water temperatures were within 1.5 ºC of each other (Schleppe *et al.,* 2010).

To ensure that the determination of submergence was accurate, the entire database for both spring and fall was reviewed and professional judgment and field experience were used to assess whether a plate was submerged or exposed to the elements. 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, and time of day. Temperature data from sites of exposure had notable highs, and we speculate that localized effects (e.g., metal frame heating) may help separate similar temperature points between exposed and submersed samplers on sunny days. Manipulations were generally greatest on sites exposed to the air for longer periods.

2.3.2 Variables and Statistical Analyses

Non-metric multidimensional scaling (NMDS) using Bray-Curtis dissimilarity was used to explore variation in benthic community composition. Data were transformed using the Bray Curtis transformation. To interpret these data, cluster diagrams using Ward clustering of the Bray Curtis matrix were constructed. Finally, ANOSIM was used to determine if groups (either Pre/Post minimum flow, Year, Season, and Transect) were significantly different in composition. NMDS was run for the genus taxonomic levels for periphyton and benthic invertebrates to investigate the effects of small and large scale taxonomic community differences within the study period.

The full set of predictor data developed by Perrin and Chapman (2010) and those developed in 2010 were collected in 2013. The temperature, light and submergence data were used to calculate a number of different predictor variables that could test the effects of hydro operations on productivity in MCR (Table 2-2, Schleppe et al, 2010 and 2011). Variables of time are often collinear, but all of the variables developed were initially considered. To reduce collinearity, multiple attempts at different model predictor combinations were considered to choose the most appropriate variables describing submergence without omitting any potentially influential factors that may affect productivity. An exploratory analysis of final production responses to explanatory variables (Table 2-2) was completed for raw and transformed data. The intent of this step was to reveal any general patterns or trends across transects or within response variables prior to any statistical analyses. We also used methods described by Zuur et al. (2009) to examine multi-collinearity among explanatory variables based on variance inflation factors (VIF) and correlation coefficients, avoiding inclusion of highly collinear variables (correlations coefficients > 0.7) together in descriptive models. Most collinearity in predictors originated from variables of submergence and variable for light. Total incubation time in the water was selected as best predictor for submergence, given previous years analysis and because this variable also addresses light attenuation with depth which is not considered in any other predictor. The final set of predictor variables chosen were the most interpretable and thus deemed the best set to address key management questions without overly inflating the variance of models due to high collinearity.

Eight response variables for both periphyton and benthic invertebrates were modeled. Periphyton responses included: 1) abundance, 2) biovolume, 3) chlorophyll-a, 4) AFDW, 5) Percent Dead Abundance, 6) Percent Dead Biovolume, 7) Simpson's Index and 8) Species Richness. Similar models for invertebrate production and diversity metrics were also prepared and included: 1) abundance, 2) biomass, 3) Simpson's Index, and 4) Hilsenhoff Biotic Index. Diversity and production data were transformed using either log10 or square root in order to adhere to the assumptions of least-squares multiple regression (i.e. normal distribution of residuals and heteroscedasticity of residuals). These eight responses were modelled for the full set of predictor variables, and then run again for permanently submerged sites using only physical predictors with measures of submergence excluded, to determine the effects of physical processes on benthic production. Finally, seasonal data is complicated, because it interacts with many of the other predictor variables, and was therefore considered independently using a separate suite of models to reduce the need to utilize complicated interactive effects within the models.

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

$$\mathrm{HBI} = \sum x_i\, t_i / n$$

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

We evaluated the relative support for the effects of these explanatory variables using an all model combinations approach. Model uncertainty was assessed using AICc and multi-model averaging (Burnham and Anderson 2002; Anderson 2008). We used the MuMIn package in R (Barton 2012) to compete models based on Δ AICc values and AICc weights (w_i), and to calculate multi-model averaged parameter estimates from 95% confidence sets for each response variable (Burnham and Anderson 2002; Grueber et al. 2011). We calculated relative variable importance (RVI), which is the sum of AICc weights from all models containing the variable of interest, with variables having RVI values above 0.6 considered to be of high importance in subsequent interpretations. We also calculated pseudo R^2 for high ranking models, derived from regressions of the observed data versus fitted values (see Cox and Snell 1989; Magee 1990; Nagelkerke 1991; Piñeiro et al. 2008 for details) which gives an indication of the proportion of the variance in response variables explained by an individual model.

We conducted the above analyses 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).

A Fish Food Index (FFI) was calculated using three criteria to assess the effects of minimum flow on food for fishes. The criteria were: 1) abundance of invertebrate taxa, 2) biomass of invertebrate taxa, and 3) a ranking of preference as fish food for different Invertebrate taxa. The index is conceptually similar to the index developed by Sass et al. (2011). The Fish Food Index is calculated as follows:

$$\text{FFI}\ (x) = \sum_{n=1}^{Ith} ((\%\ \text{Abudance})(\%\ \text{Biomass})(\text{P}))$$

where:

> 1 through the I^{th} benthic taxon at any given sampling site
> % Abundance is the percentage abundance of any given benthic taxon at that site;
> % Biomass is the biomass of the taxon / total benthic invertebrate biomass at the site; and,
> P which is a Fish Food Preference determined by a literature review and brief analysis of stomach content data in MCR.

For each different benthic taxon encountered, a fish food preference rank was assigned. The Fish Food Preference rank was assigned using stomach contents data from MCR, literature reviews, and professional judgment of foraging behaviours. Fish food preference rankings were determined for each different fish species / life stage of importance. Finally, the fish food preference for the analysis was determined by averaging the score of all fish species / life stages. Future calibration of the fish food preference values can be completed as more data becomes available, or the FFI can be used to consider only specific fish species / life stages.

The final FFI index score for each site represents the abundance of benthic taxon as fish food, the size or biomass availability of benthic taxon as fish food, and the availability of more preferred types of benthic foods. The FFI score ranges from 0 to variable maximum (dependent upon the number of species), with higher overall scores indicating a greater presence of benthic invertebrates preferred as fish food. Future iterations of the index will attempt to standardize scores within a specified range to help aid interpretation of results and facilitate comparisons to other rivers or data collected by BC Hydro. The FFI score for each site was subsequently modeled using the same independent variables as other models for periphyton and invertebrates.

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

All statistical tests were conducted using R (R Development Core Team 2006), and model averaging was completed using the R package "MuMIn" (Barton 2009). In all analyses, we assumed that each sampler was independent both within each transect and across sites. This assumption does not reflect the hierarchical sampling structure of Reach / Site / Transect previously established. This model is improved from previous years because high collinearity among predictors has been addressed. As well, both annual and site-level effects were treated as random variables.

Table 2-2: Variables used in the prediction of periphyton and benthic invertebrate response in relation to BC Hydro operations and physical conditions during deployment. The full set of variables developed in 2010 were prepared for 2013 data. Environmental predictors used in 2013 modelling are shown in bold, while the non-bold variables were considered but subsequently removed. Variable names are in brackets after variable units and these names are used throughout the text.

Variable	Definition
Average Daily Light Intensity (lux)	**Average daily light intensity observed over the duration of deployment. This predictor was removed because it does not discriminate between submerged and exposed samplers.**
Total Incubation Time (tot_inc_time_water_light_hrs) (hrs)	**The total incubation time that the sampler was within the water and in sunlight which means it can be producing periphyton. Thus, this this is the total time spent submerged during daytime hours. This is a measure of the total production time at any given sampler. This variable was chosen as the primary measure of production time.**
Mean Temperature (C)	**Average temperature over the duration of deployment (C). This variable was chosen because it gives some indication of temperature related responses. This predictor does not discriminate between time submerged and time exposed.**
Sampler Velocity (m/s)	**Water velocity at the sampler, measurements approximately 25 to 50 cm above the bed of the river (m/s). This variable was included because periphyton responses to velocity are well documented**
Rel. Abundance Cobble / Boulder	**Relative abundance of cobble and boulder substrates**
Embeddedness Score	**Embeddedness was assigned a score of 1 (0-5%), 2 (5-25%, 3 (25-50%), 4 (50-75%) or 5 (75-100%)**
Distance to Thalweg	**The thalweg of MCR was determined as the center of the channel at a normal operating range of 400 m^3/s to 800 m^3/s. The distance to the thalweg was then measured perpendicular from each site to the constructed thalweg line.**
Rel. Abundance of Silts, Sands (Fines), and Gravels	Relative abundance of silts, sands, and gravels in MCR
Frequency of 12 hour submergence events (Freq_Submer_.12.Hrs) (hrs)	A count of the number of days where submergence time was greater than 12 hours. This variable is directly linked to BC Hydro operations and was included because it provides some insight regarding production responses to an operational pattern.
Maximum Cumulative Submergence (max_cum_sub) (hrs)	The maximum cumulative number of hours a sampler was submerged. Every time the sampler was exposed the maximum cumulative exposure time started over. This variable was removed because it has a non-linear relationship.
Submergence ratio (sub_ratio)	The percentage of time the artificial sampler was submerged in water compared to total incubation time (daytime submergence) i.e. Total Submergence Time / Total Incubation Time. A sampler in the water for the entire deployment would have a submergence ratio of 1. This variable was kept because it provided indication of time spent in the water.
Cumulative Intensity Accrued During Deployment While Producing (lux)	Cumulative total of light intensity observed at the sampler location while the sampler was submerged in water and considered producing. Excludes all times when sampler was exposed to air and considered "not producing".
Site Class	An initial attempt was made to classify observed site level effects. Sites tested included Backwater (BW's), Bedrock (BR's), and Main stem large (upstream large substrate Reach 4), and Main stem small (downstream Reach 3 and Big Eddy). Future spatial mapping of these sites will be conducted to better address site level effects in MCR.

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.

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. Foraging intensity on samples is still considered to be small when compared to each sample as a whole, reducing any potential data skewing effects that may result from invertebrate grazing. Further, it is probable that invertebrate distributions around plates were clumped, reducing the potential for effects across multiple replicates. Finally, the populations of invertebrates in MCR were low relative to other large rivers, and their influence on productivity would be low as well.

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

Sampler assessments were not intended to address immigration, sloughing, or any other aspects of the periphyton community. Thus, artificial substrate samples that were obviously biased due to sloughing from rock turnover, etc. were excluded from collection. This was a field decision and was easy to make because large boulders rolling over artificial substrates left distinct trails of compressed Styrofoam. This field decision reduced the potential area available to sample, but we do not suspect that it biased the results. It is acknowledged that substrate mobility and periphyton sloughing/drift are important components of periphyton production in MCR.

3.0 RESULTS

3.1 Biophysical Characteristics of the Middle Columbia River

3.1.1 Light and Temperature in Submerged areas of MCR

Overall water temperature ranges in 2013 were similar to temperatures collected in 2010 through 2012 (Figure 3-1). During the 2013 deployment, there were numerous small spikes in temperature, as there were in other years. Reservoir conditions upstream are the most probable factor affecting the daily variation in observed temperature because downstream river temperatures were most dependent upon upstream reservoir conditions and the temperature/flow of tributaries (Larratt et al., 2011; Schleppe et al., in prep). During the fall deployment period, temperature varied from 10 to 15 ºC at the start to 5 to 7 ºC at the end. During the spring, initial river temperatures were typically 5 to 7 ºC at the start, and increased near the end of deployment to 8 to 10 ºC. Temperatures in the Jordan River were a contributing factor to the variation in temperature observed in Reach 3, but have not been fully investigated.

Light intensity during 2013 was similar to 2010 – 2012 and the observed intensity patterns were similar for both the spring and fall. In accordance with the physics of light transmission through moving water, light intensity on submerged samplers increased from deep sites at T1 locations to shallow sites at T6 locations (Figure 3-2, Figure 3-3). When samplers were in shallow water they received more energy to support periphyton production. Peak light intensities occur around noon, a period when flows were usually higher. It is important to note that as sites become shallower, the rate of exposure increased and the data presented considers only periods when a sampler was submerged. Point sampling of turbidity and suspended solids data suggest that the reduction of light penetration they caused would be minor compared to water depth.

Fall light intensities were less than half of those during spring deployment and results from 2013 were unchanged from the mean of earlier years, with the possible exception of the shallowest T6 position (Figure 3-2). This site showed higher light intensities in 2013, indicating these samplers were at shallower depths which may be the result of minimal back-watering compared to earlier years.

Spring light intensities in 2013 were consistently lower than in 2011 and 2012 (Figure 3-3), at all transect locations, indicating greater water depth in spring 2013.

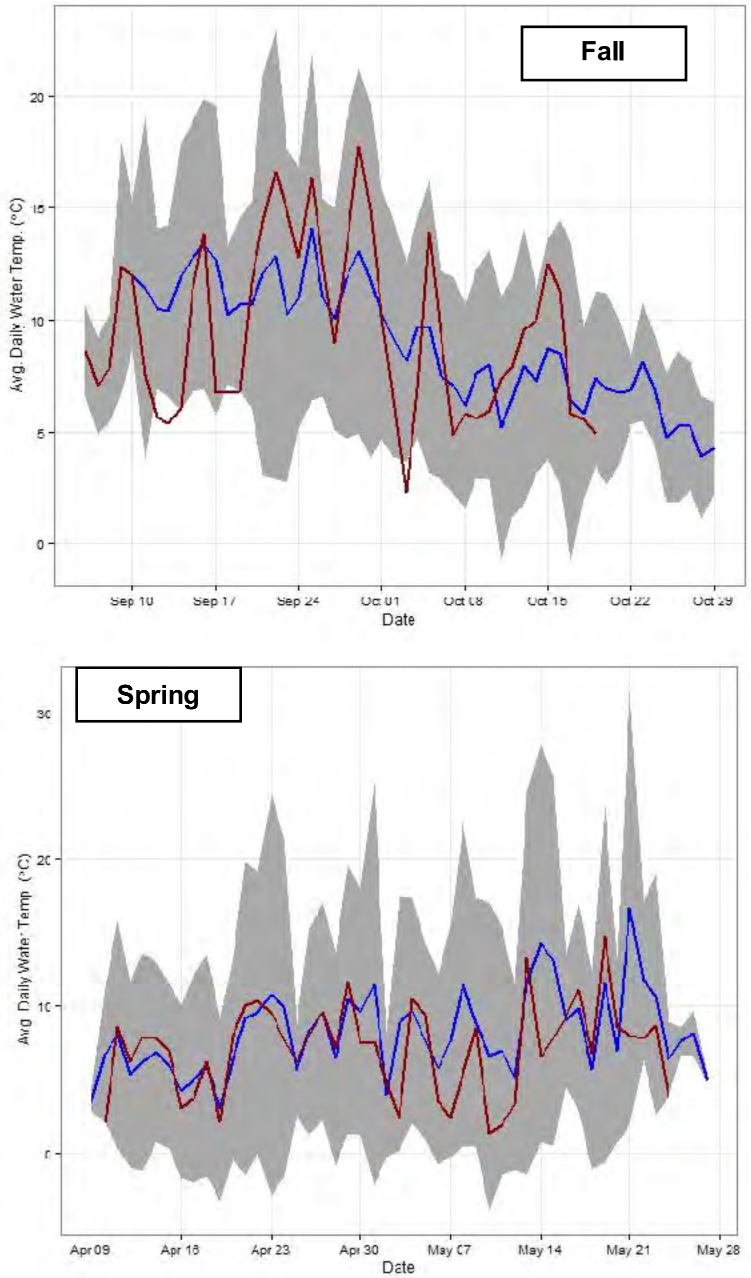


Figure 3-1: The pattern of daily temperature in MCR during the fall (top) and spring (bottom) study periods. The blue line represents the mean from 2010 to 2012 and red represents the mean 2013 data from all submerged samplers. Data were pooled for fall periods between 2010 – 2012 and for spring periods between 2011 – 2012 (±SD in grey).

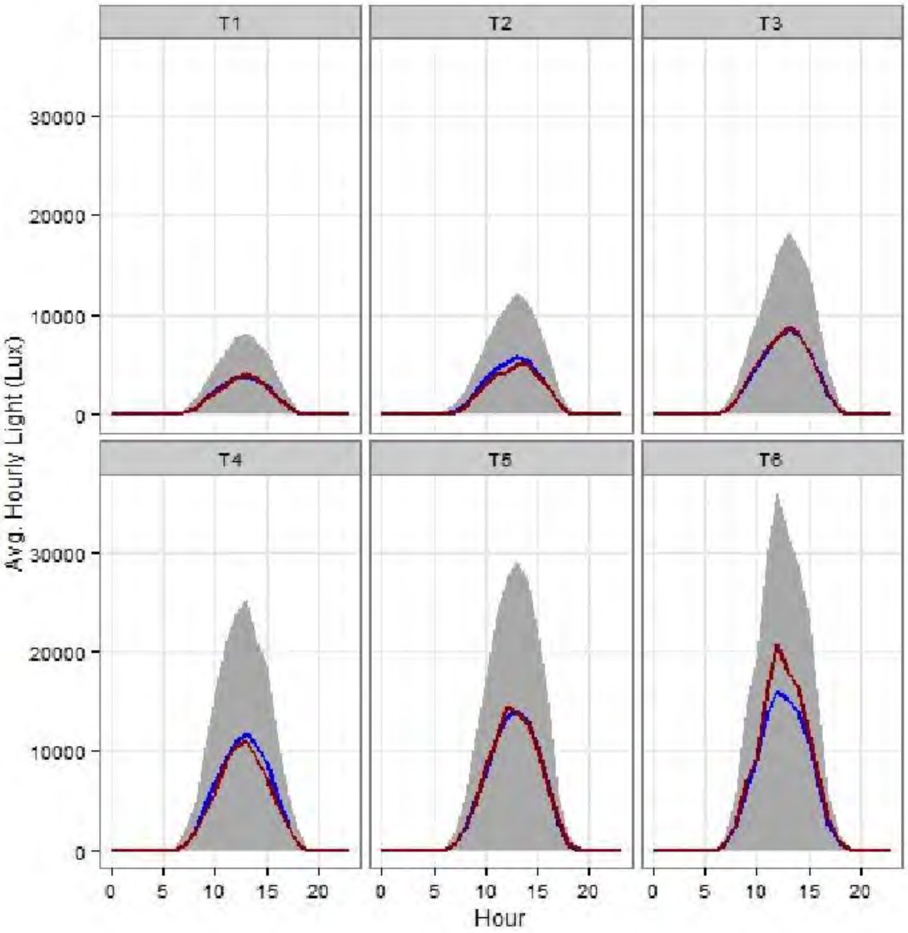


Figure 3-2: Fall daily pattern of light intensity (lux) in MCR at varying depths, where T1 is the deepest and T6 is the shallowest for samplers. The blue line represents the mean from 2010 to 2012 (±SD in grey) and red represents the mean 2013 data from all submerged samplers.

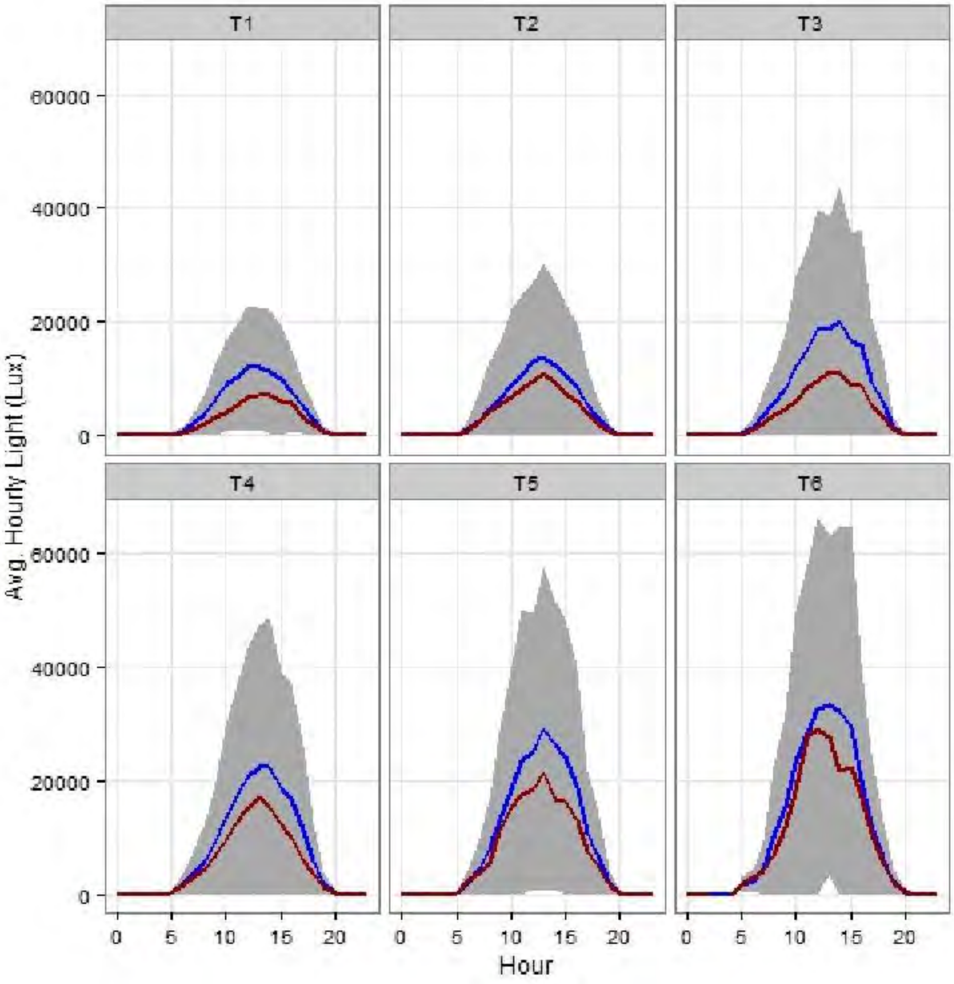


Figure 3-3: Spring daily pattern of light intensity (lux) in MCR at varying depths, where T1 is the deepest and T6 is the shallowest for samplers. The blue line represents the mean from 2010 to 2012 (±SD in grey). And red represents the mean 2013 data from all submerged samplers.

3.1.2 Pattern of Flow in MCR

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

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

- 2011 and 2012 were extremely high water years resulting from a combination of higher than normal snowpack and possibly higher use of REV 5. Small morphological and biological channel changes were observed. For instance, in 2010, there was a noticeable fungal/bacterial black colouration to substrates in Reach 4, and this was less apparent following the high water years.
- Very high flows exceeding 2000 m^3/s were concentrated in the winter months but also occurred in August of 2011 and 2012. The frequency of these events was greater in 2012 than 2011 or 2013.
- Flows followed a similar pattern between years, with low flows occurring during evening periods after midnight and high flows occurring during daytime periods from 10 a.m. until 7 p.m. At all other times, flows were either ramping up or down from high or low flow periods (Figure 3-4).
- High variability in high, low, and ramping flow periods was observed both between years and seasons.Daily flow patterns were similar to previous years in spring and fall 2013, with the exception that daily high flows were lower (<100 m^3/sec difference) than what had been observed in 2007 – 2012 (Figure 3-4).
- The magnitude of flows during 2013 was most similar to years prior to 2011, which were lower flow years than 2011 and 2012. This means that samplers deployed at deep sites (T1) were usually submerged at depths of 4 to 6 m during the day, whereas sites at T6 were only submerged in approximately 1 m of water during the day when compared to 2011/2012 when depths were 6 to 8 m and 2 to3 m during the daytime.
- The Arrow Lakes Reservoir (ALR) elevation can result in extensive back watering of Reach 3 from early June through October, and can even extend into Reach 4 during the summer months. Backwatering effects have been considered through our submergence variables, and we generally do not distinguish between submergence due to backwatering from submergence due to flows in our analyses.

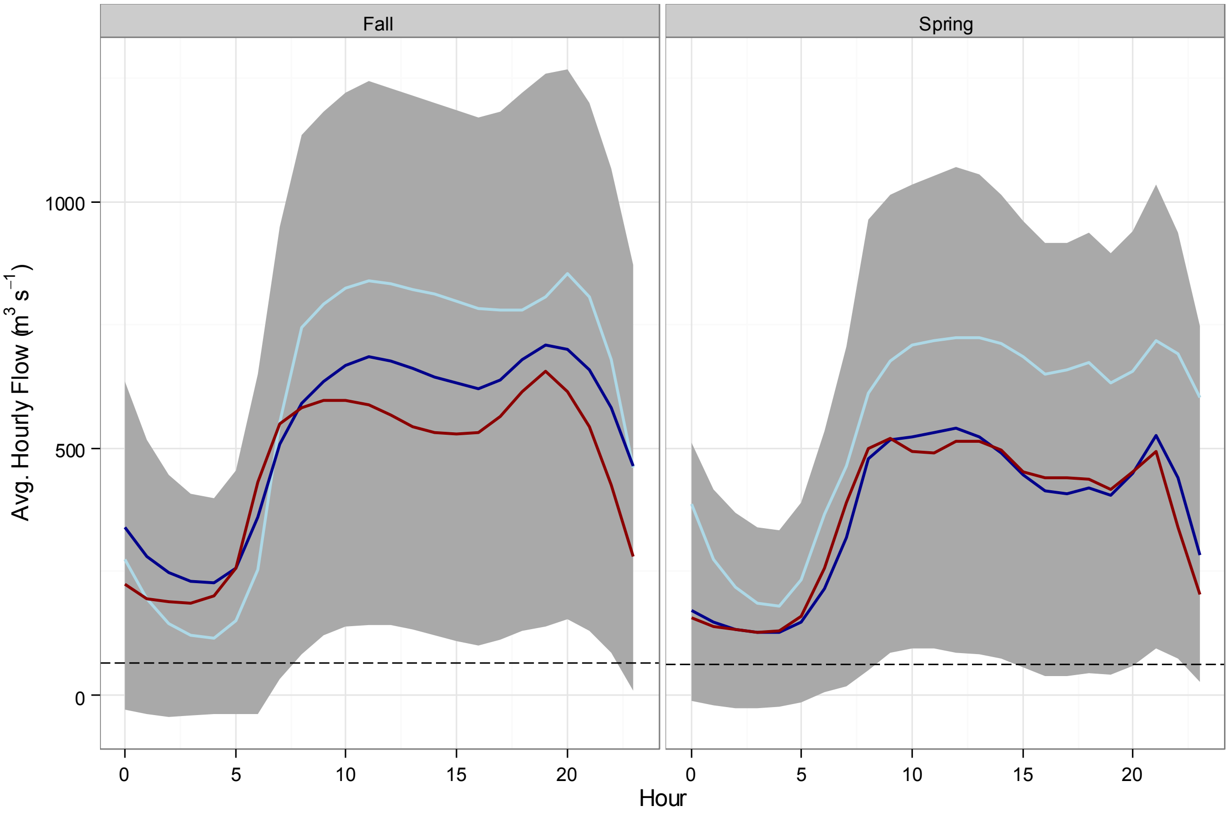


Figure 3-4: The pattern of daily flow in MCR during the fall and spring study periods. Average hourly flow from pre-minimum flow periods (2007-2010) are shown in light blue, those from post-minimum flow periods (2011-2013) are shown in dark blue, those from 2013 are shown in red, and the standard deviation of average hourly flow across all years is shown in grey. Minimum flows for each seasonis shown as a black dotted line.

3.2 Periphyton

3.2.1 Overview of MCR Periphyton Biofilms

Periphyton consists of two broad groups of micro-organisms, photosynthetic algae and bacteria, and heterotrophic (non-photosynthetic) bacteria and fungi. Algal periphyton production can only occur while substrates are submerged and exposed to sunlight, while the bacterial biofilm component also grows in the dark (Lear et al. 2009). For both components, growth in MCR slowed dramatically and mortality progressively increased during periods of desiccation.

Bacteria and fungi (moulds, yeasts) are pioneering organisms that can dominate the periphyton initially and again after the periphyton mat (biofilm) is well established (Fernandes and Esteves 2003). Heterotrophic bacteria counts on the artificial substrates deployed for 44-47 days during fall in MCR were relatively low compared to other large North American rivers at 0.2 – 5 x10^6 colony forming unit (CFU)/cm^2, suggesting oligotrophic or stressed conditions (Schleppe et al. 2013). These low counts reflect repeated desiccation. Further, our field observations indicated that the black band of heterotrophs and cyanobacteria that was evident in the upper varial zone prior to 2011 was much reduced after the peak 2012 flows. These peak flows created longer submergence and greater scouring along this zone.

Quantitative natural substrate samples were collected from R4 cobbles and suggested that the artificial substrate reduced the heterotrophic plate count (HTPC), and inflated the yeast component of the biofilm, but that the artificial substrate accurately reflected the mould component. Acknowledging these discrepancies, artificial substrates in Reach 3 had far more of all three biofilm components per sample than Reach 4 substrates with similar submergence times in both years (Schleppe, et al, 2012). The 2011 Reach 3 shallow yeast and heterotrophic bacteria counts were significantly higher at 1 and 5 x10^6 CFU/cm^2 respectively, than the other 2010 and 2011 samples. These R3 biofilm components may have been protected from 2012 flows by ALRALR backwatering.

A final contributor to MCR periphyton biofilm production was drift of viable phytoplankton cells originating from Revelstoke Reservoir, and to a lesser extent, from Arrow Lakes Reservoir during back-watering. Reservoir algae are physically distinct from true periphyton algae. These cells adhered to existing periphyton and at times, significantly augmented local productivity (Table 3-2).

3.2.2 Yearly Comparisons of Periphyton Algae Sampling

The dominant diatom species were either rapid colonizing diatoms with firm attachment strategies, or drift species from Revelstoke Reservoir that adhered to the periphyton biofilm. Like most large rivers, MCR species were dominated by diatoms representing between 85 and 98% of the biovolume in all sample sites in both natural and artificial substrates (Schleppe et al., 2013). When all years of study are considered, diatoms accounted for 90% of the fall biovolume and 93% of the spring biovolume. Green algae accounted for 6% in the fall with large filamentous species, but less than 1% 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 4% in the fall to 6% in the spring. Although cyanobacteria were functionally and numerically important, they only accounted 0.03% of total biovolume in the fall and increased to 0.4% under spring conditions that favoured species with rapid reproduction rates. The resultant growth is visible in Figure 3-5.

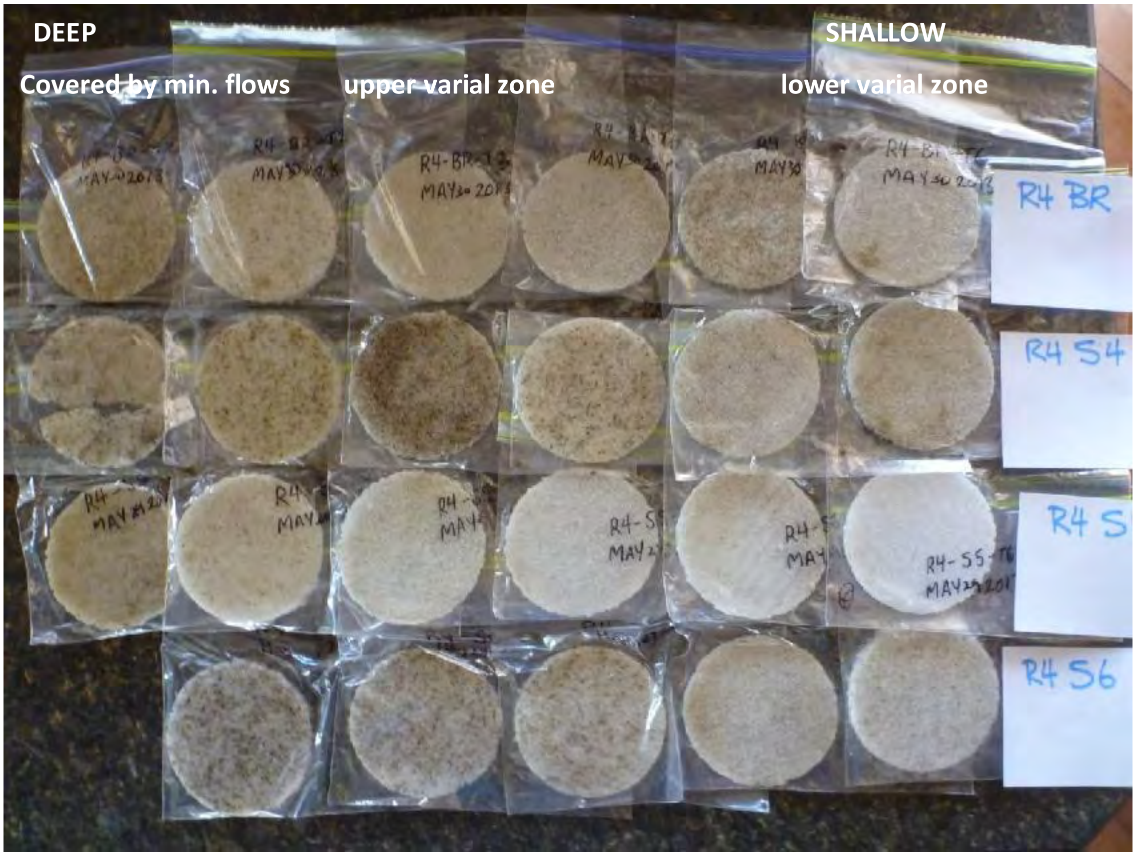


Figure 3-5: Example of spring 2013 incubated Styrofoam transects from Reach 4 MCR. BR represents the bedrock transect, while S4-S6 represent cobble transects on the mainstem.

Table 3.1: Periphyton relative abundance and biovolume in MCR in the spring and fall 2013, compared to all years

FALL 2013

Relative abundance – dominant species	Relative Abundance (%)	Relative biovolume – dominant species	Relative Biovolume (%)
Achnanthidium minutissima	27.79%	*Diatoma tenue var elongatum*	30.12%
Diatoma tenue var elongatum	18.98%	*Tabellaria fenestrata*	19.12%
Synedra ulna (small radiate sp)	8.34%	*Synedra ulna*	11.83%
Ochromonas sp.	8.10%	*Synedra ulna (small radiate sp)*	9.63%
Planktolyngbya limnetica 100L)	5.56%	*Cladophora sp. Glomerata?*	5.25%
Tabellaria fenestrata	4.53%	*Didymosphenia geminata*	4.61%
Not Identified Flagellates	4.29%	*Achnanthidium minutissima*	2.21%
Nitzschia sp.	2.63%	*Nitzschia sp.*	1.93%
Diatoma vulgare	2.49%	*Ochromonas sp.*	1.86%
Navicula spp.	1.96%	*Diatoma vulgare*	1.81%

SPRING 2013

Relative abundance – dominant species	Relative Abundance (%)	Relative biovolume – dominant species	Relative Biovolume (%)
Synedra ulna (small radiate sp)	17.46%	*Synedra ulna (small radiate sp)*	30.14%
Achnanthidium minutissima	16.14%	*Diatoma tenue var elongatum*	29.45%
Diatoma tenue var elongatum	12.76%	*Synedra ulna*	6.46%
Synechococcus sp.	5.92%	*Tabellaria fenestrata*	5.10%
Ochromonas sp.	5.91%	*Synedra nana*	3.95%
Not Identified Flagellates	5.04%	*Synedra acus*	2.98%
Coccoid chlorophyta complex	4.73%	*Ochromonas sp.*	2.54%
Planktolyngbya limnetica 100L)	4.54%	*Nitzschia sp.*	2.54%
Nitzschia sp.	3.34%	*Diatoma vulgare*	1.66%
Chrysochromulina sp.	3.05%	*Achnanthidium minutissima*	1.49%

All Years (2007-2010 -2013) FALL

Relative abundance – dominant species	Relative Abundance (%)	Relative biovolume – dominant species	Relative Biovolume (%)
Achnanthidium minutissima	18.90%	*Tabellaria fenestrata*	24.29%
Synedra ulna (small radiate sp)	11.70%	*Diatoma tenue var elongatum*	19.56%
Asterionella formosa	11.63%	*Synedra ulna (small radiate sp)*	10.95%
Diatoma tenue var elongatum	7.90%	*Synedra ulna*	7.52%
Tabellaria fenestrata	7.32%	*Synedra acus*	6.98%
Staurosira construens v ventor	5.09%	*Cladophora sp. glomerata?*	4.56%
Tabellaria flocculosa	4.20%	*Eucocconeis flexella*	3.65%
Achnanthidium linearis	3.90%	*Tabellaria flocculosa*	3.56%
Synechococcus sp.	3.52%	*Didymosphenia geminata*	2.70%
Fragilariforma virescens	2.83%	*Achnanthidium minutissima*	1.79%

All Years (2011 -2013) SPRING

Relative abundance – dominant species	Relative Abundance (%)	Relative biovolume – dominant species	Relative Biovolume (%)
Synedra ulna (small radiate sp)	16.69%	*Diatoma tenue var elongatum*	28.33%
Diatoma tenue var elongatum	12.95%	*Synedra ulna (small radiate sp)*	26.36%
Achnanthidium minutissima	12.60%	*Synedra acus*	7.06%
Synechococcus sp.	11.79%	*Synedra ulna*	5.37%
Coccoid chlorophyta complex	5.90%	*Tabellaria fenestrata*	4.86%
Anacystis cyanea	3.54%	*Diatoma vulgare*	2.63%
Synedra acus	3.31%	*Fragilariforma virescens*	2.37%
Planktolyngbya limnetica	2.78%	*Cladophora sp. glomerata?*	1.95%
Diatoma vulgare	2.70%	*Chroomonas acuta*	1.95%
Chrysochromulina sp.	2.61%	*Synedra nana*	1.94%

The taxonomic structure of all river periphyton communities displays a tendency for the predominance of a small number of taxa. In 2011, 2012 and 2013, we expanded the range of river habitats investigated to include backwater, Big Eddy and bedrock, but still found many of the same species as we did at mainstem sites. Over the years of study, ten dominant taxa accounted for 87-91 % of total biomass in the fall and an identical 86-92 % in the spring (Table 3-1). The dominant taxa distribution was typical in 2013, accounting for 88% in the fall and 86% in the spring.

The donation of Revelstoke Reservoir diatoms to MCR periphyton was highly variable from year to year, and will relate to production dynamics within the reservoir versus the timing of releases. Taxa that occurred in mid-river drift samples and therefor were most likely donated by Revelstoke Reservoir accounted for 53-70% of biomass in fall samples and 48-59% of biomass in spring samples. Example dominant species are provided in Table 3-2. They include limnoplanktonic species that can only function suspended in the water column (e.g. *Asterionella*) but persist after they become snared on MCR periphyton, and those that can reproduce after attachment to the periphyton (e.g. *Tabellaria*). In fall 2013 samples, increased periphyton biovolume occurred because there was an unusually high contribution of large diatoms from Revelstoke Reservoir.

Table 3-2: Examples of phytoplankton taxa found in Revelstoke Reservoir that were also found in MCR periphyton samples, 2007 – 2013 (% frequency by biovolume)

		% Frequency in MCR	
Taxa	Typical Growth Habit	Fall	Spring
Asterionella formosa	limnoplanktonic	1.7	>1
Diatoma tenue var elongatum	planktonic	20	28
Fragilaria crotonensis	limnoplanktonic	>1	>1
Synedra acus, nana (large spp)	limnoplanktonic	7	6.9
Synedra ulna (large sp)	limnoplanktonic	7.5	5.4
Tabellaria fenestrata	planktonic or attached	24	4.9
Tabellaria flocculosa	planktonic or attached	3.5	>1

In all spring samples the dominant diatoms were invariably *Diatoma tenue* and *Synedra ulna* (adhering species) along with large concentrations of rapidly reproducing single-celled green and blue-green algae. Spring samples had lower species diversity of 28-29 max. species/sample compared to fall samples at 33-35 max. species/sample. In fall samples, *Tabellaria fenestrata, Diatoma tenue* and *Synedra spp.* were the dominant diatoms, and there was a greater contribution made by filamentous green algae.

Throughout MCR, 2013 spring samples showed a typical species assemblage but at higher cell density, and much higher chlorophyll-a than in earlier years(Table 3-4). This increase was also reflected in time series chl-a. Light data from spring 2013 was lower than spring 2011 or 2012, indicating greater water cover on MCR substrates this year.

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

The distribution of algae groups through the range of transect depths was consistent from year to year. When all biovolume measurements were compared to chlorophyll-a (chl-a) results, strikingly similar curves emerged (Figure 3-6). Average periphyton productivity decreased with increasing exposure as the sampler positions progress from T1/T2 through T5/T6. For the transect depths that were consistently covered by minimum flows (T1 ,T2), or adjacent to the wetted edge (T3,) algae cell biovolume was stable. Chl-a dropped faster at these sites and may relate to an adaptation where algae growing in low light have more photosynthetic pigment per cell. As light penetrating the water column increased at shallower transect locations (T3 - T5), the amount of chl-a per cell decreased, and species shifted to those requiring more light. The frequently dewatered T6 and T7 locations had the lowest biovolume and chl-a because only a select few periphyton species can tolerate these conditions. There were similar patterns of abundance and productivity among depths between spring and fall, but with much lower overall production in the spring (Tables 3-4 and 3-5). In general, substrates that were wetted for periods in excess of 9 hours experienced rapid periphyton growth (Schleppe et al. 2012).

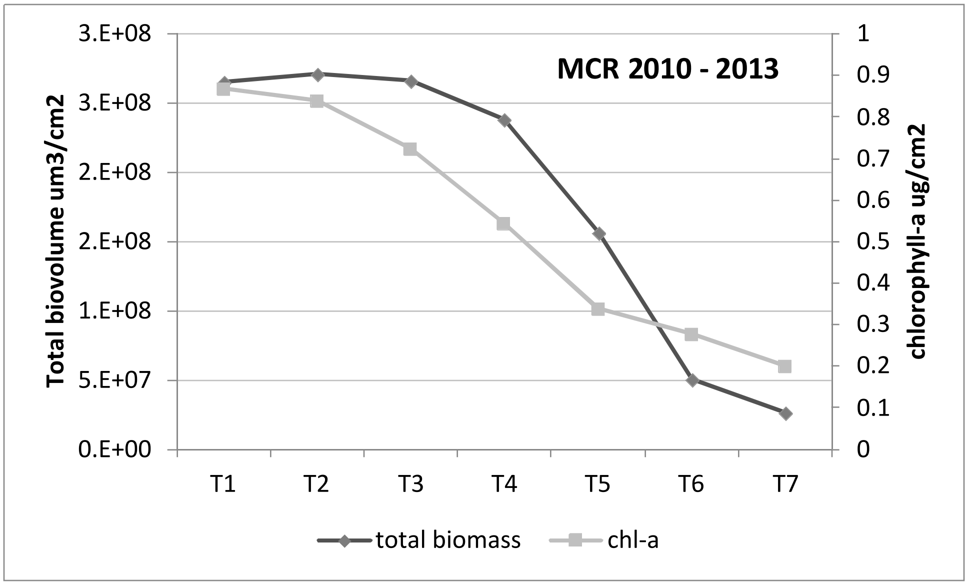


Figure 3-6: Total biomass of MCR periphyton and chlorophyll-a for the years 2010 through 2013 by sampler location (T1 deepest in thalweg to T7 shallowest on floodplain) T1 and T2 samplers were typically covered by minimum flows constantly. T3/T4 represent the mid-channel lower varial zone wetted by moderate flows (200 – 800 m^3/s), and transition to upper varial areas that were infrequently wetted (by 1000-1600 m^3/s flows) at transect T5/T6. T7 represents lower floodplain substrates that were only wetted by flows exceeding 1600-1800 m^3/s.

Average MCR ash-free dry weight (volatile solids) samples were typical of large rivers but included some samples with very high AFDW, particularly at T5 locations. For example, in 2013 samples, T1/T2 permanently wetted samplers averaged 0.49 ± 0.5 mg/cm^2, while T5 samples averaged 0.95 ± 3.14 mg/cm^2, suggesting that T5 might be a zone of organic accumulation or decomposition. Throughout MCR, samplers in the permanently wetted and lower varial zone T1 through T3 had greater autotrophic periphyton production, while frequently exposed samplers showed increasing heterotrophic dominance. Most of the organic material at heterotrophic-dominated sites was decomposer microflora and non-viable organic materials such as dead diatoms, leaf litter and detritus.

Periphyton summary statistics are provided for all seven fall sample periods in Table A3-3. The fall sampling sessions demonstrated a range of mean abundance from 2.73 to 12.5 x 10^5 cells/cm^2 , a range of mean biovolume of 0.98 – 3.78 x 10^8 microns^3/cm^2.and a range of mean chl-a of 0.49 to 1.43 ug/cm^2. For all growth metrics, the lowest year was 2012. 2012 had extremely high flows due to high snow pack and increased discharge from REV 5.

With all microflora taxa included, MCR had 5 - 52 species per sample. Among just algae taxa, mean richness of 10 ± 2 to 23 ± 6 taxa in the fall and 12 ± 4 to 20 ± 4 in the spring (Tables A3-3, 3-4) . This suggests that species richness in MCR was lower than is typical for large rivers. Average species diversity metrics have been low at 0.66 – 0.84 Simpson's index and 10 – 23 taxa, with 2007 being the lowest of 7 fall sampling campaigns.

Collection of AFDW (volatile solids) commenced in 2010 and interestingly, this metric dropped steadily from 4.89 ± 3.26 mg/cm^2 in fall 2010 to 0.81 ± 3.23 mg/cm^2 in fall 2013. AFDW provides an estimate of all components of the biofilm and these results suggest a progressive loss not seen in the other periphyton growth metrics that focus on photosynthetic members. If this trend is genuine, and our field observations of reduced black banding suggests it is, a decline in heterotrophic members of the biofilm may have occurred following the high 2012 flows. They may prefer shorter inundation periods and become displaced by algae as periods of substrate submergence increase.

Summary statistics are provided for all three spring sample periods in Table 3-4. Periphyton growth metrics were stable and low, ranging from 2.54 – 2.82 x 10^5 cells/cm^2 for mean abundance, 0.16 – 0.53 ug/cm^2 chl-a, and 1.18 – 1.36 x 10^8 microns^3/cm^2 biovolume. Average species diversity metrics were stable at 0.71 – 0.76 Simpson's index and 13 – 20 taxa. Like the fall results, AFDW results dropped from 9.28 ± 12.1 mg/cm^2 in spring 2011 to 0.35 ± 0.20 mg/cm^2 in spring 2013. Both spring means and spring maxima among growth metrics were significantly lower than fall samples from the same years. The AFDW **:** chl-a ratio was high in spring 2011 and 2012 samples however, this was not the case in spring 2013 when AFDW decreased by a factor of 10 and chl-a doubled compared to spring 2011 and 2012 (Table A-1).

Year-round implementation of 142 m^3/s minimum flows and full in-service operation of REV 5 were initiated on December 20, 2010. Samples collected before and after the December 2010 are compared in Table 3-3. Periphyton growth metrics were 25-40% lower after the flow regime change, with 2012 having the lowest periphyton metrics and the highest flows to date. Species diversity showed little change in Simpson's index and a small increase in species richness following the flow change. The contradictory trends between abundance and species diversity suggest that the area covered by minimum flows may be acting as a species reservoir with distribution when flows ramp up. The drivers behind these shifts in periphyton metrics are addressed by our statistical modelling.

Table 3-3: Comparison of fall MCR periphyton metrics before and after the flow regime change

Fall of Year (all depths)	abundance cells/cm^2	biovolume um^3/cm^2	chl-a ug/cm^2	AFDW mg/cm^2	species richness	Simpson's Index
2007 – 2010	7.10E+05	3.67E+08	1.01	0.499	17.2	0.695
2011 – 2013	4.23E+05	2.49E+08	0.76	0.556	21.1	0.700

Periphyton metrics for both reaches are compared by season in Table 3-7. All growth metrics were higher in R3 than R4 in both seasons. For example, fall chl-a measured 1.05 ± 0.84 ug/cm^2 chl-a in R3 and 0.64 ± 0.47 ug/cm^2 chl-a in R4. While cell density followed the same pattern, cell biovolume did not because Revelstoke Reservoir phytoplankton subsidies include very large diatoms and these donations diminish with distance downstream of a dam (Stanley et al. 2004). When all samples to date for both reaches are compared, R3 had 7.6% higher cell abundance and 44% higher chl-a, but R4 had 13% greater biomass.

There was no observable difference in the Simpson's index or species diversity between reaches. There are numerous mechanisms that account for similarities in species distribution in large rivers such as MCR. These include backwatering and high flow events that can move benthic species to new substrate locations. Additionally, the T1/T2 area that remained wetted by minimum flows can function as a source of organisms to re-colonize exposed habitat areas after catastrophic flow events.

Field crews noticed that as flows ramp up in MCR, air is displaced up through the river bed. Vigorous bubbling occurs in the upper varial zone and dislodges deposited or friable periphyton and may force invertebrates into the drift. This air displacement was particularly forceful in Reach 4 cobble substrates.

Elevated flows can generate water velocities in the thalweg in excess of 2 m/sec (Schleppe et al. 2013). Since 2012 was the highest flow year to date, the growth metrics at T1 positions in 2012 were compared to other years (Table 3-4). As expected with higher flows, thalweg T1 periphyton abundance dropped by 48% in Reach 3 and by 62% in Reach 4, while biovolume dropped by 60% in Reach 3 and by 77% in Reach 4 during 2012. Overall water velocities would have been higher in the narrower Reach 4 channel, possibly accounting for the larger periphyton declines detected there compared to the wider Reach 3 channel. Higher flow velocities can increase sloughing of periphyton mats, and the greater water depth also lowers light penetration to the substrates.

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

	T1 in Fall of Year	Flow conditions	Abundance cells/cm^2	n #	Biovolume um^3/cm^2	n #
R3	2009 -11,13	typical flows	5.51 ± 2.20 x10^5	14	2.90 ± 2.58 x10^8	8
	2012	very high flows	2.87 ± 4.65 x10^5	3	1.18 ± 2.04 x10^8	3
R4	2009-11,13	typical flows	6.21 ± 3.13 x10^5	16	4.57 ± 2.29 x10^8	10
	2012	very high flows	2.36 ± 1.25 x10^5	4	1.04 ± 0.08 x10^8	4

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 should reduce desiccation on substrates that would otherwise be exposed by low flow releases. It should also increase the opportunity for limnoplankton suspended in the ALR water column to drop out onto MCR periphyton. In most years, sampler deployments in spring occurred at the lowest Arrow Lakes Reservoir levels and ended when backwatering was just starting in R3, while fall deployments commenced as backwatering declined in R3 and R4. Both deployments can be affected by backwatering with R3 receiving the greatest effect. Since the hydrologic regime in the preceding week is of greater importance to periphyton production than events that occurred further in the past (Schleppe et al. 2013), fall data should give us 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). Because light loggers on T6 samplers showed increased light (less water cover) and because back-watering was minimized in 2013, we compared R3 upper varial zone T5/T6 periphyton from 2013 to T5/T6 from 2010 and 2011 (Table 3-5). Upper varial zone abundance dropped by about 30% and biovolume by 70% in 2013 with no back-watering, while very high flows in 2012 apparently caused greater losses of 80% abundance and 93% biovolume

Table 3-5: Effects of flow conditions on periphyton productivity in Reach 3 in the upper varial zone

Fall R3 T5 & T6 of year	Flow conditions	Abundance cells/cm^2	Biovolume um^3/cm^2	N #
2010 and 2011	typical flows and backwatering	4.2 ± 2.4 x10^5	3.2 ± 2.0 x10^8	12
2012	very high flows, backwatering	0.90 ± 0.33 x10^5	0.22 ± 0.074 x10^8	6
2013	average flows, no backwatering	3.0 ± 1.8 x10^5	0.96 ± 0.53 x10^8	6

The protection from desiccation afforded by back-watering was most evident at the upper varial zone T4 – T6 positions. The effects of backwatering are accounted for by our statistical models because they consider duration and timing of submergence.

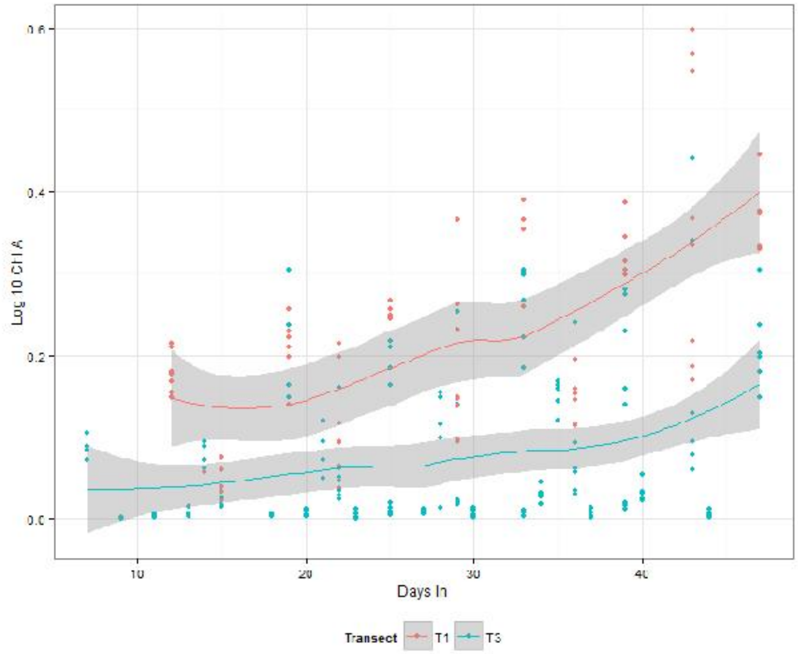
3.2.3 Periphyton Accrual

An ANCOVA was used to analyze chlorophyll-a accrual at the T1 and T3/T4 locations within the channel for data across all years during the fall and spring. Periphyton chl-a accrual rates area greater in permanently submerged locations (T1) than in varial zone locations (T3/T4) during the fall (Figure 3-7) and this trend does not differ between years ($F_{3,224} = 66.34$, $p<0.001$). Periphyton chl-a in the spring of 2013 were much higher than those observed in 2011 and 2012 (Figure 3-7, $F_{3,46}$ $=13.97$, $p=0.66$). Growth rates during the first few weeks were similar between permanently submerged and varial zone areas, but by the end of deployment, permanently submerged locations had achieved a greater quantity of chl-a ($F_{1,22} = 7.18$, $p=0.01$). These data suggest that growth was linked to submergence patterns in both spring and fall. Generally, the permanently submerged samplers are T1 benefit from increased submergence, while the T3/4 samplers experienced greater substrate exposure and likely increased rates of mortality affecting accrual. Spring and fall chl-a accrual at T1 locations did not show a plateau typical of peak biomass after the a 42 to 51 day deployment period, but rather suggested that chl-a may continue to grow to a higher level of overall productivity with an increased incubation time exceeding 50 days. This is supported by very high biomass found on samplers that were incubated in MCR for 6 months (Schleppe et al., 2011).

When MCR periphyton accrual (time series) data to date are considered together, periphyton accrual was most affected by the flow regime during the preceding 30 to 70 days, with the most recent event tending to exert the greatest influence on overall productivity. Catastrophic events occur where mortalities have exceeded 50% and have been detected within the dataset on several occasions over time series deployments. After these events, the periphyton standing crop drops to low levels, where these events act to almost “reset” the community and productivity. These events occur most often during long periods of exposure that exceed several days (i.e., greater than 72 hours or until channel substrate and interstitial spaces between the substrate is 100% dry), when temperatures are either warm (i.e., above 20 C) or cold (i.e., below -5 ˚C), and have a far greater effect on productivity than physical processes such as velocity or light intensity.

Time series chlorophyll-a data have been collected since 2009, while time series species abundance and biovolume were collected from 2010 to 2012 (Schleppe et al. 2011). In 2013, chl-a was selected as the only measure of periphyton productivity to assess accrual because it is a standard measure of production, it is available for the longest period, and it is highly correlated ($R^2 > 0.8$) with abundance and biovolume in MCR data (Schleppe et al. 2011).

Fall



Spring

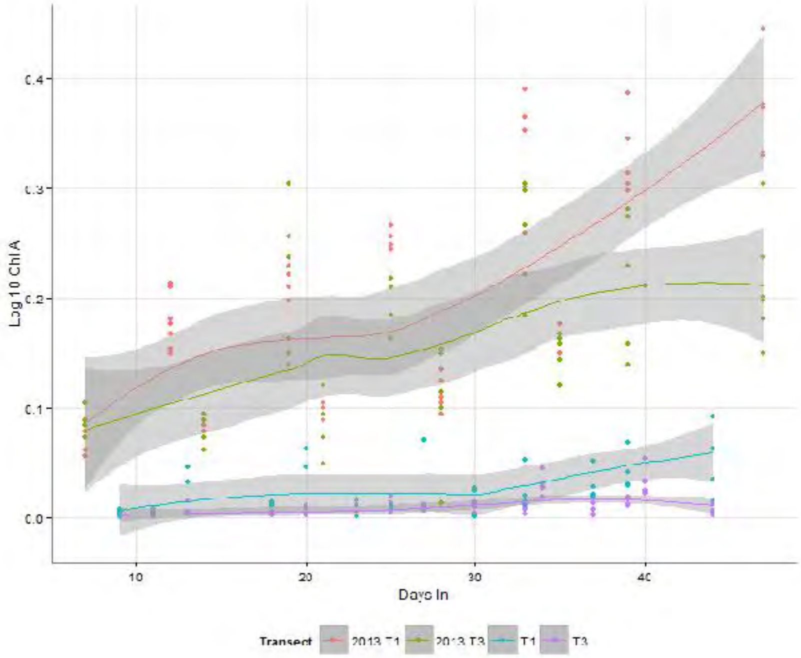


Figure 3-7: Regressions (with 95% confidence intervals (grey shade) of days submerged and chlorophyll-a. For the fall data, data is pooled at T1 and T3/T4 locations between 2009-2012. For spring data, the data is pooled for 2011 and 2012 (labelled T1 or T3) and for 2013 (labelled 2013.T1 or 2013.T3) Fitted lines were generated using a locally weighted polynomial regression method (LOWESS).

3.2.4 Periphyton Community Groupings

Community analyses of the full 2007 – 2013 database were completed at the genus level in 2013. This taxonomic level of analysis is intermediary between the species level considered in 2011 (Schleppe et al., 2012) and the family level considered in 2012 (Schleppe et al., 2013). When the analyses at all three taxonomic levels are compared, NMDS results suggest that at the species level, there was high inter-annual and seasonal variation, with potential effects of either implementation of minimum flow, operational flow patterns, or taxonomist. Therefore, analysis at the species level succeeded in identifying annual variations that are common in riverine environments, but was confounded by a change in taxonomist between 2009 and 2010. At the family level, these taxonomic differences were not observed, but at the same time, community shifts caused by implementation of minimum flow, year, season or transect, were obscured. We may conclude that over the 2007 - 2013 sample period, large-scale shifts in periphyton communities did not occur. Rather, the data infer that all differences were confined to shifts at lower taxonomic levels and were more typical of annual species shifts than of a periphyton response to minimum flows.

Similar to previous years, statistical analyses conducted at the genus level suggest that year (ANOSIM, R: 0.31, $p < 0.001$), season (ANOSIM, R: 0.15, $p < 0.001$), and flow period (ANOSIM, R: 0.07, $p < 0.001$) (pre and post minimum flows) are important determinants of the periphyton community (Figure 3-8). Patterns of submergence determined by transect location also appeared to have an influence on MCR periphyton communities (ANOSIM of Transect, 0.09, $p < 0.001$).

Although the change of taxonomist may account for some of the data differences observed between2007-2009 and 2010-2013, it appears that annual operational patterns affect periphyton community at some lower level (i.e., species/genus) either because they created specific habitat conditions that favoured different species and/or because species donation from Revelstoke Reservoir changed by year and by season. This is supported by the significant effect of transect depth, resulting in differing communities when the periphyton data were evaluated at the genus level (Figure 3-8).

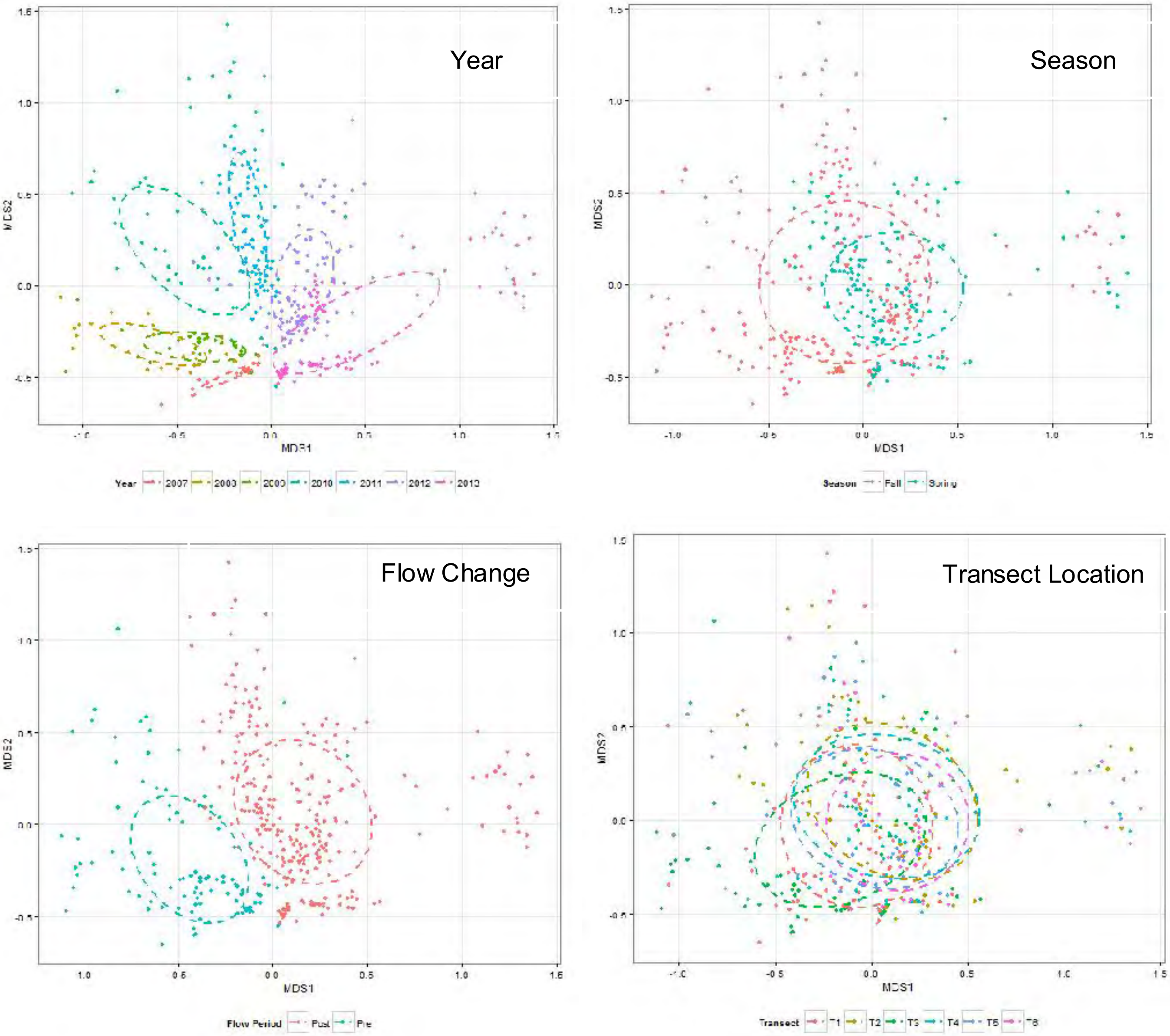


Figure 3-8: NMDS of periphyton abundance at the genus level, grouped by year, by season, by Pre and Post flow regime change, and by transect location for data collected between 2007 and 2013. These figures suggest that there were distinct differences between years, between flow periods, and smaller differences between spring vs. fall or between transect locations.

3.2.5 Periphyton Production Models

Results of periphyton production models are considered in a broad sense below. The intent is to understand the underlying processes that affect periphyton production rather than explain specific results of any given production response. This approach is advantageous because it allows us to consider more production responses than previous years (n=8 vs. n=4), and to facilitate future development of spatial models that can predict productivity under different flow scenarios.

Graphical analysis of data suggested that some sites, and the backwater sites in particular, had high leverage, and affected the outcome of the analyses. As a result, we reduced the dataset to only include mainstem sites (R3 and R4, S1 through S7, and T1 through T6) and sites that did not have a relative abundance of large substrate (either 100% or 0% large substrate) in the final models. This step improved both adherence to model assumptions and the interpretation of larger-scale processes that affect periphyton productivity. A cursory analysis of the removed data suggested that backwater and eddy sites experienced large, site-level effects that are yet to be accounted for in our models. Future model iterations should consider methods to incorporate these site-level effects.

3.2.5.1 Fall and Spring Full River Transect

This section considers the entire river cross section for transect location spanning the thalweg to the upper varial zone, while the next section considers only the permanently wetted transects. Model averaging clarifies the influence of the key drivers of periphyton production in the MCR system. Data for the fall sample periods indicated that there were numerous plausible models (those with an AICc<2.0) for the eight production metrics (Table 3-6).

Several significant trends were observed across all measures of periphyton production, most notably that production increased with total daytime incubation (i.e., total time in the water during daylight), and decreased with mean temperature and mean light intensity (Figure 3-9 and 3-10; Appendix A, Figures A1-A3). When substrates were exposed, temperature and light both increased. Thus, the data strongly suggests that submergence is the most important determinant of periphyton production because water and light intensity are surrogates of submergence.

The relative abundance and biovolume of dead cells was inversely related with measures of live production. Dead abundance and biovolume increased with decreasing total incubation time and increased with both mean temperature and light intensity (Figure 3-11; Appendix Figures A-1 to A-3). We can assume that substrate exposure increases periphyton mortality.

Other periphyton response measures including AFDW and Simpson's index described less variance, and were not useful in the determination of predominant effects of submergence or minimum flow on MCR during the fall (Figure 3-12).

Table 3-6: Summary of the number of plausible models identified using model averaging (those with a ∆AIC <2) and the range of pseudo R^2 values for selected models for samplers across all transects.

MCR - Full Transect Periphyton Response	Fall # of plausible models	 range of pseudo R^2	Spring # of plausible models	 range of pseudo R^2
Abundance	11	0.70 - 0.72	8	0.58 - 0.59
biovolume	15	0.68 - 0.69	5	0.68
chlorophyll-a	11	0.51 - 0.52	4	0.72 - 0.74
ash-free dry weight	21	0.09 - 0.11	19	0.17 - 0.19
% dead abundance	32	0.35 - 0.38	22	0.22 - 0.25
% dead biovolume	10	0.39 - 0.40	7	0.37 - 0.39
Simpson's Index	9	<0.001	5	0.22 - 0.25
species richness	13	0.52 - 0.53	17	0.69 - 0.70

Model averaging of the spring data was similar to the fall results. Numerous plausible models (those with an AICc<2.0) were identified. The variance described by the top models (pseudo R^2) varied between periphyton metrics (Table 3-6). Several key and significant trends were observed across all measures of spring periphyton production. Like the fall results, abundance and biovolume increased with total daytime submergence (i.e., incubation time in the water during daylight), and decreased with mean temperature and mean light intensity (Figure 3-9 and 3-10; Appendix A Figure A1-A3). Also, periphyton biovolume increased with increasing velocity, noting that sites that were regularly exposed usually had lower velocities (Figure 3-9). The percent dead abundance and biovolume were inversely related to measures of production. Specifically, dead abundance and biovolume increased with both mean temperature and light intensity, which are both surrogate measures of substrate exposure (Figure 3-13, Figure 3-14). Figures 3-9 to 3-12 confirm that spring MCR productivity was lower than fall productivity and that spring exposure resulted in very low abundance and frequent non-detectable chlorophyll-a results.

Other response measures including AFDW and Simpson's index were not useful to ascertain effects of submergence or minimum flow on MCR during the spring (Figure 3-12).

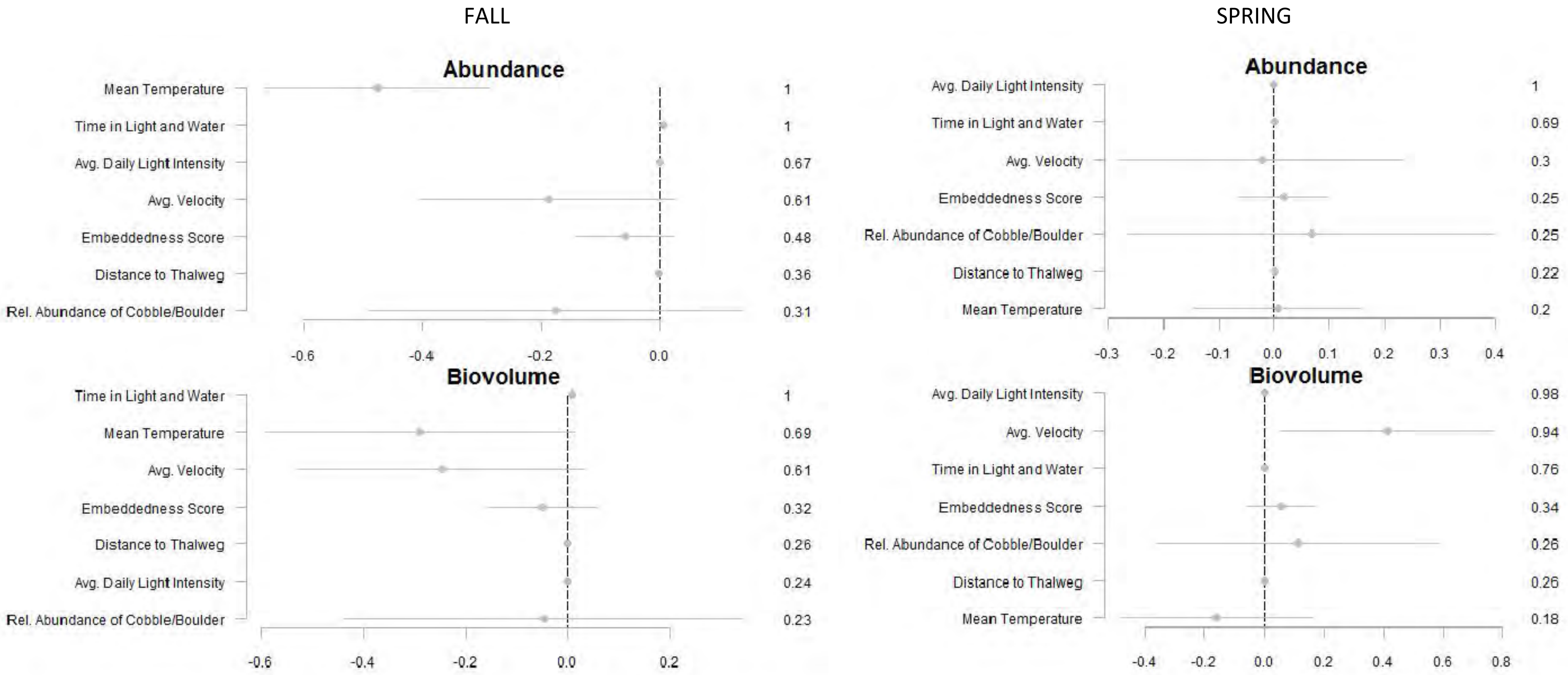


Figure 3-9: Model averaged parameter coefficients and 95% confidence limits from model averaged linear mixed effects models of the effects of mean temperature, time in the light and water, average daily light intensity, average velocity, embeddedness score, distance to thalweg, and the relative abundance of cobble/boulder substrates on periphyton production in the MCR. Response variables of periphyton production included both abundance and biovolume in the fall (left) and spring (right). Coefficients are centered and standardized to allow direct comparisons of the direction and size of effects. Those explanatory variables with coefficients falling to the right of the zero line have a positive effect on the response, while those falling to the left have a negative effect. Those variables with 95% confidence intervals spanning zero are considered of low significance as the direction of their effects are inconsistent among models. Parameter coefficients are sorted by their relative variable importance to the averaged model on a scale of 0 to 1 on the right y-axis of each panel.

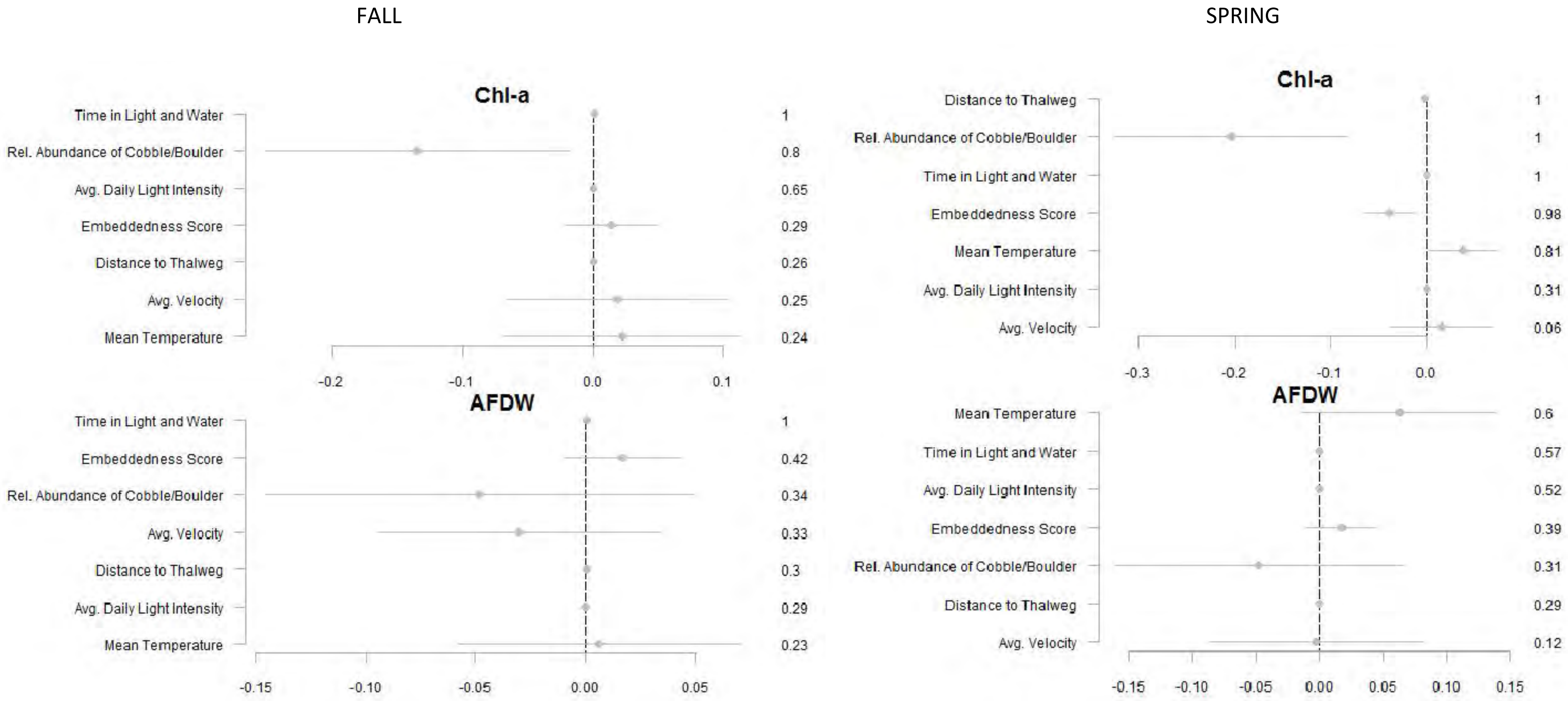


Figure 3-10: The coefficients and their 95% confidence limits of standardized explanatory variables of periphyton production in MCR. Periphyton responses included Chlorophyll-a (chl-a) and ash-free dry weight (AFDW) for the fall and spring. Explanatory variables included mean temperature, time in the light and water, average daily light intensity, average velocity, embeddedness score, distance to thalweg, and the relative abundance of cobble/boulder substrates. Coefficients were standardized to allow direct comparisons of the direction and size of effects, noting that variables with confidence limits that encompass zero can have either a positive or negative effect depending upon which model is considered. Key explanatory variables are those that have a relative variable importance (RVI) of greater than 0.6-0.7 and the RVI is shown on the right-hand side of each figure.

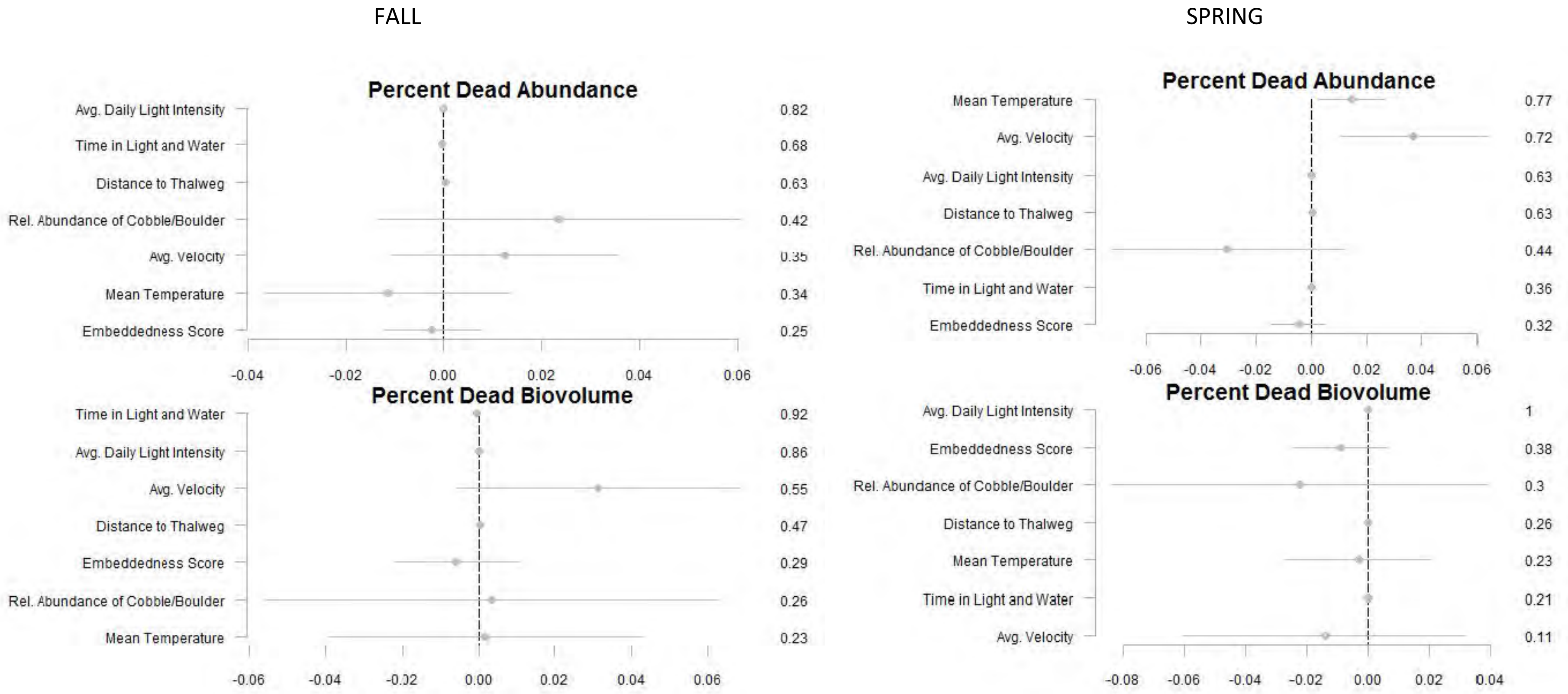


Figure 3-11: The coefficients and their 95% confidence limits of standardized explanatory variables of periphyton production in MCR. Periphyton responses included percent dead abundance and biovolume for the fall (left) and spring (right). Explanatory variables included mean temperature, time in the light and water, average daily light intensity, average velocity, embeddedness score, distance to thalweg, and the relative abundance of cobble/boulder substrates. Coefficients were standardized to allow direct comparisons of the direction and size of effects, noting that variables with confidence limits that encompass zero can have either a positive or negative effect depending upon which model is considered. Key explanatory variables are those that have a relative variable importance (RVI) of greater than 0.6-0.7 and the RVI is shown on the right-hand side of each figure.

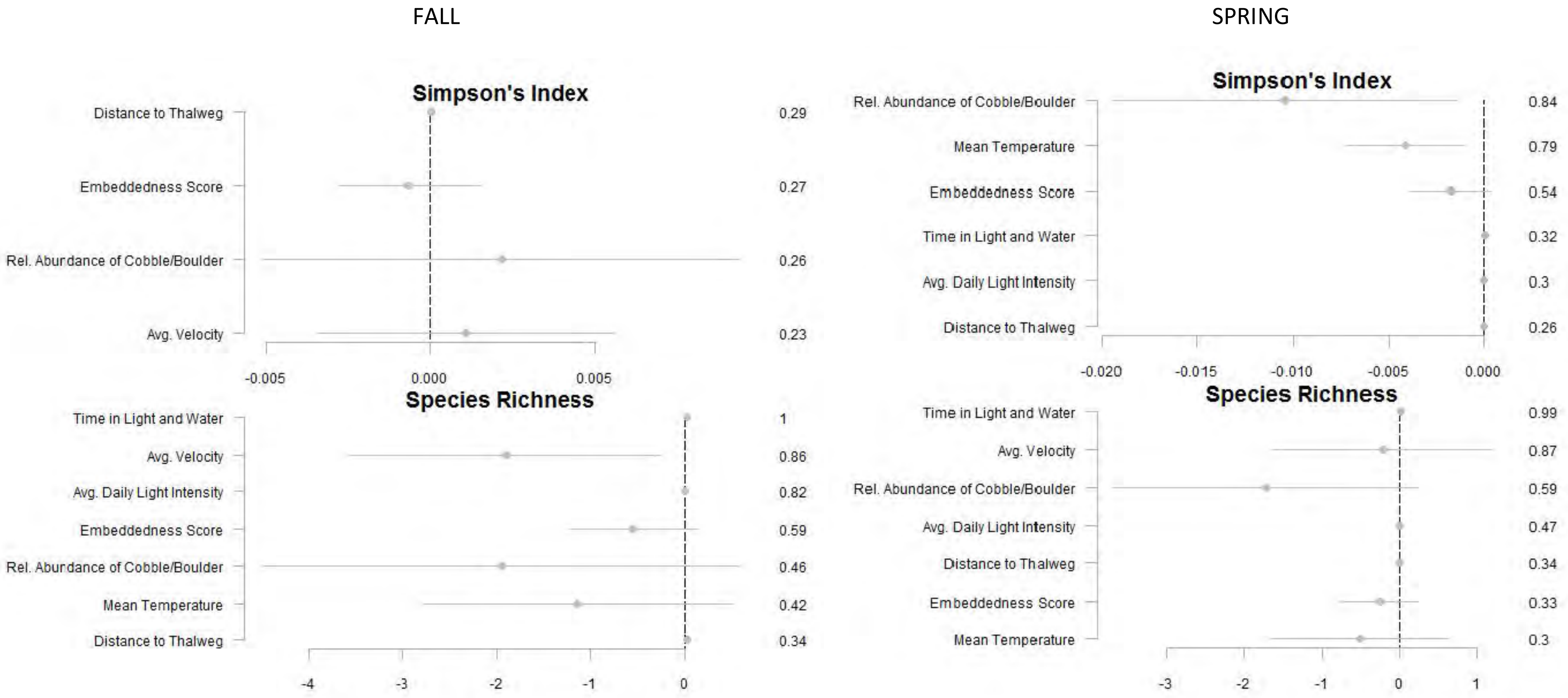


Figure 3-12: The coefficients and their 95% confidence limits of standardized explanatory variables of periphyton production in MCR. Periphyton responses included Simpson's Index and Species Richness for the fall (left) and spring (right). Explanatory variables included mean temperature, time in the light and water, average daily light intensity, average velocity, embeddedness score, distance to thalweg, and the relative abundance of cobble/boulder substrates. Coefficients were standardized to allow direct comparisons of the direction and size of effects, noting that variables with confidence limits that encompass zero can have either a positive or negative effect depending upon which model is considered. Key explanatory variables are those that have a relative variable importance (RVI) of greater than 0.6-0.7 and the RVI is shown on the right-hand side of each figure.

3.2.5.2 Fall and Spring Submerged Transects

The model averaging exercise was re-run, but instead of including the entire river transect, only those sampler transects that were submerged 100% of the time were considered. Model averaging data for the fall indicated that there were numerous plausible models (those with an AICc<2.0) that could explain aspects of MCR periphyton metrics. The top models described a range of variance in the periphyton metrics (Table 3-7). These models help us understand the main drivers of periphyton production on zones in MCR wetted by minimum flows.

The models between the responses and predictors in sites submerged for 100% of the time described less variance than those considering all sites and this was observed across multiple production metrics suggesting other factors are potentially important determinants of the periphyton community (e.g., ramping rates and magnitude). Fall data suggest that abundance and biovolume increased with increasing light intensity and decreased with increasing velocity (Figure 3-13 to 3-16). These results are consistent with periphyton behaviour in unregulated rivers, suggesting that the permanently wetted substrates in the MCR have similar production constraints to a natural river system. The percent dead abundance and biovolume appeared to increase with embeddedness.

Table 3-7: Summary of the number of plausible models identified using model averaging (those with ∆AIC <2) and the range of pseudo R^2 values for selected models for permanently submerged samplers.

MCR - Permanently Submerged Samplers	Fall		Spring	
Periphyton response metric	# of plausible models	range of pseudo R^2	# of plausible models	range of pseudo R^2
abundance	5	0.34	5	0.01 - 0.16
biovolume	7	0.29 - 0.31	11	0.10 - 0.23
chlorophyll-a	14	0.04 - 0.13	9	0.09 - 0.33
ash-free dry weight	6	0.19 - 0.28	8	<0.10
% dead abundance	7	0.21 - 0.27	9	<0.13
% dead biovolume	7	0.33 - 0.37	5	<0.06
Simpson's Index	15	0.07 - 0.30	9	0.01 - 0.25
species richness	10	0.01 - 0.10	7	0.27 - 0.33

Model averaging data for the permanently submerged spring data also indicated that there were numerous plausible models (i.e., combinations of predictive variables). The variance described by the top models (pseudo R^2) was lower than that of permanently submerged fall models, indicating our set of predictor variables were not as strong or that variability was greater (Table 3-7). During the spring, the data suggest that abundance and biovolume increased with increasing amounts of large substrate, and decreased with increasing distance from the thalweg. The percent dead abundance and biovolume increased with increasing embeddedness, as they did in the fall.

Several key trends were observed for both seasons, even though the data from submerged transect sites had less predictive capability (i.e., lower R^2) than data from both submerged and varial zone samplers. The data suggest that samplers occurring in sites with increased light intensity and lower velocities, and with larger, stable substrates (lower embeddedness), had higher overall production. These results fit well with Figure 3-12; as light intensity increased, periphyton production increased, provided that the substrate stayed water-covered. Additionally, as velocity increased, productivity decreased, presumably by increased shear and saltation. Taken together, the depth of maximum productivity within the permanently wetted substrates should shift as the balance of velocity and light intensity are changed by flow patterns. These model results correspond to our field observations of shifting bands of periphyton productivity.

In summary, the model averaging analyses demonstrated that the key drivers of periphyton production were different for continuously submerged substrates than for varial zones of MCR. While varial zone productivity was largely determined by time spent submerged or exposed, the productivity in the deeper zones continuously wetted by minimum flows was determined by light intensity, water velocity and substrate stability. Within these zones, the key drivers remained the same between spring and fall.

Inevitably our model averaging cannot account for all of the variability in a complex system like MCR, and some variability remains unexplained.

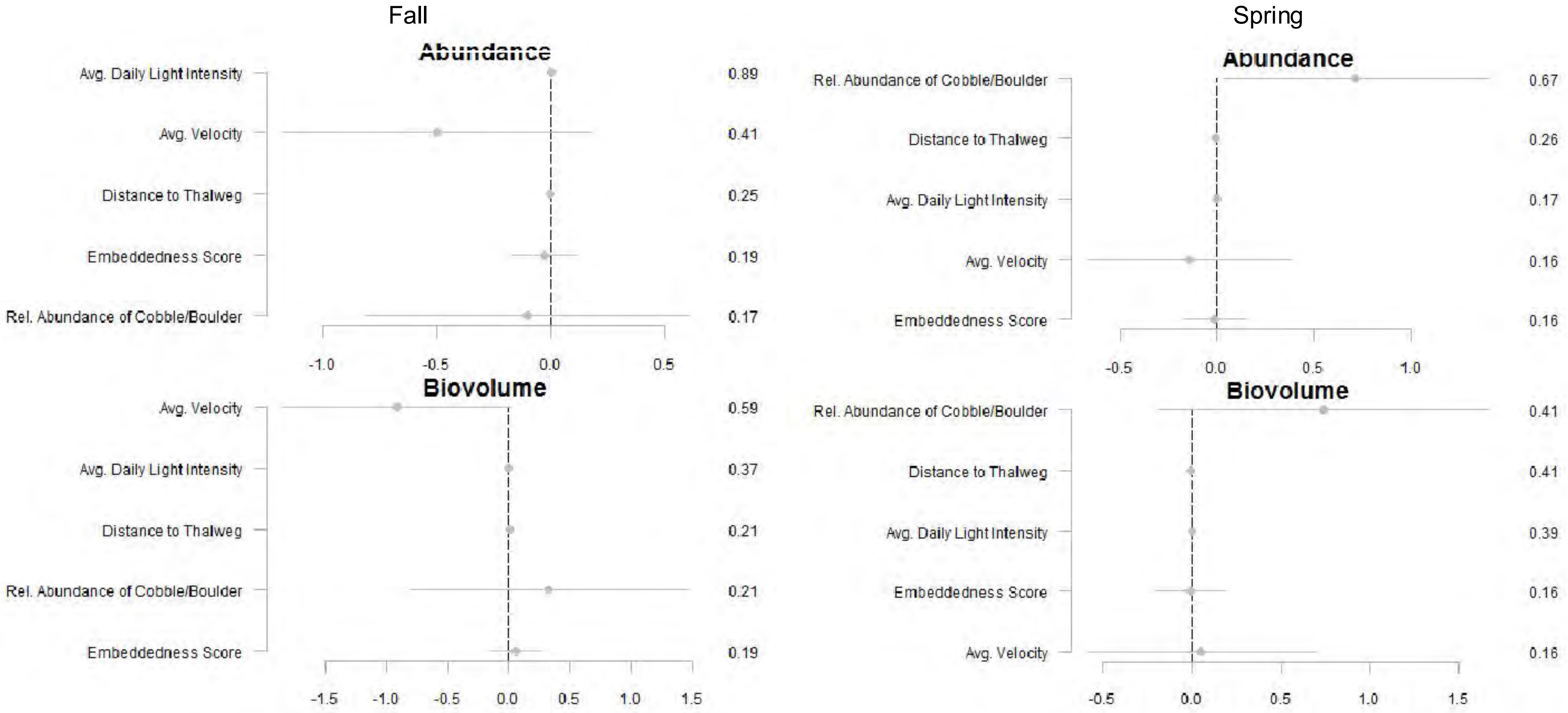


Figure 3-13: The coefficients and their 95% confidence limits of standardized explanatory variables of periphyton production in MCR. Periphyton responses included abundance and biovolume for the fall (left) and spring (right). Explanatory variables included mean temperature, average daily light intensity, average velocity, embeddedness score, distance to thalweg, and the relative abundance of cobble/boulder substrates. Coefficients were standardized to allow direct comparisons of the direction and size of effects, noting that variables with confidence limits that encompass zero can have either a positive or negative effect depending upon which model is considered. Key explanatory variables are those that have a relative variable importance (RVI) of greater than 0.6-0.7 and the RVI is shown on the right-hand side of each figure.

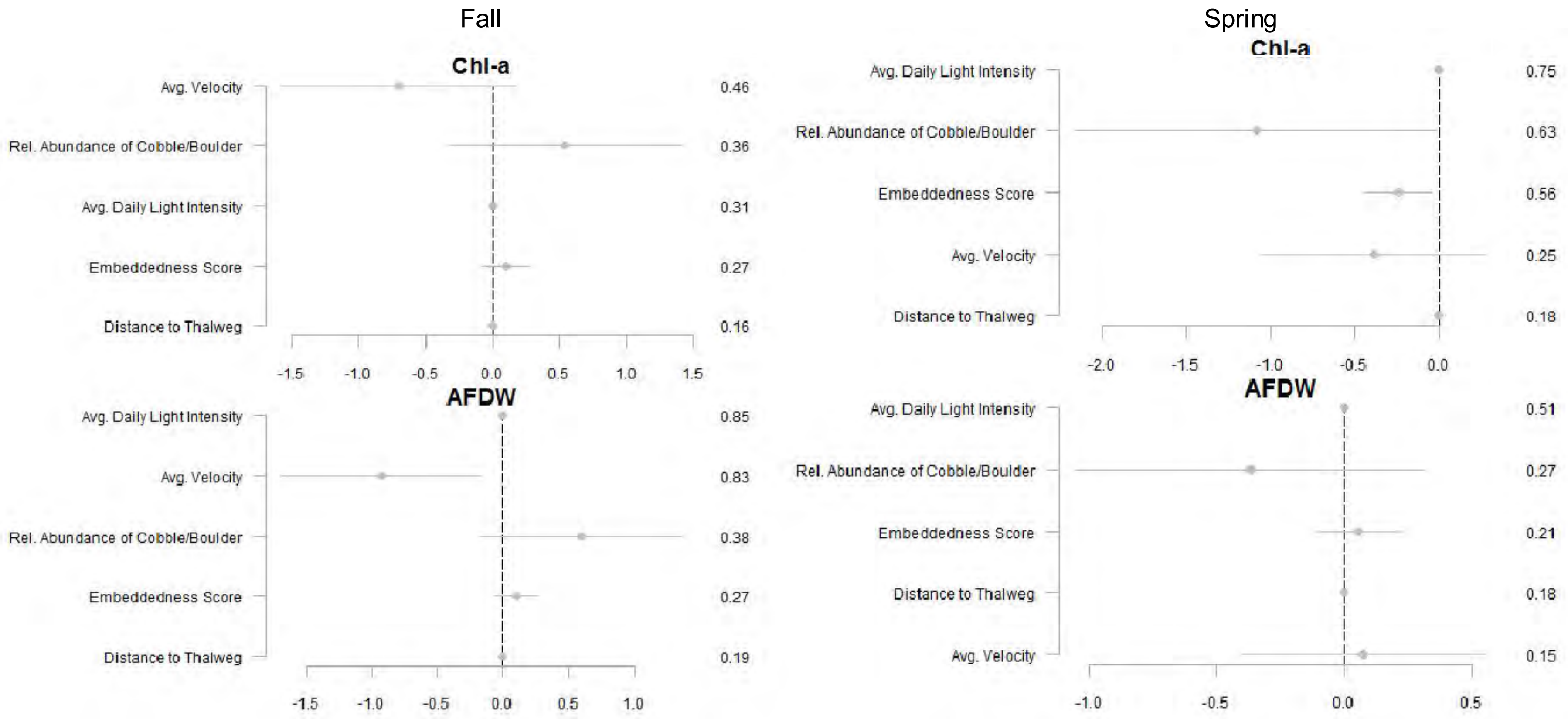


Figure 3-14: The coefficients and their 95% confidence limits of standardized explanatory variables of periphyton production in MCR. Periphyton responses included chlorophyll-a (Chl-a) and ash-free dry weight (AFDW) for the fall (left) and spring (right). Explanatory variables included mean temperature, average daily light intensity, average velocity, embeddedness score, distance to thalweg, and the relative abundance of cobble/boulder substrates. Coefficients are standardized to allow direct comparisons of the direction and size of effects, noting that variables with confidence limits that encompass zero can have either a positive or negative effect depending upon which model is considered. Key explanatory variables are those that have a relative variable importance (RVI) of greater than 0.6-0.7 and the RVI is shown on the right-hand side of each figure.

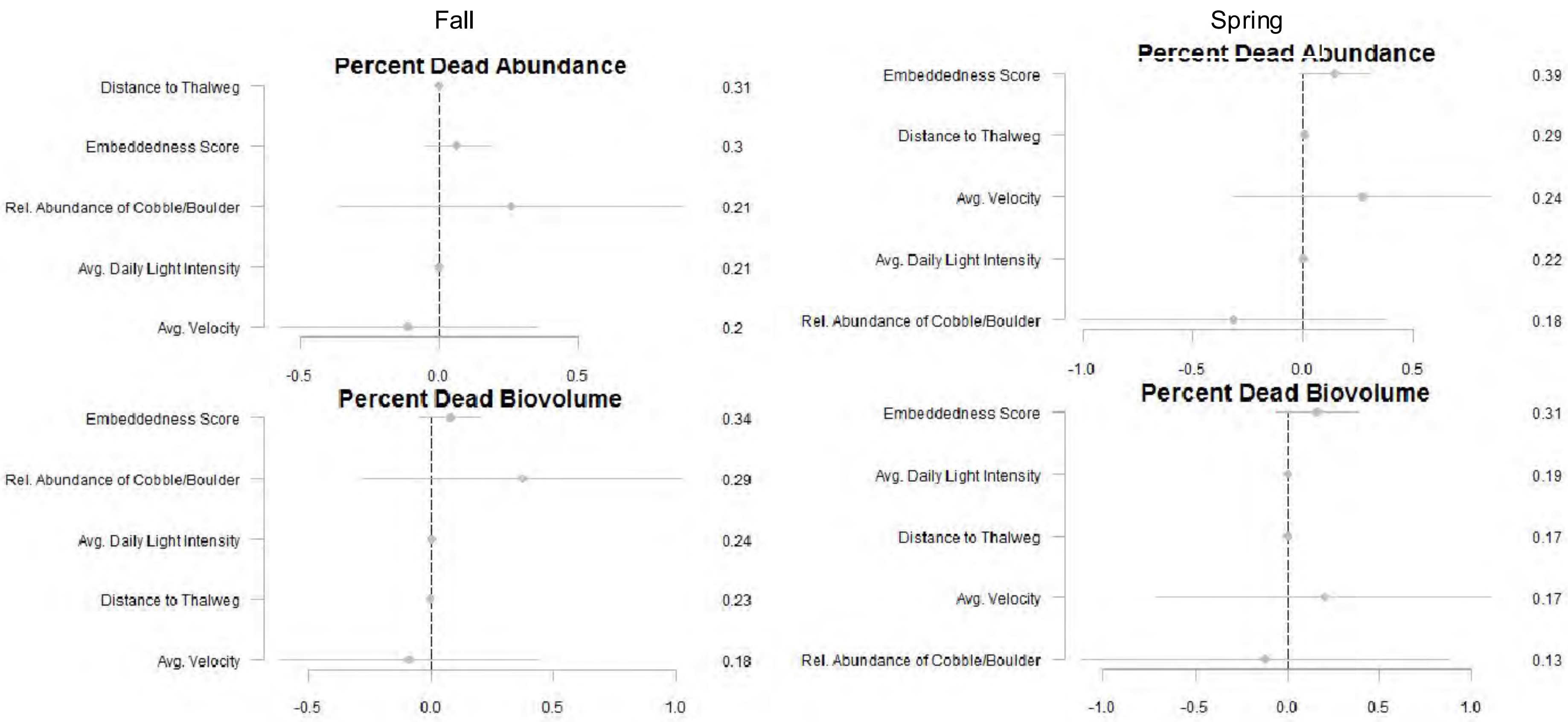


Figure 3-15: The coefficients and their 95% confidence limits of standardized explanatory variables of periphyton production in MCR. Periphyton responses included percent dead abundance and biovolume for the fall (left) and spring (right). Explanatory variables included mean temperature, average daily light intensity, average velocity, embeddedness score, distance to thalweg, and the relative abundance of cobble/boulder substrates. Coefficients are standardized to allow direct comparisons of the direction and size of effects, noting that variables with confidence limits that encompass zero can have either a positive or negative effect depending upon which model is considered. Key explanatory variables are those that have a relative variable importance (RVI) of greater than 0.6-0.7 and the RVI is shown on the right-hand side of each figure.

Fall Spring

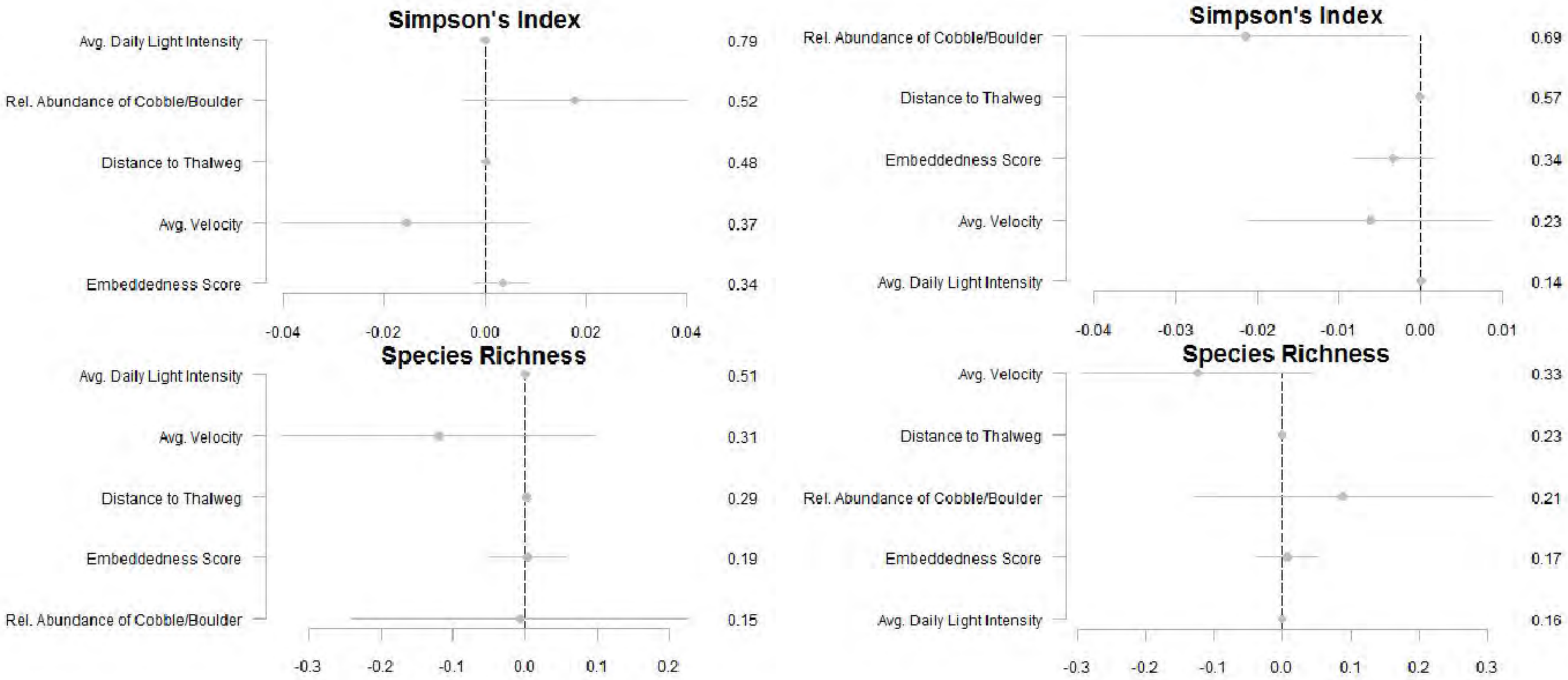


Figure 3-16: The coefficients and their 95% confidence limits of standardized explanatory variables of periphyton production in MCR. Periphyton responses included Simpson's Index and Species Richness for the fall (left) and spring (right). Explanatory variables included mean temperature, average daily light intensity, average velocity, embeddedness score, distance to thalweg, and the relative abundance of cobble/boulder substrates. Coefficients are standardized to allow direct comparisons of the direction and size of effects, noting that variables with confidence limits that encompass zero can have either a positive or negative effect depending upon which model is considered. Key explanatory variables are those that have a relative variable importance (RVI) of greater than 0.6-0.7 and the RVI is shown on the right-hand side of each figure.

3.3 Benthic Invertebrates

3.3.1 Yearly Comparisons of Benthic Invertebrate Sampling

Relative biomass and relative abundance of benthic invertebrates varied between years at the lowest taxonomic level of identification (Family to Genus). Generally, members of *Hydra* sp., Chironomids, and small Tubificid worms were the most abundant, accounting for over 75% of the total abundance in all years and seasons studied. When present, although not as numerically abundant, members of the EPT taxonomic groups increased relative biomass greatly when compared to their contribution to relative abundance (Table A-5). These trends were consistently observed in both spring and fall data (Table A-4). In most samples, less than 10 species made up over 98% of the total abundance or biomass at any sampling location.

Benthic abundance and biomass varied greatly among different reaches, with standard deviation within a given year consistently higher than the mean. Species richness also varied among years in the fall with the lowest values in 2009-2010, and highest in the fall sampling periods of 2011 and 2013. However, species richness was low and stable among years in the spring (Tables A-6, A-7). In contrast, while some variability was observed in percent EPT, percent Chironomidae, Simpson's Index, and Hilsenhoff index, these more general metrics were much more consistent among years and season. Benthic invertebrates were usually more abundant in the fall than in spring, however effects of flow, season, or year were not readily apparent. Chironomidae were much more prevalent than EPT taxa, and accounted for 30-75% of the total abundance in the spring or fall at any site. EPT taxa were most prevalent in 2012-2013, when they accounted for 4-5% of the total abundance. Greater abundance of EPT taxa corresponded with years of higher average flow and associated increased submergence of substrates within varial zones. Although we did not sample the Jordan River in 2013, it is considered to be an important source of invertebrates for areas within Reach 3.

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 (Tables A-8, A-9), with highest levels observed in T2 and the lowest values in the upper varial zone (T5-T7). Contrary to these trends, Simpson’s and Hilsenhoff indices were relatively consistent across all portions of the channel.

3.3.2 Benthic Invertebrate Community Groupings

Community analyses of the full 2007 – 2013 data were completed at the genus level in 2013. This taxonomic level of analysis is intermediary between the species level considered in 2011 (Schleppe et al., 2012) and the family level considered in 2012 (Schleppe et al., 2013). Similar to previous years, genus data suggest that year (ANOSIM, R: 0.35, $p < 0.001$), season (ANOSIM, R: 0.07, $p < 0.001$), and flow period (ANOSIM, R: 0.43, $p < 0.001$) (pre and post minimum flows) are important determinants of the invertebrate community (Figures 3-17 and 3-18). Patterns of submergence also appeared to affect the invertebrate community (ANOSIM of Transect, 0.07, $p < 0.001$).

Similar to periphyton, there was high inter-annual and seasonal variation when data were analyzed at the species level. At the family level of taxonomic identification, these trends were not as apparent but were still present. This infers that over the sample period, large-scale shifts in benthic communities were not observed and that trends were associated with high inter-annual variation, season, and location within the river channel. Difference in taxonomist are only expected to account for some of the differences observed between years, while most of the observed inter-annual variation is associated with the BC Hydro operating regime over the sample period (i.e., see ANOVA's of groupings of flow over the study period during stable high and low flow periods).

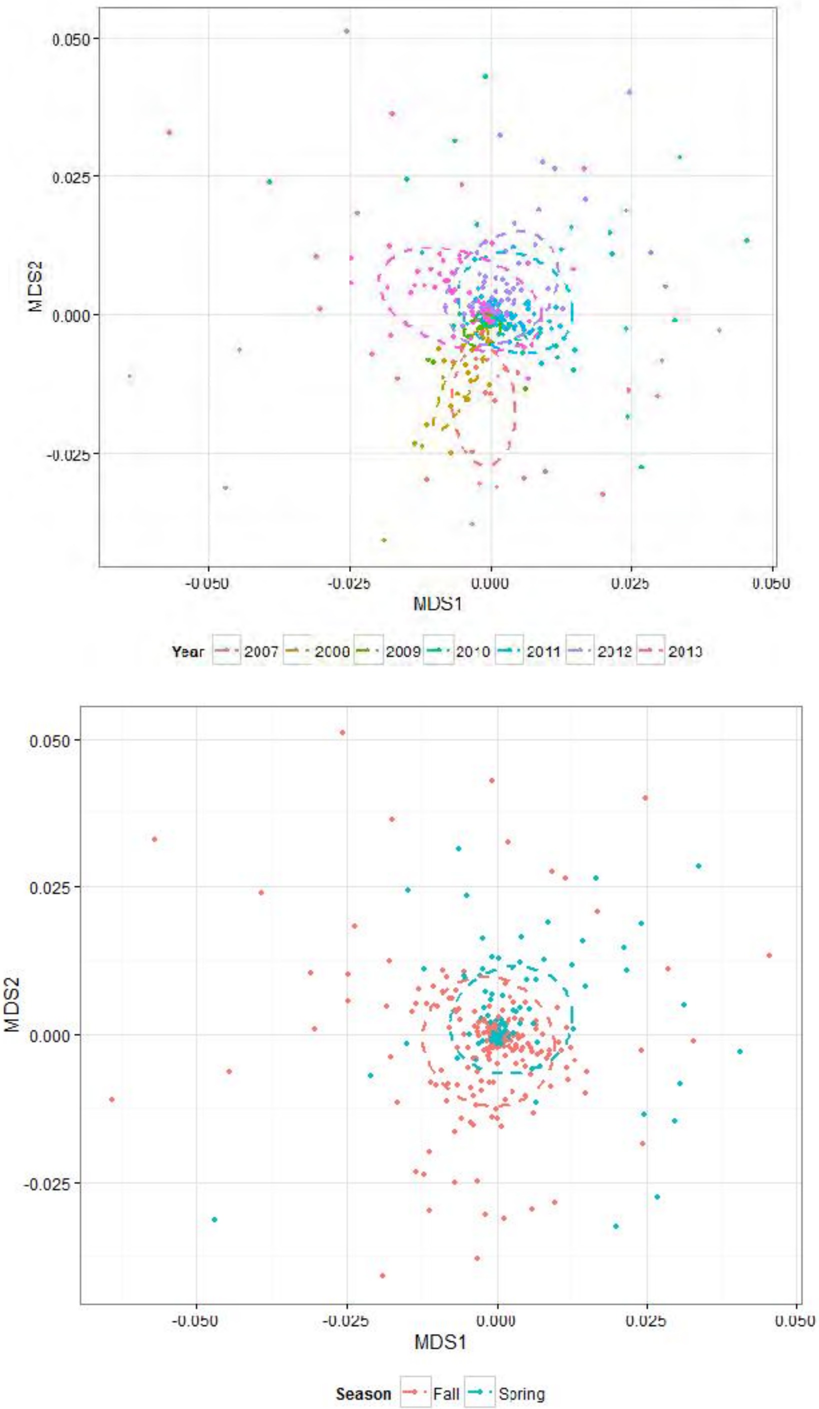


Figure 3-17: NMDS of benthic abundance at the genus level grouped by Year and Season for data collected between 2007 and 2013.

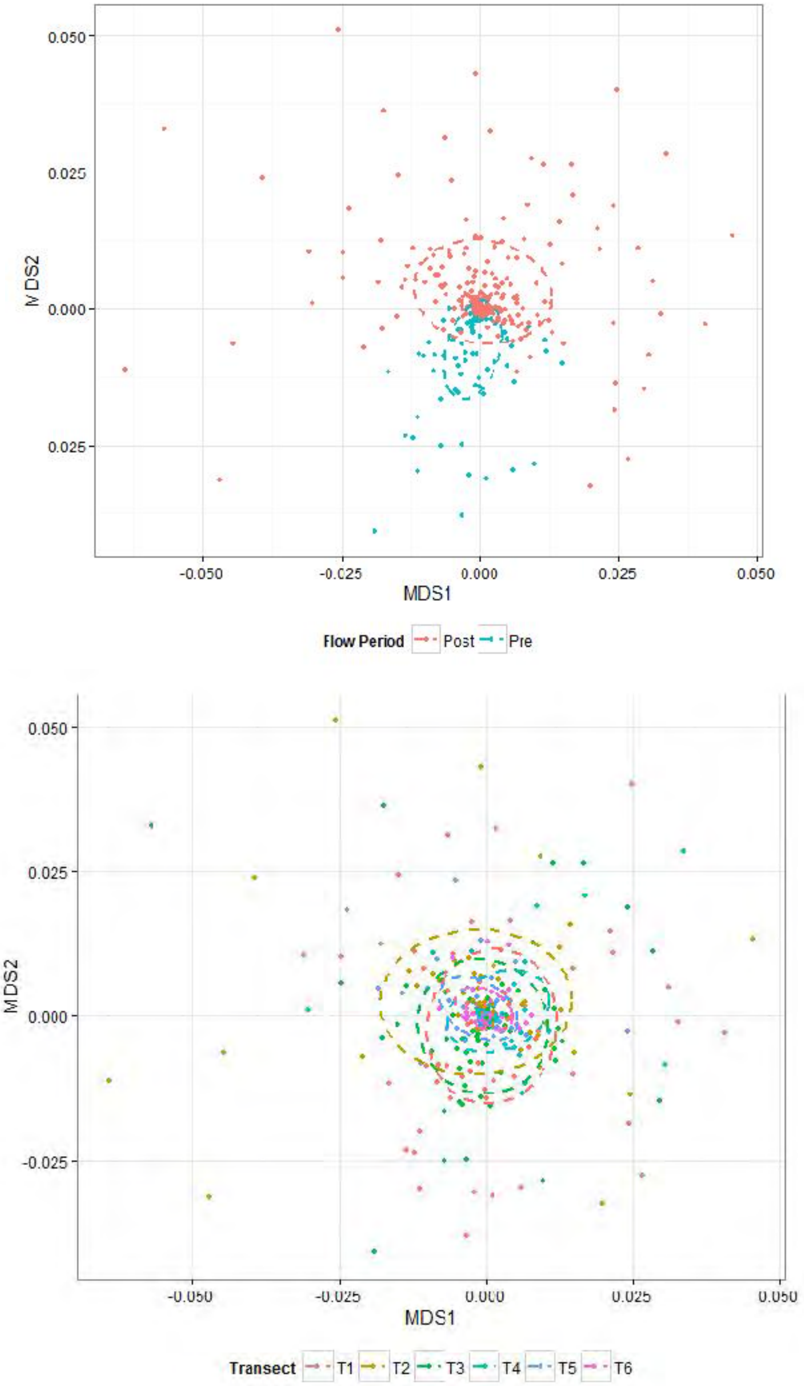


Figure 3-18: NMDS of benthic abundance at the genus level grouped by flow period (per and post minimum flows) and Transect (T1 Deep to T6-shallow) for data collected between 2007 and 2013.

3.3.3 Benthic Invertebrate Production Models

The results of invertebrate production models are similar to that of periphyton in a broad sense. The intent is to understand the underlying processes that affect invertebrate production rather than explain specific results of any given production response. This approach is advantageous because it allows us to evaluate more production responses than previous years (n=8 vs. n=4), and to facilitate future development of spatial models that can predict productivity under different flow scenarios.

3.3.3.1 Fall and Spring Full River Transect

This section evaluates the entire river cross section for transect locations spanning the thalweg to the upper varial zone, while the next section considers only the permanently wetted transects. Model averaging clarifies the influence of the key drivers of periphyton production in the MCR system. Data for the fall sample periods indicated that there were numerous plausible models (those with an AICc<2.0) for the eight production metrics (Table 3-8).

Several key and significant trends were observed across all measures of production, most notably that production increased with submergence time and velocity, and decreased with increasing abundance of cobble/boulder (Figure 3-19 to Figure 3-22). The quantity of food for fish (i.e., EPT taxa and Chironomids) increased with increasing relative abundance of cobble boulder, and increasing velocity, as shown by both the fish food index and Hilsenhoff Index (trends are inverse with the HBI because EPT increase with decreasing HBI score). Submergence measures also affected the quantity of fish food, with increased food occurring in sites with increased submergence (as determined by EPT, Hilsenhoff, and FFI). Species richness and Simpson's Index suggest that diversity is negatively associated with increasing relative abundance of larger substrates.

In the spring, invertebrate production increased with submergence time and velocity, and decreased with mean light intensity and distance to thalweg (Figure 3-19 to Figure 3-22). The quantity of food for fish increased with increasing relative abundance of cobble boulder, and increasing velocity, similar to the fall, noting that trends are inverse with the HBI because EPT increase with decreasing HBI score. Species richness and Simpson's Index suggest that diversity is negatively associated with increasing relative abundance of larger substrates.

Although numerous different predictors appear to influence benthic community establishment, the most important factors all relate to some measure of submergence. Similar to previous years, submergence time appears to be the most important factor influencing the invertebrate community and ultimately food for fish in permanently submerged areas of the MCR during 2013.

Table 3-8: Summary of the number of plausible models identified using model averaging (those with a ΔAIC <2) and the range of pseudo R^2 values for selected models for samplers across all transects.

MCR - Full Transect	Fall		Spring	
Invertebrate response metric	# of plausible models	range of pseudo R^2	# of plausible models	range of pseudo R^2
abundance	12	0.87-0.89	15	0.56-0.58
Biomass	11	0.82-0.83	5	0.41-0.43
EPT Abundance	6	0.47-0.49	8	0.37-0.39
% Chironomidae	8	0.42-0.43	10	0.35-0.39
Fish Food Index	6	0.34-0.35	29	0.29-0.33
Hilsenhoff Biotic Index	14	0.22-0.23	17	0.28-0.33
Simpson's Index	8	0.93-0.94	6	0.16-0.18
species richness	10	0.11-0.13	6	0.16-0.18

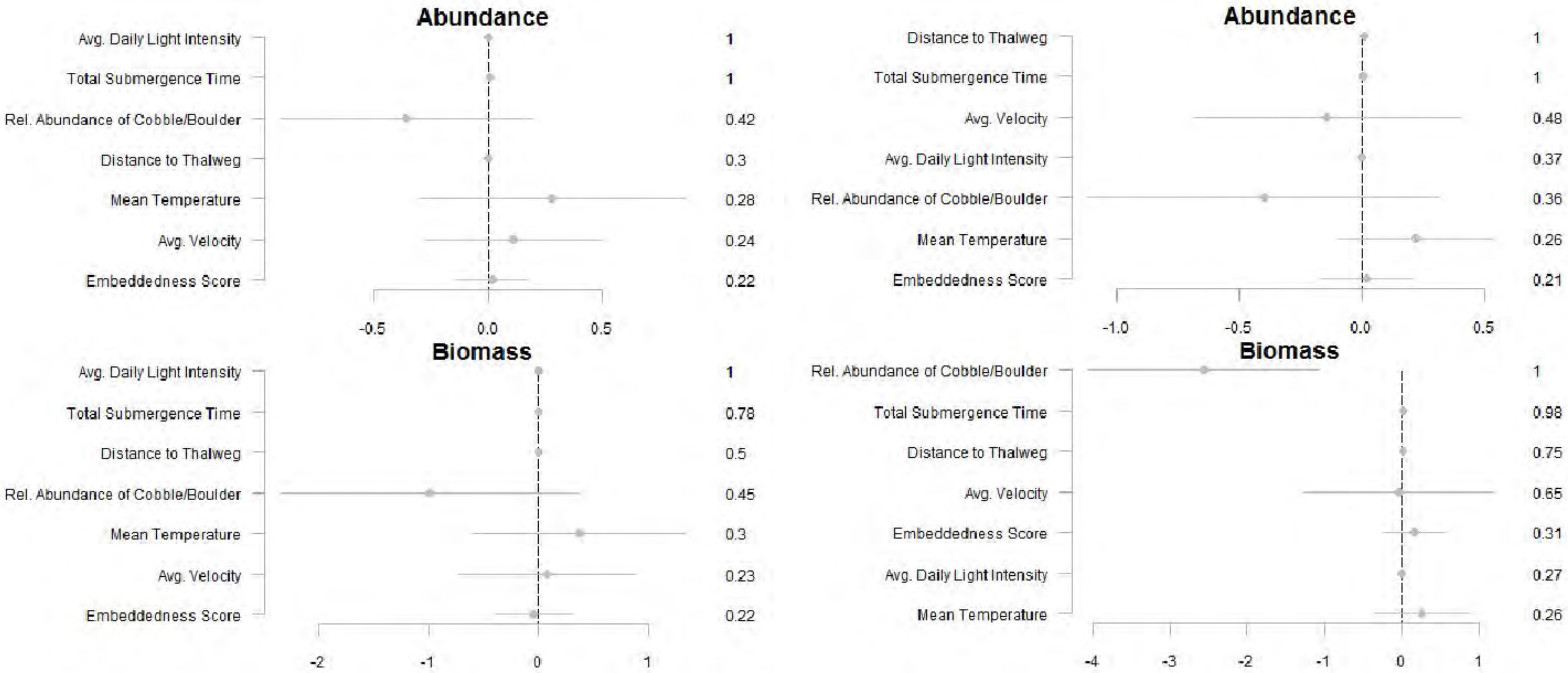


Figure 3-19: The coefficients and their 95% confidence limits of standardized explanatory variables of benthic production in the MCR. Periphyton responses included abundance and biomass for the fall (left) and spring (right). Explanatory variables included mean temperature, total submergence time, average daily light intensity, average velocity, embeddedness score, distance to thalweg, and the relative abundance of cobble/boulder substrates. Coefficients are standardized to allow direct comparisons of the direction and size of effects, noting that variables with confidence limits that encompass zero can have either a positive or negative effect depending upon which model is considered. Key explanatory variables are those that have a relative variable importance (RVI) of greater than 0.6/0.7 and the RVI is shown on the right hand side of each figure.

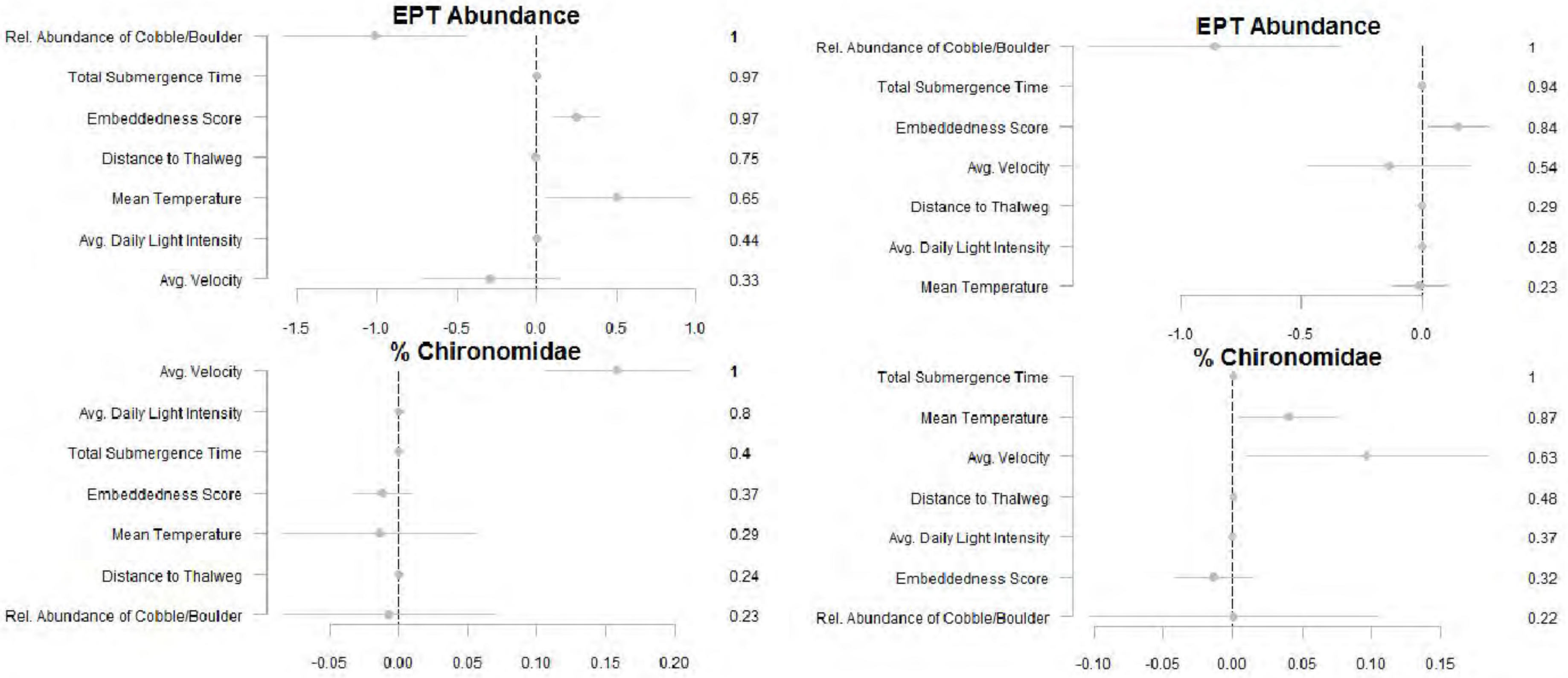


Figure 3-20: The coefficients and their 95% confidence limits of standardized explanatory variables of benthic production in the MCR. Benthic responses included abundance and biovolume for the fall (left) and spring (right). Explanatory variables included mean temperature, total submergence time, average daily light intensity, average velocity, embeddedness score, distance to thalwege and the relative abundance of cobble/boulder substrates. Coefficients are standardized to allow direct comparisons of the direction and size of effects, noting that variables with confidence limits that encompass zero can have either a positive or negative effect depending upon which model is considered. Key explanatory variables are those that have a relative variable importance (RVI) of greater than 0.6/0.7 and the RVI is shown on the right hand side of each figure.

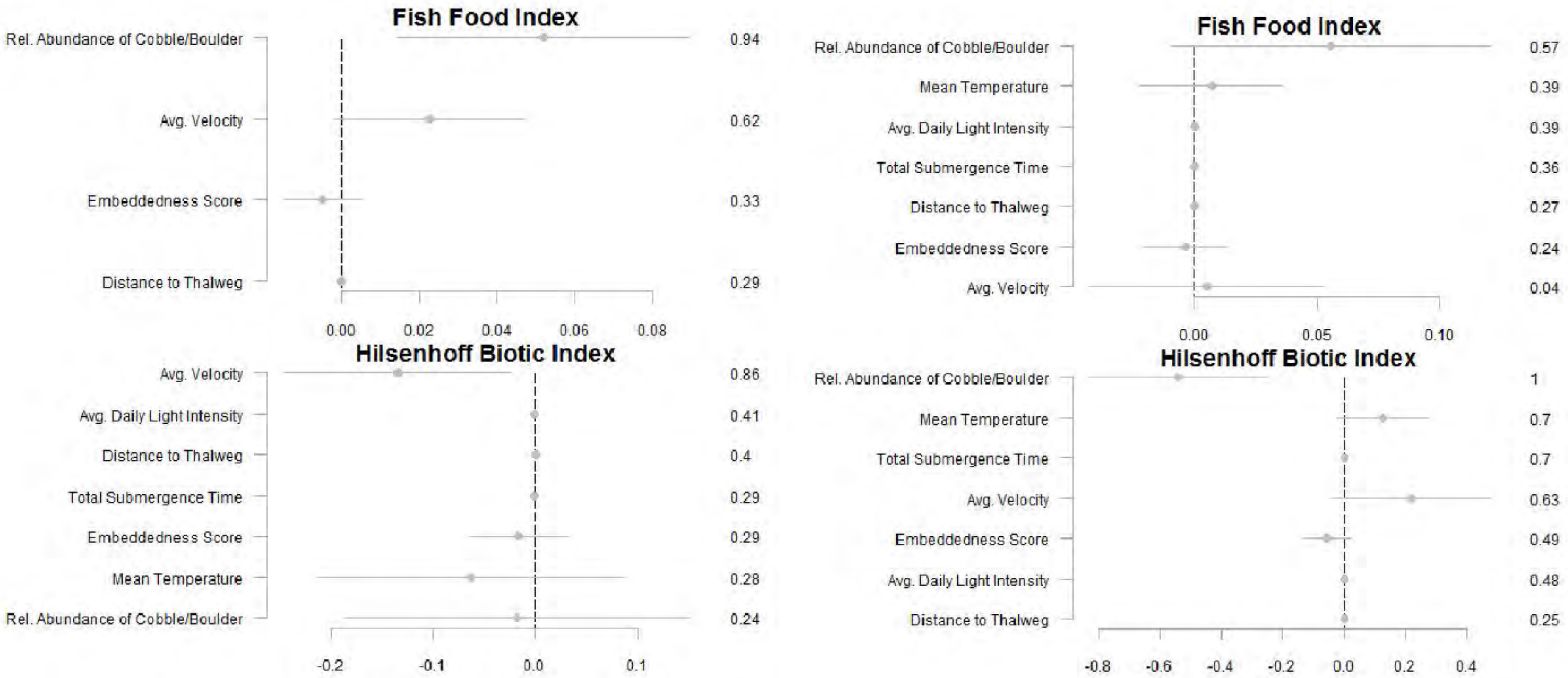


Figure 3-21: The coefficients and their 95% confidence limits of standardized explanatory variables of benthic production in the MCR. Benthic responses included abundance and biovolume for the fall (left) and spring (right). Explanatory variables included mean temperature, total submergence time, average daily light intensity, average velocity, embeddedness score, distance to thalweg, and the relative abundance of cobble/boulder substrates. Coefficients are standardized to allow direct comparisons of the direction and size of effects, noting that variables with confidence limits that encompass zero can have either a positive or negative effect depending upon which model is considered. Key explanatory variables are those that have a relative variable importance (RVI) of greater than 0.6/0.7 and the RVI is shown on the right hand side of each figure.

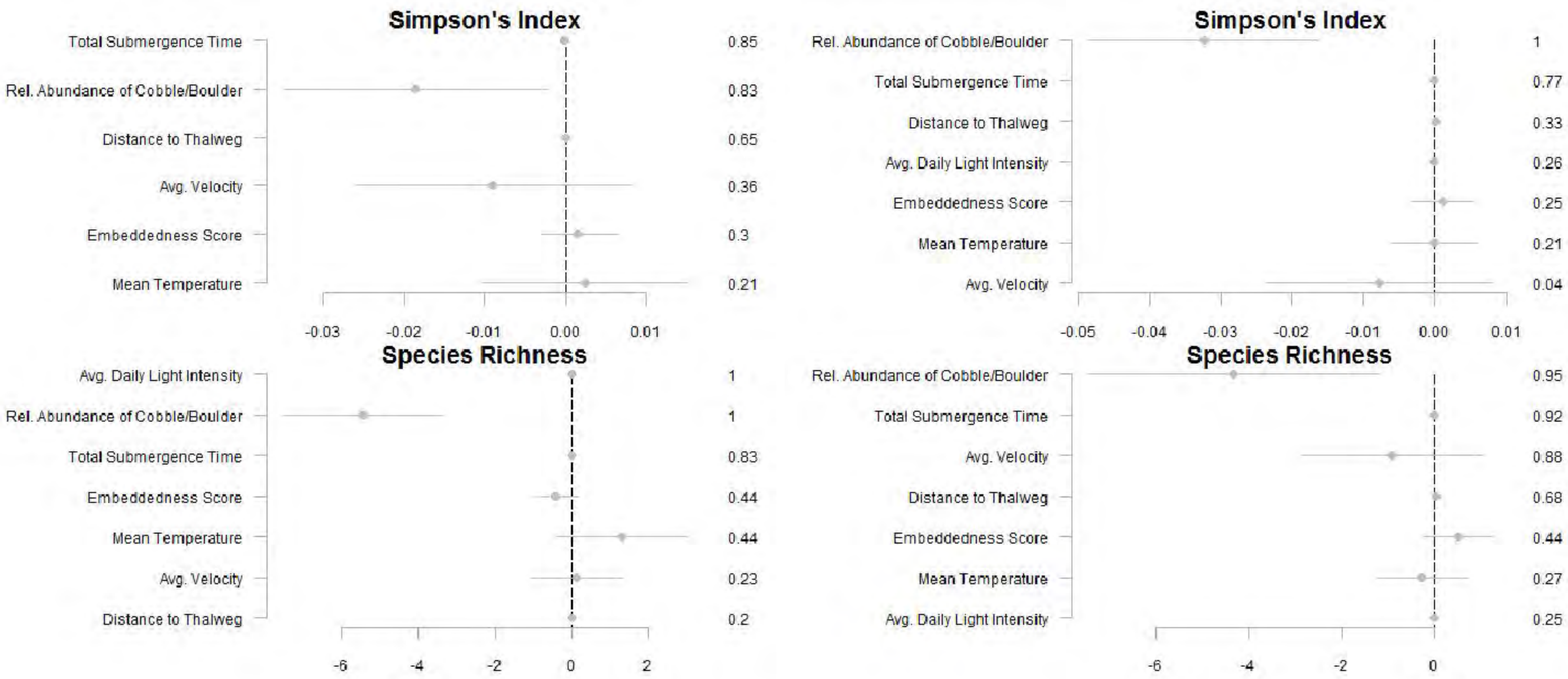


Figure 3-22: The coefficients and their 95% confidence limits of standardized explanatory variables of benthic production in the MCR. Benthic responses included abundance and biovolume for the fall (left) and spring (right). Explanatory variables included mean temperature, time in the light and water, average **daily light intensity, average velocity, embeddedness score, distance to thalweg, and the relative abundance of cobble/boulder substrates. Coefficients are standardized to allow direct comparisons of the direction and size of effects, noting that variables with confidence limits that encompass zero can have either a positive or negative effect depending upon which model is considered. Key explanatory variables are those that have a relative variable importance (RVI) of greater than 0.6/0.7 and the RVI is shown on the right hand side of each figure.**

3.3.3.2 Fall and Spring Submerged River Transect

The model averaging exercise was re-run, but instead of including the entire river transect, only those sampler transects that were submerged 100% of the time were considered. Model averaging data for the fall indicated that there were numerous plausible models (those with an AICc<2.0) that could explain aspects of the MCR invertebrate metrics. The top models described a range of variance in the invertebrate metrics (Table 3-9). These models help us understand the main drivers of invertebrate production on zones in MCR wetted by minimum flows.

In the fall, invertebrate production in permanently submerged areas increased with light intensity and decreased with velocity. Invertebrate abundance also increased with increasing embeddedness. In contrast, the abundance of EPT taxa and *Chironomidae* increased with increasing velocity (Figure 3-23 to Figure 3-26).

In the spring, invertebrate density increased with light intensity and decreased with velocity, while EPT abundance and percent *Chironomidae* decreased with increasing velocity which is , the opposite of the trend observed in the fall.

Substrates and other physical parameters such as distance to thalweg appeared to play a role in benthic community establishment in permanently submerged areas, but the influence was variable between season and more data is required determine the overall relative importance of these factors compared to velocity or light intensity.

In summary, it appears the invertebrate density is greater in areas of higher light intensity and lower velocity. These sites typically occur at T2 locations, adjacent to the deeper, faster T1 locations.

Table 3-9: Summary of the number of plausible models identified using model averaging (those with a ΔAIC <2) and the range of pseudo R^2 values for selected models for samplers across all transects.

MCR - Submerged Transect	Fall		Spring	
Invertebrate response metric	# of plausible models	range of pseudo R^2	# of plausible models	range of pseudo R^2
abundance	4	0.89-0.90	3	0.54-0.64
biomass	5	0.87	7	0.03-0.12
EPT Abundance	7	0.36-0.46	10	0.08-0.21
% Chironomidae	7	0.36-0.40	10	0.05-0.21
Fish Food Index	4	0.36	5	0.21-0.39
Hilsenhoff Biotic Index	5	0.56-0.57	6	0.01-0.04
Simpson's Index	5	0.18-0.20	2	0.21-0.26
species richness	4	0.74-0.75	4	0.34-0.40

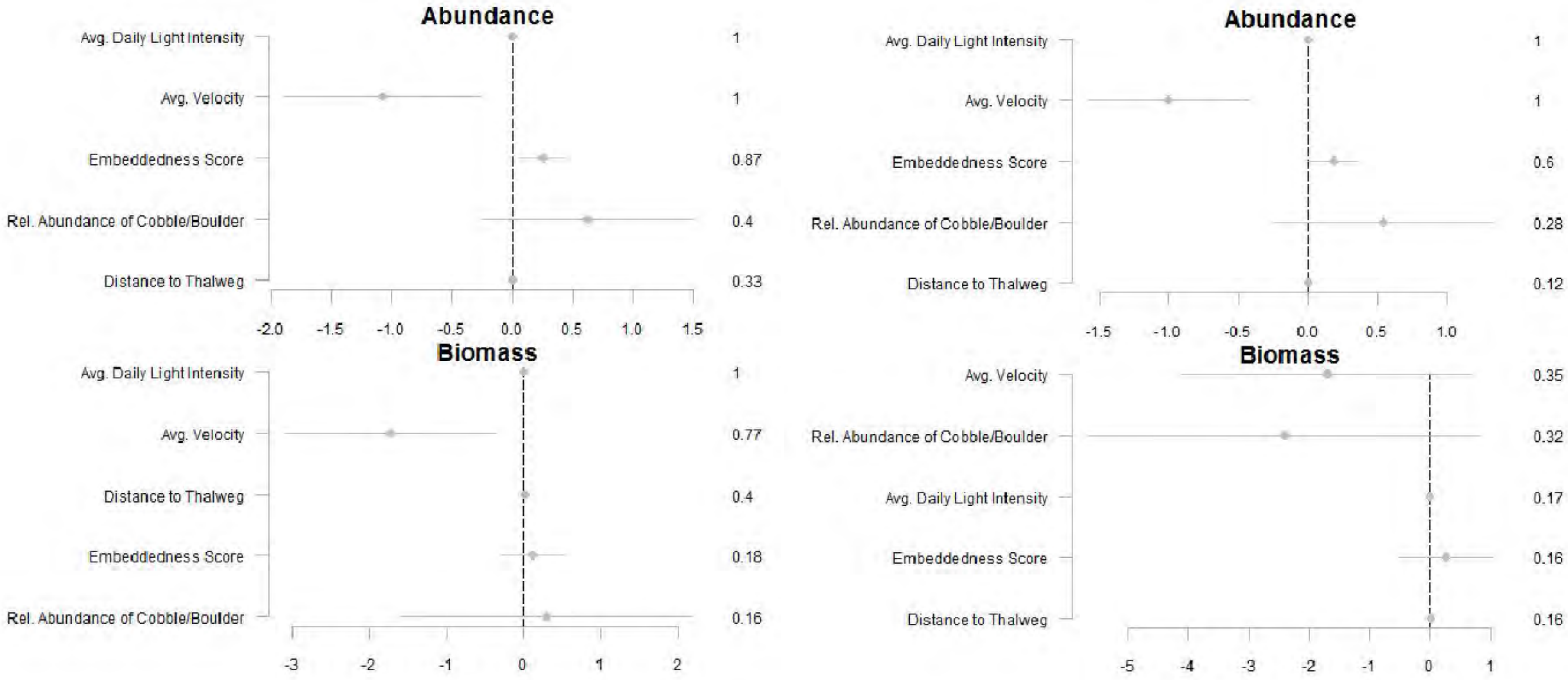


Figure 3-23: The coefficients and their 95% confidence limits of standardized explanatory variables of benthic production in the MCR. Periphyton responses included abundance and biomass for the fall (left) and spring (right). Explanatory variables included mean temperature, total submergence time, average daily light intensity, average velocity, embeddedness score, distance to thalweg, and the relative abundance of cobble/boulder substrates. Coefficients are standardized to allow direct comparisons of the direction and size of effects, noting that variables with confidence limits that encompass zero can have either a positive or negative effect depending upon which model is considered. Key explanatory variables are those that have a relative variable importance (RVI) of greater than 0.6/0.7 and the RVI is shown on the right hand side of each figure.

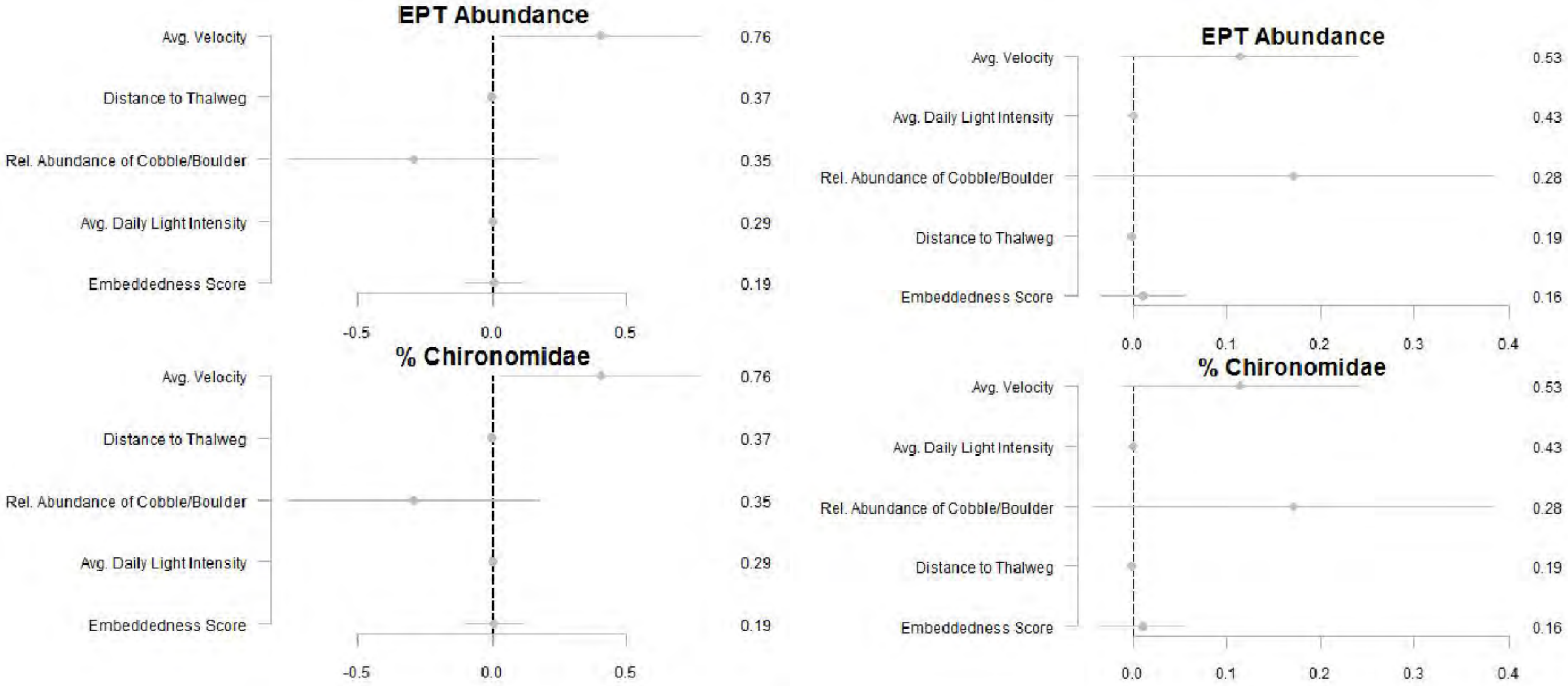


Figure 3-24: The coefficients and their 95% confidence limits of standardized explanatory variables of benthic production in the MCR. Benthic responses included abundance and biovolume for the fall (left) and spring (right). Explanatory variables included mean temperature, total submergence time, average daily light intensity, average velocity, embeddedness score, distance to thalweg, and the relative abundance of cobble/boulder substrates. Coefficients are standardized to allow direct comparisons of the direction and size of effects, noting that variables with confidence limits that encompass zero can have either a positive or negative effect depending upon which model is considered. Key explanatory variables are those that have a relative variable importance (RVI) of greater than 0.6/0.7 and the RVI is shown on the right hand side of each figure.

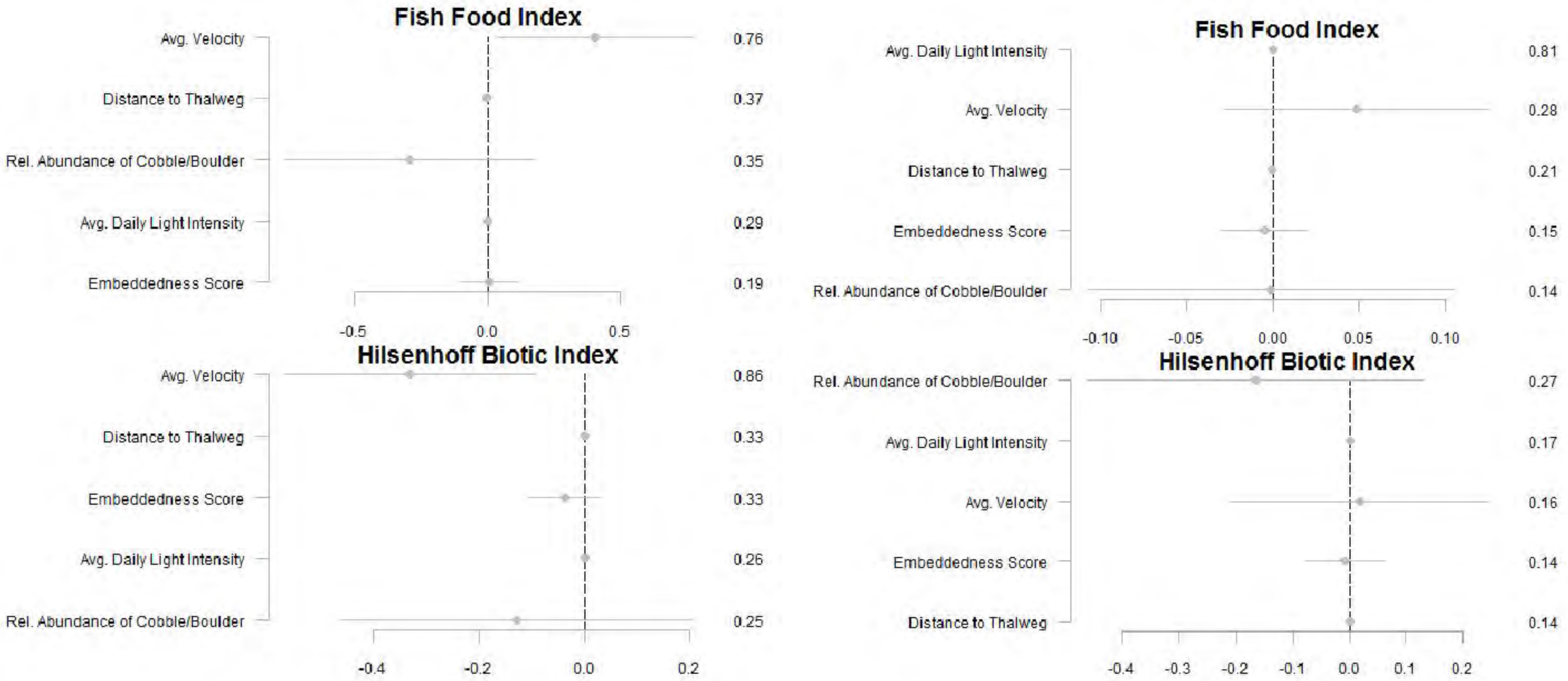


Figure 3-25: The coefficients and their 95% confidence limits of standardized explanatory variables of benthic production in the MCR. Benthic responses included abundance and biovolume for the fall (left) and spring (right). Explanatory variables included mean temperature, total submergence time, average daily light intensity, average velocity, embeddedness score, distance to thalweg, and the relative abundance of cobble/boulder substrates. Coefficients are standardized to allow direct comparisons of the direction and size of effects, noting that variables with confidence limits that encompass zero can have either a positive or negative effect depending upon which model is considered. Key explanatory variables are those that have a relative variable importance (RVI) of greater than 0.6/0.7 and the RVI is shown on the right hand side of each figure.

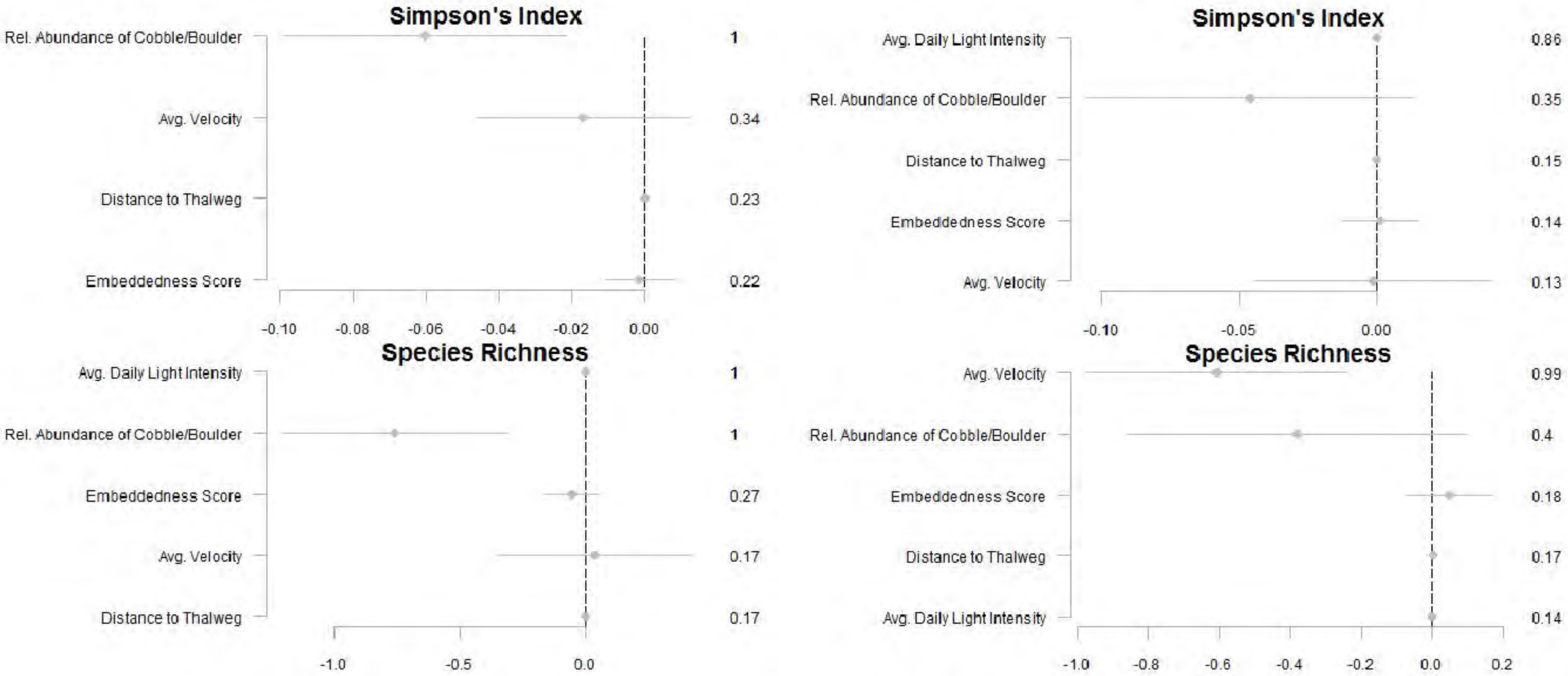


Figure 3-26: The coefficients and their 95% confidence limits of standardized explanatory variables of benthic production in the MCR. Benthic responses included abundance and biovolume for the fall (left) and spring (right). Explanatory variables included mean temperature, time in the light and water, average daily light intensity, average velocity, embeddedness score, distance to thalweg, and the relative abundance of cobble/boulder substrates. Coefficients are standardized to allow direct comparisons of the direction and size of effects, noting that variables with confidence limits that encompass zero can have either a positive or negative effect depending upon which model is considered. Key explanatory variables are those that have a relative variable importance (RVI) of greater than 0.6/0.7 and the RVI is shown on the right hand side of each figure.

4.0 DISCUSSION

4.1 Overview of MCR Habitat Zones and Conditions

Like all regulated rivers, periphyton and benthic invertebrate components of the MCR benthic community 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 ongoing to determine the effects of minimum flows and REV 5 flows. The key objective of the 142 m^3/s minimum flow strategy is to enhance the productivity and diversity of benthic communities in the MCR by increasing the permanently wetted area by an estimated 32–37% (Golder 2012). This discussion summarizes the findings from the 2007 to 2013 field surveys and subsequent analyses.

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

The 2007-2013 data suggests that benthic communities in the MCR occurred in three large zones created by the operating regime over the preceding 30 to 70 days. First, there were permanently submerged areas that were sampled at T1 (thalweg, mid channel) and T2 (channel edge at minimum flow) transect locations. These permanently wetted habitats functioned like those in other large rivers, with physical habitat attributes such as velocity, light, substrate stability and water temperature controlling periphyton and invertebrate community structure and productivity. MCR data suggests that within these areas wetted by minimum flows, densities and biomass of both periphyton and invertebrate communities mimicked those of a more natural large river system that is oligotrophic or stressed (Table 4-1). Similar to most large rivers, MCR periphyton production in permanently wetted areas was negatively correlated with velocity and substrate embeddedness, and positively correlated with increasing light intensity and substrate size. Peak production occurred near the edge of the permanently wetted channel at T2 locations where shear stress was less, light penetration was greater, substrates were stable, and the effects of scour and saltation were not as pronounced as they were near the thalweg at T1 locations. Furthermore, time series data suggests that extreme high flow events that generated velocities in excess of 2 m/s coincided with thinning of the periphyton community in the T1 thalweg zones. These high velocities were theoretically sufficient to cause shearing of filamentous algae (Flinders and Hartz 2009), and to mobilize sand particles that cause further periphyton thinning through abrasion (Gregory et al. 1991; Goudie 2006; Luce et al. 2010). Prolonged high flows in 2012 increased water velocity in the narrower Reach 4 channel, which coincidentally had lower periphyton accrual than in Reach 3. 2012 had the highest flows of this study, and their adverse effect on periphyton production suggests that flows equal to or exceeding the 2012 frequency and magnitude can significantly impact MCR productivity, particularly in the thalweg.

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 our T3-T4 sampler locations. The width of the productive area in the lower varial zone varied depending upon the BC Hydro operating regime and the channel morphology at any given location. The fluctuations between submergence and exposure usually occurred at night and resulted in less desiccation than the equivalent exposure period in daylight hours (Self and Larratt, 2013; Vincent 2007). Further, these areas were submerged during moderate flow events (between 600 to 800 m^3/s), which occurred more frequently than higher flow events. The heterotrophic components of the biofilm can continue growing in damp substrates in the dark, while the photosynthetic components cannot, resulting in greater heterotrophic contributions to overall production. The invertebrate community underwent periods of growth and decline depending on how the recent operating regime concided with their life cycles. Not unexpectedly, the variable hydrologic conditions of MCR tended to select for rapid colonizers and rapid reproducers, resulting in high biomass communities of diatoms and filamentous green algae where nutrient conditions allow (Biggs 2000; Biggs and Kilroy 2000). The lower varial zone is productive and an important component of the overall productivity of MCR. However, the time series accrual rate at T3 positions was significantly slower than T1 positions during most seasons and years. Our modelling data demonstrated that 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.

The third habitat unit found in the MCR was the upper varial zone, located in the frequently dewatered area and typified by our T5 through T7 locations. It was less productive than the lower varial zone because its productivity was curtailed by 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. Periphyton production halted when the substrates were dewatered during the day because normal cell processes couldn't continue and desiccation stress reduced survival. The upper varial zone became more heterotrophic as the frequency or duration of drying events increased. This finding is also supported by the importance of frequency of 12-hour submergence events and total incubation time in the water and light, identified in modelling data for the periphyton autotrophic index in previous years (Schleppe et al., 2013).

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

The boundaries between these zones were dynamic, and depended upon the average flow regime during the preceding 30-70 days, based on our time series data. Growth within these zones occurred rapidly until least 6 months (Table 4-1), provided conditions were appropriate for benthic community development. The width of the productive lower varial zone was expanded by stable flows in the 400 to 800 m^3/s range. The ever-changing hydrologic patterns in the varial zone induced a benthic invertebrate community that was in a constant state of recovery following periods of exposure of >48 consecutive hours. Further, invertebrate recovery after a catastrophic event could take several weeks or more and was dependent upon the life-stage of the invertebrates at the time of the event. 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 and extracellular mucilage. Even with these strategies, the rate of desiccation can exceed the rate at which these structures can be produced, particularly during daytime drying (Stanley et al. 2004). Periphyton species that do not have strategies capable of allowing them to withstand repeated exposure would presumably become eliminated from the varial zones of MCR, resulting in the observed homogeneity of the periphyton community structure throughout the varial zone. Such pressures on the invertebrate and periphyton communities are common to all large rivers, however, BC Hydro operations create a larger, and more dynamic varial zone in the MCR than would otherwise be expected.

For many reasons, the rates of de-watering influence the mode of periphyton and benthic invertebrate recovery. 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). Periphyton originating from the Revelstoke Reservoir is therefore expected to be important to periphyton recovery, as our fall 2013 data suggests, while drift of invertebrates from tributaries is expected to be important to benthic invertebrate recovery in MCR.

The rate at which periphyton biofilms recover is dependent on their complexity. Biofilm bacteria are capable of division every 20-30 minutes and cyanobacteria every 6 – 24 hours. Five hours of saturating light per day can support a diatom division every 2-3 days in summer and every 4-6 days in winter (Capblanco and Decamps 1978; DeRuyter van Steveninick et al. 1992; Gosselain et al. 1994) As a result, bacteria can colonize natural and artificial surfaces within a few hours (Gerchakov et al., 1976; Fletcher, 1980; Dempsey, 1981), while diatoms and other microbes immigrate onto substrates within a day to several weeks (Cundell and Mitchell 1977; Colwell et al. 1980; Hoagland et al. 1993).

Most of the artificial substrate periphyton data collected to date indicate that the MCR is moderately productive. However, the open-celled Styrofoam used in these trials may exaggerate production from 20% (Perrin et al. 2004) to as much as 400% (median = 200%) based on our preliminary natural substrate samples from the upper varial zone (Schleppe et al. 2013). If the artificial sampler data are corrected by the median potential inflation of periphyton production, the corrected results suggest that MCR production is consistent with an oligotrophic or stressed river system (Table 4.1). Furthermore, the natural substrate samples had far higher proportions of cyanobacteria, particularly in the sand from the cobble interstices in Reach 4. The natural cobble samples also had higher proportions of the slower-growing filamentous green algae than the comparable artificial substrate samplers. Other researchers have found a similar under-representation of these algae groups on artificial substrates (Cattaneo and Amireault 1992).

Table 4-1: Summary of typical MCR periphyton metrics from spring and fall 2010 - 2013, with comparison to oligotrophic, typical, and productive large rivers

Metric	**Oligotrophic or stressed**	**Typical large rivers**	**Eutrophic or productive**	**MCR (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+)	0.04 – 4.1 **(0.59-2.0)**
Algae density cells/cm^2	<0.2 x10^6	1 - 4 x10^6	>1 x10^7	<0.02 – 1.5 x10^6 **(0.9 – 13.1x10^6)**
Algae biovolume cm^3/m^2	<0.5	0.5 – 5	20 - 80	0.03 - 10 **(0.6 - 5.9)**
Diatom density frustules/cm^2	<0.15 x10^6	1 - 2 x10^6	>20 x10^6	<0.01 – 0.6 x10^6 **(0.2-1.0 x10^6)**
Biomass –AFDW mg/cm^2	<0.5	0.5 – 2	>3	0.12 – 4.8 **(0.35-3.5)**
Biomass –dry wt mg/cm^2	<1	1 – 5	>10	0.7 – 80 **(6-99)**
Organic matter (% of dry wt)		4 – 7		1 – 10 **(2-7)**
Bacteria count sediment. HTPC CFU/cm^2	<4 -10 x10^6	0.4 – 50 ×10^6	>50×10^6 – >10^{10}	0.2 – 5 x10^6
Bacteria count water CFU/mL	0.1 – 10 x10^4	0.1 – 100 x10^5	2.4 x10^7	Not sampled
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	0.001 - 0.1 shallow; 0.005 - 0.38 deep

Comparison data obtained from Flinders and Hartz 2009; Biggs 1996; Peterson and Porter 2002; Freese et al. 2005; Durr and Thomason 2009; Romani 2010; Biggs and Close 2006.

In summary, an oligotrophic or stressed river is expected to have <20 – 40 species richness (Table 4.1), whereas MCR had 5 - 52 species per sample. This suggests that species richness in MCR was lower than is typical for large rivers.

4.2 Overview of Benthic Communities

The physical habitat condition on the MCR created three spatial zones of productivity during the study period: 1) those that are permanently submerged, 2) those in the lower varial zone, and 3) those in the upper varial zone. Despite the establishment of three distinct benthic communities with variable dominant species, both periphyton and invertebrate communities were relatively stable when viewed at the family taxonomic level. Benthic communities also followed annual and seasonal patterns of growth. Periphyton production metrics measured in the spring were all less than half of the fall deployments. We expect this is because night outages exposed both the upper and lower varial zone substrates to freezing temperatures, and because low water temperatures reduce enzymatic activity and slow growth even in the rapidly reproducing bacterial biofilm (Wetzel 2001). The MCR benthic community structure is stable but is still subject to seasonal variation, in addition to habitat condition over the preceding 2 to 6 months.

MCR periphyton communities were dominated by diatoms representing between 85 and 95% of the biovolume at all sample sites. Other species, such as filamentous green algae were more prevalent near the edge of permanently wetted areas (T2), and in the lower varial zone (T3/T4) where stable substrates were present. The small-celled flagellates, cyanobacteria, and colonial greens were numerous but rarely exceeded 1.5% of the biovolume in MCR samples. Finally, in upper varial zone areas, periphyton communities transitioned from "producers" to "consumers", as indicated by the Autotrophic Index at T5/T6 locations. AFDW (volatile solids) results have dropped steadily from fall 2010 to fall 2013, suggesting a progressive loss of consumers or detritus not seen in the other periphyton growth metrics that focus on photosynthetic members. If this trend is genuine, and our field observations of reduced black banding suggests it is, a decline in heterotrophic members of the biofilm may have occurred following the high 2012 flows.

Benthic invertebrate communities were also dominated by those that are more tolerant of disturbance, such as chironomids (Tonking et al. 2009) which are often overrepresented in regulated rivers (e.g., Orthoclad chironomids (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. Although the major taxonomic group contributions of periphyton and benthic taxa remained the same, the dominant species were variable with annual BC Hydro operations, weather conditions (e.g., freezing temperatures during night time low flows or hot weather and lower flows during daylight hours), and other prevailing MCR conditions.

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

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

In MCR, the total area of productive habitat in these three zones depends upon more than just minimum flows. The effectiveness of minimum flows at increasing the area of productive benthic habitat was difficult to determine given the highly variable flow regime, variable episodes of ALR backwatering and the timing of benthic life cycles and flow releases. Despite difficulties in determining the exact benefits in spatial area of productive habitats attributable to minimum flows, we conclude that minimum flow increased the spatial area of productive habitat because it provided a minimum wetted habitat area that is productive.

4.4 Effects of Minimum Flows on Periphyton and Accrual (Q#1 & Q#3) – Composition, distribution, abundance and biomass of periphyton in areas subjected to minimum flows, and determination of long term trends in benthic productivity in these areas

Historically, BC Hydro avoided daytime dewatering and this operating regime was implemented prior to the establishment of 142 m^3/s minimum flows. After the initiation of this study, the REV 5 turbine also came online. This means that we do not have clear before/after periods where we can study the benefits of minimum flows in isolation from other flow changes in MCR over the study period. We therefore contrasted production in the regularly dewatered varial zones with production in the permanently wetted zones to address questions 1 and3.

The benefits of minimum flows were most evident in the periphyton communities at T2 and T3 locations because these locations occur directly above or adjacent to the wetted edge at minimum flows. Peak production was most apparent at T2 locations because higher velocities at T1 thalweg locations had higher sheer stresses that reduced the periphyton community. However, productivity at T3 locations was similar to T2 locations under the current operating regime of nightly low flow periods with daytime high flows frequently exceeding 800 m^3/s. The lower varial zone (T3/T4) was an important productive area bounded by minimum flows and a mobile upper limit created by average daily submergence during the preceding 30 – 70 days. Unlike the permanently wetted zone, productivity in the lower varial zone was entirely dependent upon submergence caused by the recent operating regime. Extended minimum flow events in excess of one week would cause extensive periphyton losses in the lower varial zone and required a recovery period of several weeks with consistent submergence by flows greater than the 142 m^3/s minimum. Productivity of the frequently dewatered upper varial zone (T5/T6) was consistently less than half of the high productivity zones.

These data suggest that MCR periphyton communities may be more dependent upon the overall operating regime (daily, monthly, and annual patterns of flow release, ALR backwatering, etc.) than the specific effects of minimum flow because the normal operating regime determined the wetted edge of the channel during daytime periods, a key explanatory variable in our modelling data.

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

The effects of season and peak flows were also important when considering the benefits of minimum flows. Minimum flows were particularly advantageous during the fall when rates of periphyton recovery were highest, while the benefits were less evident in the winter/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 MCR occurred at slow rates similar to other large oligotrophic rivers (Table 4.1). The combined time series data collected across year, season and river depth suggest that accrual on MCR continued linearly to the end of the 46-51 day deployment period. Therefore, incubation periods of greater than 46 days are required to achieve peak periphyton biomass in MCR. Limited six month MCR deployments indicated that peak biomass in the varial zone required many months to accrue. Since periphyton communities can take from weeks in mesotrophic and eutrophic habitats to as many as three years in oligotrophic habitats to stabilize following a change in flow regime (Wu et al. 2009; Biggs 1989), assessing the overall effects of minimum flow in MCR will take years to fully understand. Further, the daily, weekly, and yearly patterns of operation, Arrow Lakes Reservoir backwatering, and seasonal growth cycles can all affect accrual. Although improved periphyton production stemming from the implementation of minimum flows is already occurring, it will be 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 backwaters and back-eddies as a source of recruitment and maintenance of some planktonic and periphytic species cannot be doubted (Reynolds and Descy 1996). Similarly, many researchers have concluded that shallows with lower velocities also act as important areas for periphyton recruitment (Butcher 1932; Reynolds and Descy 1996). Thus, back-water and Big Eddy areas of MCR that retain water for longer, but still undergo fluid exchange with the main flow, can act as reservoirs of periphyton inocula. These areas are more abundant in Reach 3 than in Reach 4, and may cause Reach 3 periphyton to recover faster after catastrophic flow events.

Patterns of periphyton accrual and recovery in MCR are further complicated by drifting limnoplankton exported by flows from Revelstoke Reservoir. Phytoplankton that becomes trapped in the periphyton matrix (Middleton 2010) can subsidize the periphyton for many kilometers below a dam (Doi et al 2008; Larratt et al. 2013). The distinction between periphyton that grow on surfaces and those that live a wholly planktonic existence is not clear-cut, but is blurred by species that can grow in either habit, and some limnoplankton can pass a benthic survival stage (Reynolds and Descy 1996). Contributions of phytoplankton to MCR periphyton may also occur from the Arrow Lakes Reservoir to Reach 3 during backwatering, but the few plankton hauls we have completed showed that the ALR phytoplankton was impoverished, likely by turbidity (Schleppe et al. 2012). Species contributed by Revelstoke Reservoir appeared to account for a significant proportion of the MCR periphyton, particularly in the fall. 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.

4.5 Effects of Minimum Flows on Benthic Invertebrates and Accrual (Q# 1 and Q#4)

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

However, MCR invertebrate models explained substantially less variation than periphyton models. This occurred for several reasons, including patchily distributed 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, and microhabitat factors that could not be accounted for in our analysis. Further, invertebrates are more sensitive to desiccation than periphyton (Schleppe et al. 2012; Golder 2012). Invertebrate habitat was probably more heavily influenced by periods of daytime exposure than periphyton because of their reduced tolerances to desiccation. The spatial area of the lower varial zone available to invertebrates was probably smaller than that of periphyton. For these reasons, explicitly determining the effectiveness of minimum flows on improving benthic conditions for invertebrates is difficult, but it is known that minimum flows benefited the invertebrate community and that dewatering of habitat had a direct, negative effect on benthic abundance, biomass, and community composition. The permanently wetted area can function as a source of benthic organisms to re-colonize previously exposed habitat areas after extensive low flow events lasting longer than 24 hours.

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

The area of productive MCR habitat is directly correlated with submergence. Our data suggest that the abundance, biomass, and overall availability of fish food (using the Fish Food Index and other benthic responses) were also directly dependent upon submergence. Fish food varies depending upon the species considered, and generally the EPT taxa and chironomids are the most important forage for fish. It is for this reason that we developed the fish food index, to consider how fish food availability may be affected for different fish foraging groups. Generally, any increase in wetted productive habitat should cause a subsequent increase in fish food availability. The overall fish food availability was greatest at T1 through T3 locations, and coincided with the areas identified as being the most productive benthic habitats in our models. For these reasons, minimum flows increased fish food availability, but other key influences on productivity such as frequency and duration of daytime submergence events must also be considered. When considering specific fish species, EPT taxa were most commonly observed in areas of boulder or cobble substrate, whereas overall benthic abundance was greatest at sites with finer substrates. This suggests that food for salmonids should be greatest within areas of larger substrates. Furhter analysis is required to understand all the dynamics of fish species, and fish food interactions and how they relate to the implementation of minimum flows.

4.7 Possible Alternate Flow Regimes to Enhance Productivity

Operating regimes which reduce the frequency of catastrophic drying may expand the highly productive lower varial zone in MCR. Before the December 2010 implementation of minimum flows, BC Hydro attempted to avoid zero discharge during daylight hours for ecological and social reasons (BC Hydro 1998).

Based on the artificial substrate results, areas experiencing daytime submergence for longer than 9 hours can maintain measures of periphyton production and diversity similar to areas permanently submerged by minimum flows. Thus, a small shift in water releases would increase the area of productive habitat, and could occur under an operating regime that included brief excursions to <10 m^3/s flow, provided that flows of 400 to 600 m^3/s occurred every day for at least 9 daytime hours. It is probable that there are many operating regimes that could benefit MCR production, but more data is required to assess the merits of alternate operating regimes.

Minimum flows management may not be as helpful to MCR productivity as avoiding dewatering the highly productive lower varial zone (T3/T4) in daytime outages, although more data is required to fully understand the interactions between BCH operating regimes and benthic productivity. The consequences of, and recovery from, substrate exposure are explored in Table 4-2. Operating regimes that reduce the frequency and duration of catastrophic drying events could be more beneficial than always maintaining minimum flows. It may be possible to conserve minimum flow water during periods where backwatering extends through the MCR, and then use the conserved water to maintain higher releases during daytime low flow periods at a later date, thereby increasing the size of the valuable lower varial zone.

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

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

Data obtained from this study 2010 – 2013; Usher and Blinn 1990; Angradi and Kubly 1993; and Blinn et al. 1995, Hodoki 2005

We further propose that the strongly selective variable submergence of MCR varial zone substrates limits algae diversity, and provision of a stable flow regime would allow a more varied flora, including species with slower rates of reproduction. Furthermore, even in areas that are covered by minimum flows, an abrupt increase in the underwater light field can induce photoinhibition in some diatoms and exacerbate diatom loss to increased shear. Many of the species found in the T1 thalweg locations have adaptations allowing them to thrive under light-deficient regimes such as increased pigment density or flattened shape. They may experience photoinhibition when minimum flows occur during the day. This will favour species that are photo-adaptive, such as the pennate diatoms that currently dominate in MCR. Therefore, both the varial zones and the thalweg areas covered by minimum flows could benefit from stable flows in excess of minimum flows during the day, particularly when ALR back-watering is not present to protect the upper varial zones of Reach 3.

5.0 RECOMMENDATIONS

5.1 Review of Previously Recommended Project Directions

Table 5.1: Previously Recommended Project Directions and Actions Completed in 2013

Recommendations from earlier CLBMON 15b Reports	Project Action in 2013
A spatial model of productivity should be developed	Further data from 2013 confirmed that development of a spatial model is feasible
Compare natural substrate adjacent to T4-6 samplers to develop adjustment factor	Not possible with current budget structure
Study *in situ* desiccation and recovery of benthics on natural substrates	Not possible with current budget structure
Conduct in-stream nutrient assay	Not possible with current budget structure

5.2 Recommended Work Program Elements

The following are recommendations for consideration as part of the longer-term CLBMON15b work program.

- Collect a series of plankton hauls during the fall deployment and retrieval from the top of Reach 4 to the bottom of Reach 3 to track how fast the limnoplankton from Revelstoke Reservoir settle and augment MCR periphyton. This would involve a total of 30 samples, with three collected at 10 locations between Reach 4 and 3.
- Spring sampling is not proposed for 2014. However, our data strongly suggest an influence of season on productivity. Thus, sampling during the spring is likely necessary to better understand the effects of minimum flow on benthic productivity.
- Finally, to develop a full spatial model of the MCR, sampling during the spring, and winter will be necessary to elucidate the effects of season, and to ultimately predict the benefits of minimum flow or other operational regimes on productivity within the MCR.

6.0 REFERENCES

Anderson, D. R. (2008). *Model Based Inference in the Life Sciences: A Primer on Evidence*. *Biometrics* (Vol. 64, p. 184). Springer. doi:10.1111/j.1541-0420.2008.01138_13.x

Angradi, T. R., & Kubly, D. M. (1993). Effects of atmospheric exposure on chlorophyll a, biomass and productivity of the epilithon of a tailwater river. *Regulated Rivers: Research & Management*, *8*(4), 345–358. doi:10.1002/rrr.3450080405

Barton, K. (2009). MuMIn – multi-model inference (An R statistical package). Retrieved from http://r-forge.r-project.org/projects/mumin/

Barton, K. (2012). MuMIn: Multi-model inference. R package version 1.7. 7. Retrieved from http://r-forge.r-project.org/projects/mumin/

BC Hydro. (1998). System Operating Order No. 4P-30, Revelstoke Project Prepared by BC Hydro Power Facilities.14 p

BC Hydro. (2005). *Consultative Committee Report: Columbia River Water Use Plan, Volumes 1 and 2. Report prepared for the Columbia River Water Use Plan Consultative Committee*. Burnaby, BC.

BC Hydro. (2006). *Revelstoke Unit 5 Project Environmental Assessment Certificate Application. Volume 1: Supplemental Information Report*.

BC Hydro. (2010). *Columbia River Water Use Plan – Revelstoke Flow Management Plan; Monitoring Program Terms of Reference Resubmission; Monitoring Program No. CLBMON-15b: Middle Columbia River Ecological Productivity Monitoring. Reference #RFP-385.*

Benke, A. C., Huryn, A. D., Smock, L. A., & Wallace, J. B. (1999). Length-mass relationships for freshwater macroinvertebrates in North America with particular reference to the southeastern United States. *Journal of the North American Benthological Society*, *18*(3), 308–343. doi:10.2307/1468447

Biggs, B. (2000). *New Zealand periphyton guideline: detecting, monitoring and managing enrichment of streams*. *Ministry for the Environment Wellington*.

Biggs, B. J. F. (2000). *Stream periphyton monitoring manual. NIWA*. Ministry for the Environment, P.O. Box 8602. Christchurch, New Zealand.

Biggs, B. J. F., & Close, M. E. (1989). Periphyton biomass dynamics in gravel bed rivers: the relative effects of flows and nutrients. *Freshwater Biology*, *22*(2), 209–231. doi:10.1111/j.1365-2427.1989.tb01096.x

Blinn, W., Shannon, J., Stevens, L., & Carder, J. (1995). Consequences of fluctuating discharge for lotic communities. *Journal of North American Benthological Society*, *14*(2), 233–248. Retrieved from http://www.jstor.org/stable/10.2307/1467776

Bunn, S. E., & Arthington, A. H. (2002). Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. *Environmental Management*, *30*(4), 492–507. Retrieved from http://www.springerlink.com/openurl.asp?genre=article&id=doi:10.1007/s00267-002-2737-0

Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: a practical information-theoretic approach*. (Springer-Verlag, Ed.)*Ecological Modelling* (Vol. 172, p. 488). Springer. doi:10.1016/j.ecolmodel.2003.11.004

Butcher, G. A. (1992). *Ambient Water Quality Objectives For The Lower Columbia River Hugh Keenleyside Dam To Birchbank : Overview Report*. Retrieved from http://www.env.gov.bc.ca/wat/wq/objectives/birchbank/birchbank.html

Capblanco, J., & Decamps, H. (1978). Dynamics of the phytoplankton of the River Lot. *Vehr. Int. Verein. Limnol.*, *20*, 1479–1484.

Cattaneo, A., & Amireault, M. C. (1992). How artificial are artificial substrata for periphyton? *Journal of the North American Benthological Society*, *11*(2), 244–256. Retrieved from http://www.jstor.org/stable/1467389

Colwell, R. R., Belas, M. R., Zachary, A., Austin, B., & Allen, D. (1980). Attachment of microorganisms to surfaces in the aquatic environment. *Devel. Indust. Microbiol.*, *21*, 169–178.

Cox, D., & Snell, E. (1989). Analysis of binary data. 2nd. *London: Chapman and Hall*.

Cundell, A. M., & Mitchell, R. (1977). Microbial succession on a wooden surface exposed to the sea. *Int. Biodeterior. Bull.*, *13*(3), 67–73.

De Ruyter van Steveninck, E. D., Admiraal, W., Breebaart, L., Tubbing, G. M. J., & van Zanten, B. (1992). Plankton in the River Rhine: structural and functional changes observed during downstream transport. *Journal of Plankton …*. Retrieved from http://plankt.oxfordjournals.org/content/14/10/1351.short

Doi, H. (2009). Spatial patterns of autochthonous and allochthonous resources in aquatic food webs. *Population Ecology*. doi:10.1007/s10144-008-0127-z

Doi, H., Chang, K.-H., Ando, T., Imai, H., Nakano, S., Kajimoto, A., & Katano, I. (2008). Drifting plankton from a reservoir subsidize downstream food webs and alter community structure. *Oecologia*, *156*(2), 363–371. doi:10.1007/s00442-008-0988-z

Dürr, S., & Thomason, J. (2009). *Biofouling*. New York: John Wiley and Sons.

Fernandes, V. O., & Esteves, F. A. (2003). The use of indices for evaluating the periphytic community in two kinds of substrate in Imboassica Lagoon, Rio de Janeiro, Brazil. *Brazilian Journal of Biology Revista Brasleira de Biologia*, *63*(2), 233–243. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/14509845

Fletcher, M. (1980). Adherence of marine micro-organisms to smooth surfaces. *Bacterial Adherence*. Retrieved from http://link.springer.com/chapter/10.1007/978-94-009-5863-0_11

Flinders, C. A., & Hart, D. D. (2009). Effects of pulsed flows on nuisance periphyton growths in rivers: a mesocosm study. *River Research and Applications*, *25*(10), 1320–1330. doi:10.1002/rra.1244

Freese, H. M., Karsten, U., & Schumann, R. (2006). Bacterial abundance, activity, and viability in the eutrophic River Warnow, northeast Germany. *Microbial Ecology*, *51*(1), 117–127. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/16395540

Gelman, A. (2008). Scaling regression inputs by dividing by two standard deviations. *Statistics in Medicine*, *27*(October 2007), 2865–2873. doi:10.1002/sim

Gerchakov, S., Marszalek, D., & Roth, F. (1976). Observations on Microfouling Applicable to OTEC Systems. Retrieved from http://oai.dtic.mil/oai/oai?verb=getRecord&metadataPrefix=html&identifier=ADA047302

Golder and Associates. (2012). *CLBMON-15a Mid-Columbia River Physical Habitat Monitoring. Annual Technical Report – 2011. Report No. 11-1492-0084* (p. 44). Castlegar, B.C.

Golder and Associates, ESSA Technologies, & Limnotek. (2012). *Baseline Aquatic Productivity in the Upper Peace River. Site C Clean Energy Project. Project Number: 10-1373-0028/3000.*

Gosselain, V., Descy, J.-P., & Everbecq, E. (1994). The phytoplankton community of the River Meuse, Belgium: seasonal dynamics (year 1992) and the possible incidence of zooplankton grazing. *Hydrobiologia*. doi:10.1007/BF00007419

Gregory, S., Swanson, F., McKee, W., & Cummins, K. (1991). An ecosystem perspective of riparian zones. *BioScience*, *41*(8), 540–551. Retrieved from http://www.jstor.org/stable/10.2307/1311607

Grueber, C. E., Nakagawa, S., Laws, R. J., & Jamieson, I. G. (2011). Multimodel inference in ecology and evolution: challenges and solutions. *Journal of Evolutionary Biology*, *24*(4), 699–711. doi:10.1111/j.1420-9101.2010.02210.x

Hoagland, K. (1983). Short-term standing crop and diversity of periphytic diatoms in a eutrophic reservoir. *Journal of Phycology*, *19*, 30–38. Retrieved from http://onlinelibrary.wiley.com/doi/10.1111/j.0022-3646.1983.00030.x/abstract

Hoagland, K. D., Rosowski, J. R., Gretz, M. R., & Roemer, S. C. (1993). Diatom Extracellular Polymeric Substances: Function, Fine Structure, Chemistry, and Physiology. *Journal of Phycology*, *29*(5), 537–566. doi:10.1111/j.0022-3646.1993.00537.x

Hodoki, Y. (2005). Bacteria biofilm encourages algal immigration onto substrata in lotic systems. *Hydrobiologia*. doi:10.1007/s10750-004-3082-5

Hynes, H. (1989). Keynote address. Proceedings of the international large river symposium. Canadian Special Publications of Fisheries and Aquatic Sciences 106. In D. Dodge (Ed.), (pp. 5–10).

Larratt, H., Schleppe, J., Olson-Russello, M., & Swain, N. (2013). *Monitoring Study No. CLBMON-44 (Year 5) Lower Columbia River Physical Habitat and Ecological Productivity, Study Period: 2012. Report Prepared for BC Hydro by Ecoscape Environmental Consultants Ltd.* (p. 96). Castlegar, B.C.

Lear, G., Turner, S. J., & Lewis, G. D. (2008). Effect of light regimes on the utilisation of an exogenous carbon source by freshwater biofilm bacterial communities. *Aquatic Ecology*, *43*(2), 207–220. doi:10.1007/s10452-008-9193-8

Luce, J. J., Cattaneo, A., & Lapointe, M. F. (2010). Spatial patterns in periphyton biomass after low-magnitude flow spates: geomorphic factors affecting patchiness across gravel–cobble riffles. *Journal of the North American Benthological Society*. doi:10.1899/09-059.1

Magee, L. (1990). R2 Measures Based on Wald and Likelihood Ratio Joint Significance Tests. *American Statistician*, *44*(3), 250–253. doi:10.2307/2685352

Middleton, R.G. (2010) Cattle access affects periphyton community structure in Tennessee farm ponds. Master's Thesis, University of Tennessee, 2010. http://trace.tennessee.edu/utk_gradthes/732

Nagelkerke, N. (1991). A note on a general definition of the coefficient of determination. *Biometrika*. Retrieved from http://www.cesarzamudio.com/uploads/1/7/9/1/17916581/nagelkerke_n.j.d._1991_-_a_note_on_a_general_definition_of_the_coefficient_of_determination.pdf

Neal, C., & Robson, A. J. (2000). A summary of river water quality data collected within the Land-Ocean Interaction Study: Core data for eastern UK rivers draining to the North Sea. *Science of the Total Environment*, *251-252*, 585–665.

Perrin, C. J., & Chapman, B. (2010a). *Columbia River Project Water Use Plan: Middle Columbia River Ecological Productivity Monitoring. Study Period: 2009. Golder Associates. Report No. 09-1480-0036* (p. 54).

Perrin, C. J., & Chapman, B. (2010b). *Middle Columbia River ecological productivity monitoring, 2009. Report Prepared by Golder Associates Ltd. and Limnotek Research and Development Inc. for BC Hydro* (p. 52).

Perrin, C. J., Korman, J., & Schmidt, D. (2004). *A monitoring protocol for benthic invertebrates and periphyton in the Middle and Lower Columbia River* (p. 59). Report prepared by Limnotek Research and Development Inc., Ecometric Research Ltd. and Golder Associates Ltd. for BC Hydro.

Peterson, C., & Jones, T. (2003). Diatom viability in insect fecal material: comparison between two species, Achnanthidium lanceolatum and Synedra ulna. *Hydrobiologia*. Retrieved from http://link.springer.com/article/10.1023/A:1026259403351

Peterson, D., & Porter, S. (2002). *Biological and chemical indicators of eutrophication in the Yellowstone River and major tributaries during August 2000*. Retrieved from http://wy.water.usgs.gov/projects/yell/nwqmc/

Piñeiro, G., Perelman, S., Guerschman, J. P., & Paruelo, J. M. (2008). How to evaluate models: Observed vs. predicted or predicted vs. observed? *Ecological Modelling*, *216*(3-4), 316–322. doi:10.1016/j.ecolmodel.2008.05.006

Plafkin, J., Barbour, M., & Porter, K. (1989). Rapid bioassessment protocols for use in rivers and streams: benthic macroinvertebrates and fish. *Washington DC: Office of …*.

R Development Core Team. (2008). *A language and environment for statistical computing.* Vienna, Austria: R Foundation for Statistical Computing. Retrieved from http://www.r-project.org

Reynolds, C., & Descy, J. (1996). The production, biomass and structure of phytoplankton in large rivers. *Large Rivers*. Retrieved from http://www.schweizerbart.de/papers/rs/detail/10/80138/The_production_biomass_and_structure_of_phytoplankton

Robinson C.T., Aebischer, S. & Uehlinger U. (2004). Immediate and habitat-specific responses of macroinvertebrates to sequential, experimental floods. Journal of the North American Benthological Society23(4):853-867.

Romaní, A. M. (2010) Freshwater Biofilms, in Biofouling (eds S. Dürr and J. C. Thomason), Wiley-Blackwell, Oxford, UK. doi: 10.1002/9781444315462.ch10

Sass, G. G., Carpenter, S. R., Gaeta, J. W., Kitchell, J. F., & Ahrenstorff, T. D. (2011). Whole-lake addition of coarse woody habitat: response of fish populations. *Aquatic Sciences*, *74*(2), 255–266. doi:10.1007/s00027-011-0219-2

Schleppe, J., Bio, R., Larratt, H., & Olson-Russello, M. (2011). *MIDDLE COLUMBIA RIVER ECOLOGICAL PRODUCTIVITY MONITORING* (CLBMON–15b ed.). Kelowna, B.C: Ecoscape Environmental Consultants Ltd. & Larratt Aquatic Consulting Ltd. Retrieved from http://www.bchydro.com/content/dam/hydro/medialib/internet/documents/planning_regulatory/wup/southern_interior/2011q3/clbmon-15b_yr4_2011-08-01.pdf

Schleppe, J., Bio, R., Larratt, H., & Olson-Russello, M. (2011). *MIDDLE COLUMBIA RIVER ECOLOGICAL PRODUCTIVITY MONITORING* (CLBMON–15b ed.). Kelowna, B.C: Ecoscape Environmental Consultants Ltd. & Larratt Aquatic Consulting Ltd. Retrieved from http://www.bchydro.com/content/dam/hydro/medialib/internet/documents/planning_regulatory/wup/southern_interior/2011q3/clbmon-15b_yr4_2011-08-01.pdf

Schleppe, J., Larratt, H., & Olson-Russello, M. (2012). *CLBMON-15b Middle Columbia River ecological productivity monitoring, annual report 2011. Ecoscape Environmental Consultants Ltd. & Larratt Aquatic. Ecoscape File No. 10-599*. Kelowna, B.C.

Schleppe, J., Larratt, H., & Olson-Russello, M. (2013). *CLBMON-15b Middle Columbia River ecological productivity monitoring, annual report 2012. Ecoscape Environmental Consultants Ltd. & Larratt Aquatic. Ecoscape File No. 10-599*. Kelowna, B.C.

Self, J., & Larratt, H. (2013). *Limiting the Spread of Aquatic Invasive Species into the Okanagan. Prepared for the Okanagan Basin Water Board and the Glenmore-Ellison Improvement District* (p. 84). Retrieved from http://www.obwb.ca/fileadmin/docs/2013_obwb_ais_report.pdf

Smock, L. A. (1980). Relationships between body size and biomass of aquatic insects. *Freshwater Biology*, *10*(4), 375–383. doi:doi: 10.1111/j.1365-2427.1980.tb01211.x

Stanley, E. H., Fisher, S. G., & Jones, Jr., J. B. (2004). Effects of water loss on primary production: A landscape-scale model. *Aquatic Sciences - Research Across Boundaries*. doi:10.1007/s00027-003-0646-9

Stockner, J., & F.A.J., A. (1971). Periphyton of the Experimental Lakes Area. *Journal of the Fisheries Research Board of Canada*, *28*, 215–229.

Stockner, J. G. (1991). Autotrophic picoplankton in fresh-water ecosystems - the view from the summit. *Internationale Revue Der Gesamten Hydrobiologie*, *76*(4), 483–492. Retrieved from <Go to ISI>://A1991HE11500001

Tonkin, J. D., Death, R. G., & Joy, M. K. (2009). Invertebrate drift patterns in a regulated river: dams, periphyton biomass or longitudinal patterns? *River Research and Applications*, *25*(10), 1219–1231. doi:10.1002/rra.1213

Usher, H., & Blinn, D. (1990). Influence of various exposure periods on the biomass and chlorophyll-a of Cladophora glomerata (Chlorophyta). *Journal of Phycology*. Retrieved from http://onlinelibrary.wiley.com/doi/10.1111/j.0022-3646.1990.00244.x/abstract

Vincent, W. (2007). Cold tolerance in cyanobacteria and life in the cryosphere. *Algae and Cyanobacteria in Extreme Environments*. Retrieved from http://link.springer.com/chapter/10.1007/978-1-4020-6112-7_15

Wetzel, R. (2001). *Limnology: lake and river ecosystems* (3rd ed.). New York: Academic Press.

Wetzel, R. G., & Likens, G. E. (1991). *Primary Productivity of Phytoplankton. Limnological Analysis* (pp. 207–226). Springer.

Wu, N., Tang, T., Zhou, S., Jia, X., Li, D., Liu, R., & Cai, Q. (2009). Changes in benthic algal communities following construction of a run-of-river dam. *Journal of the North American Benthological Society*. doi:10.1899/08-047.1

Zuur, A. F., Leno, E. N., Walker, N. J., Saveliev, A. A., & Smith, G. M. (2009). *Mixed effects models and extensions in ecology with R*. New York: Springer Science. Retrieved from http://books.google.com/books?hl=en&lr=&id=vQUNprFZKHsC&oi=fnd&pg=PA1&dq=mixed+effects+models+and+extension+in+ecology&ots=kaxItP4HXp&sig=zfaOaGTw9Ug4YT5Tp7oobf_VKn4

APPENDIX A DATA TABLES AND FIGURES

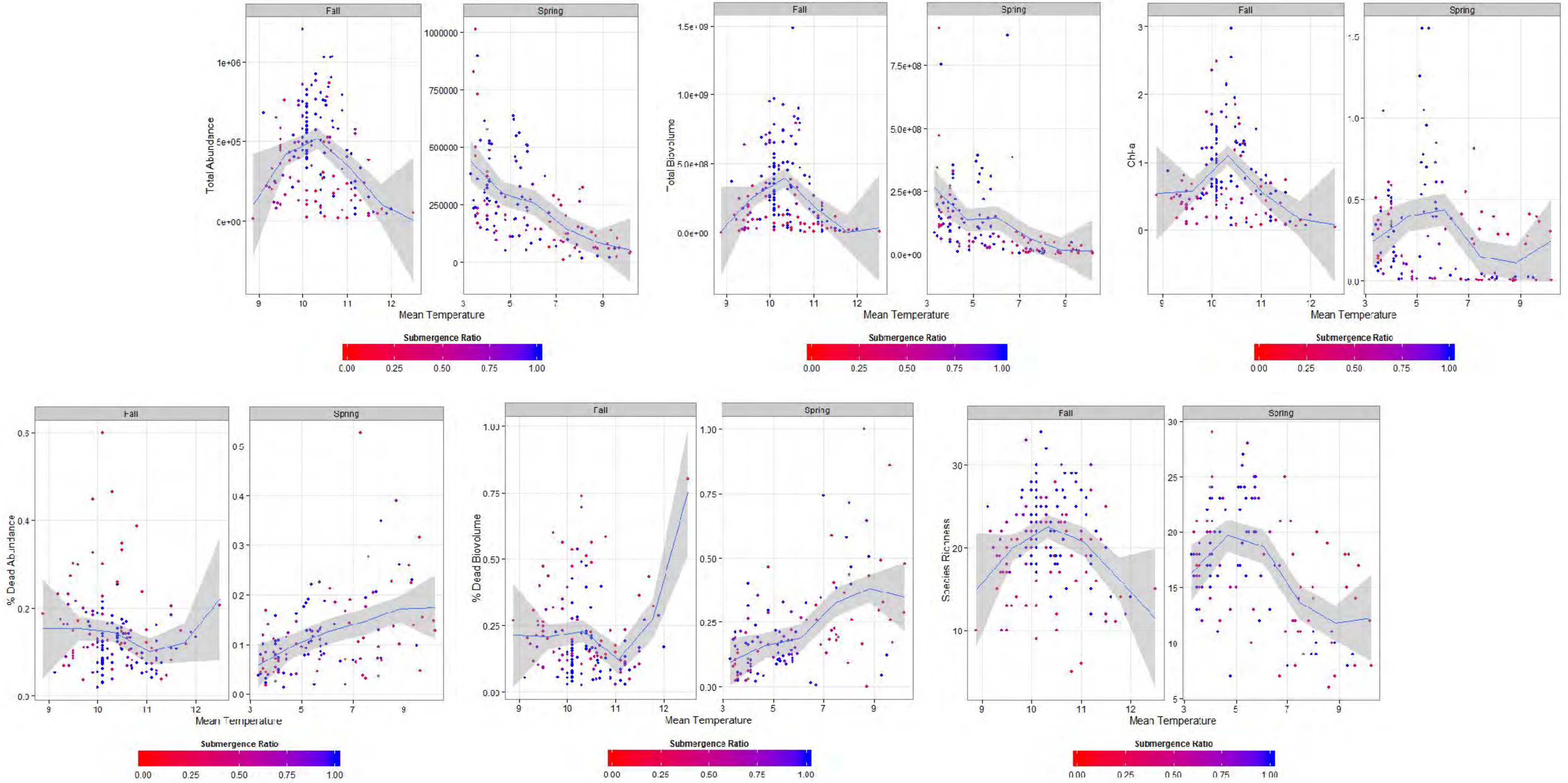


Figure A-1: **Production responses to mean sampler site temperature (ºC) for spring and fall data. Metrics include total abundance (cells/cm^2), total biovolume (cm^3/cm^2), chl-a (ug/cm^2), percent dead cell abundance, percent dead biovolume, and species richness. Sampler sites are coloured by submergence ratio to highlight the relationships between temperature and submergence, where red represents no time in the water (0%) and blue (100%) represents 100% submergence.**

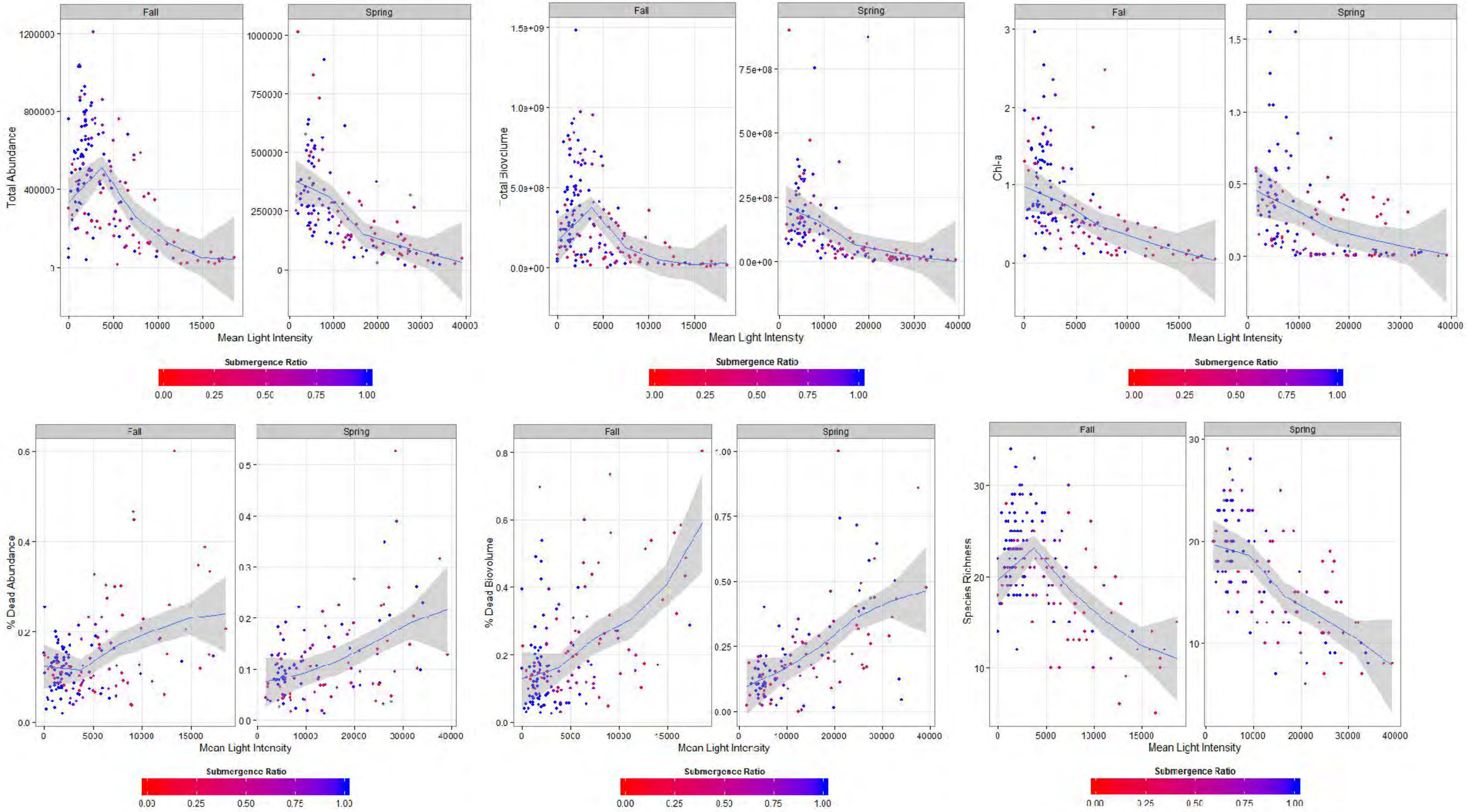


Figure A-2: Production responses to mean sampler site light intensity (Lux) for spring and fall data. Metrics include total abundance (cells/cm^2), total biovolume (cm^3/cm^2), chl-a (ug/cm^2), percent dead cell abundance, percent dead biovolume, and species richness. Sampler sites are coloured by submergence ratio to highlight the relationships between temperature and submergence, where red represents no time in the water (0%) and blue (100%) represents 100% submergence.

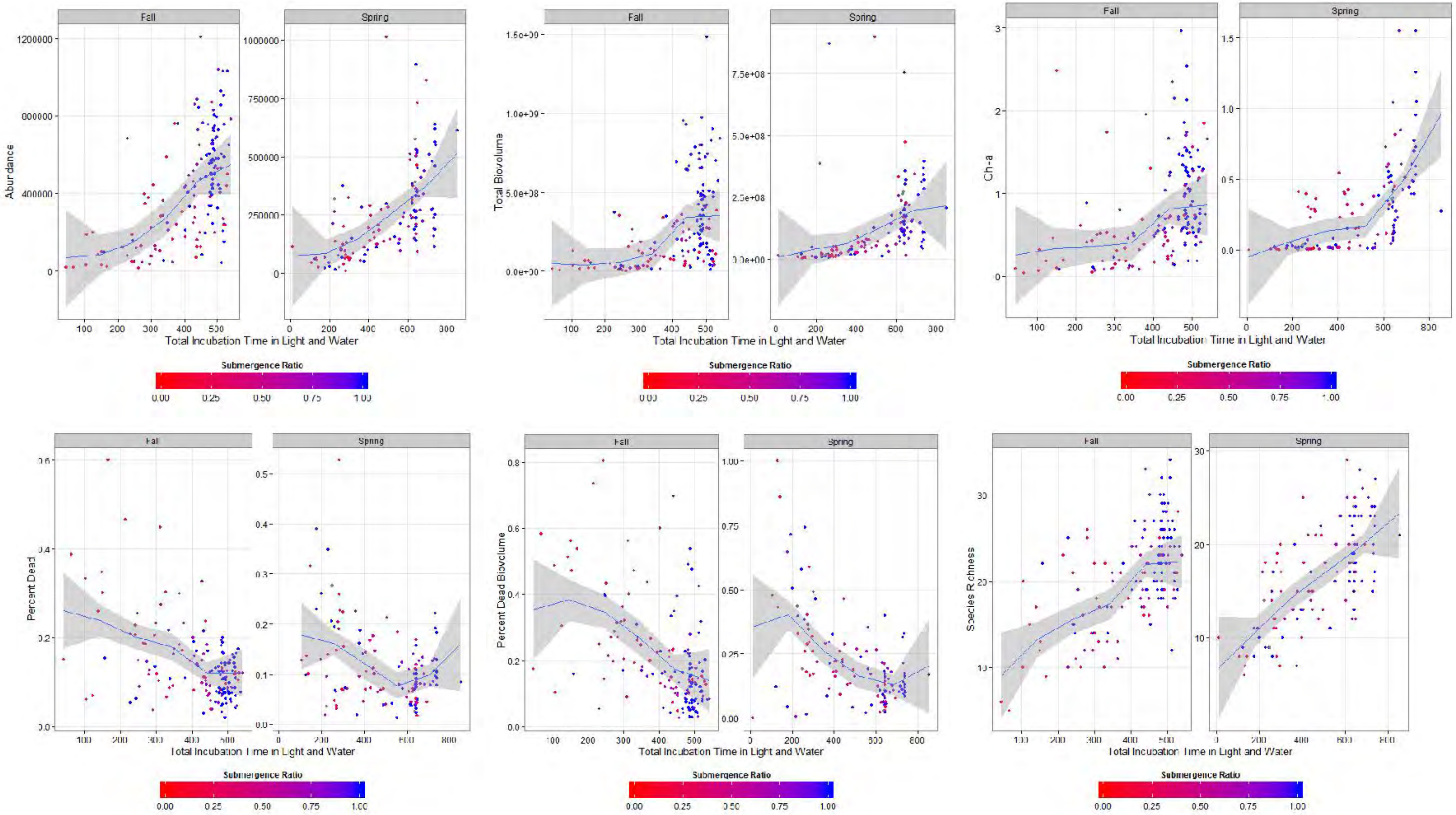


Figure A-3: Production responses to mean sampler incubation time in the light and water (hrs) for spring and fall data. Metrics include total abundance (cells/cm^2), total biovolume (cm^3/cm^2), chl-a (ug/cm^2), percent dead cell abundance, percent dead biovolume, and species richness. Sampler sites are coloured by submergence ratio to highlight the relationships between temperature and submergence, where red represents no time in the water (0%) and blue (100%) represents 100% submergence.

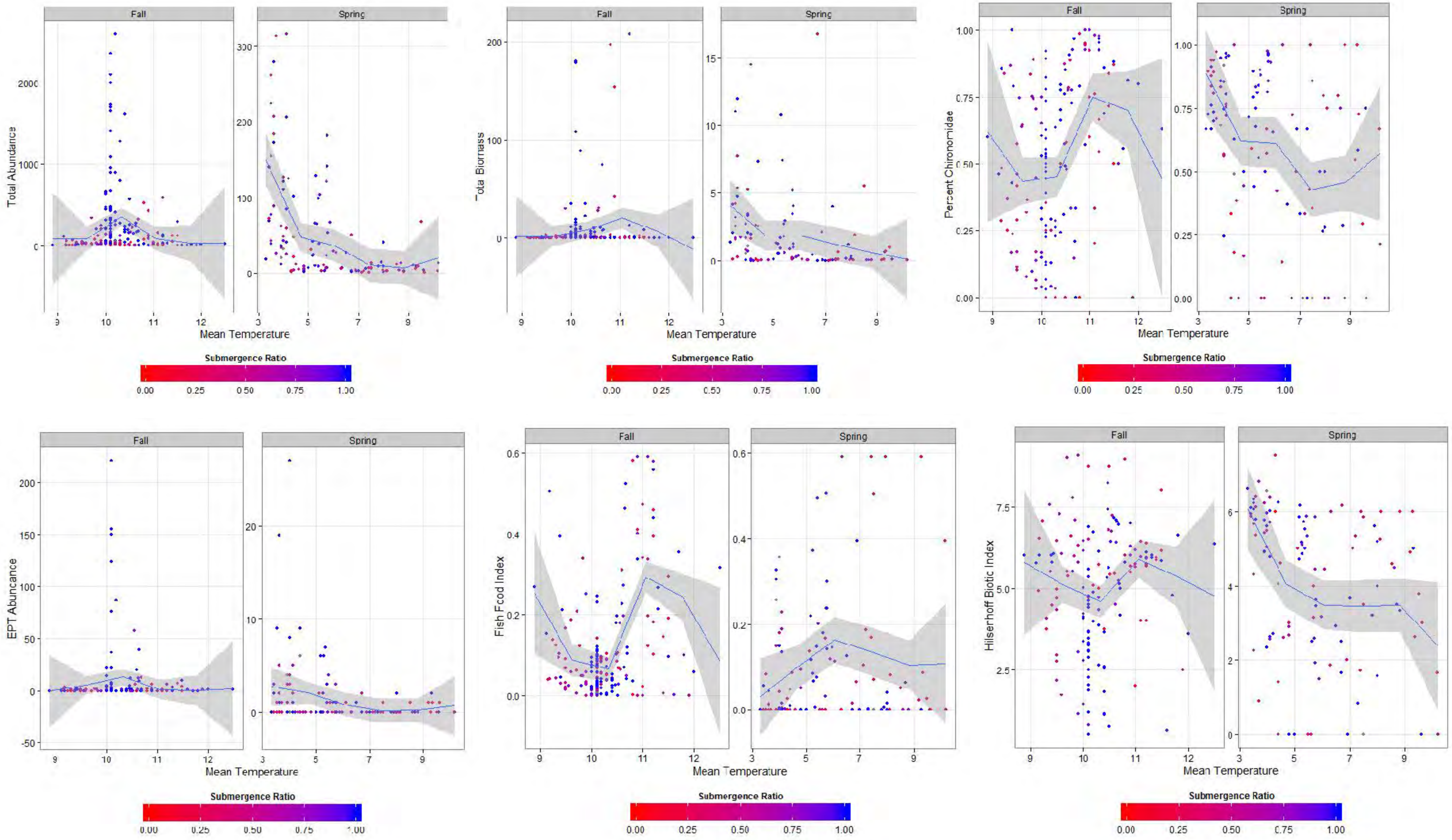


Figure A-4: Total abundance, total biomass, percent chironomidae, EPT abundance, fish food index, and Hilsenhoff Biotic Index production responses to mean sampler site temperature (ºC) for spring and fall data. Sampler sites are coloured by submergence ratio to highlight the relationships between temperature and submergence. The submergence data explains the relationship between the response and predictor.

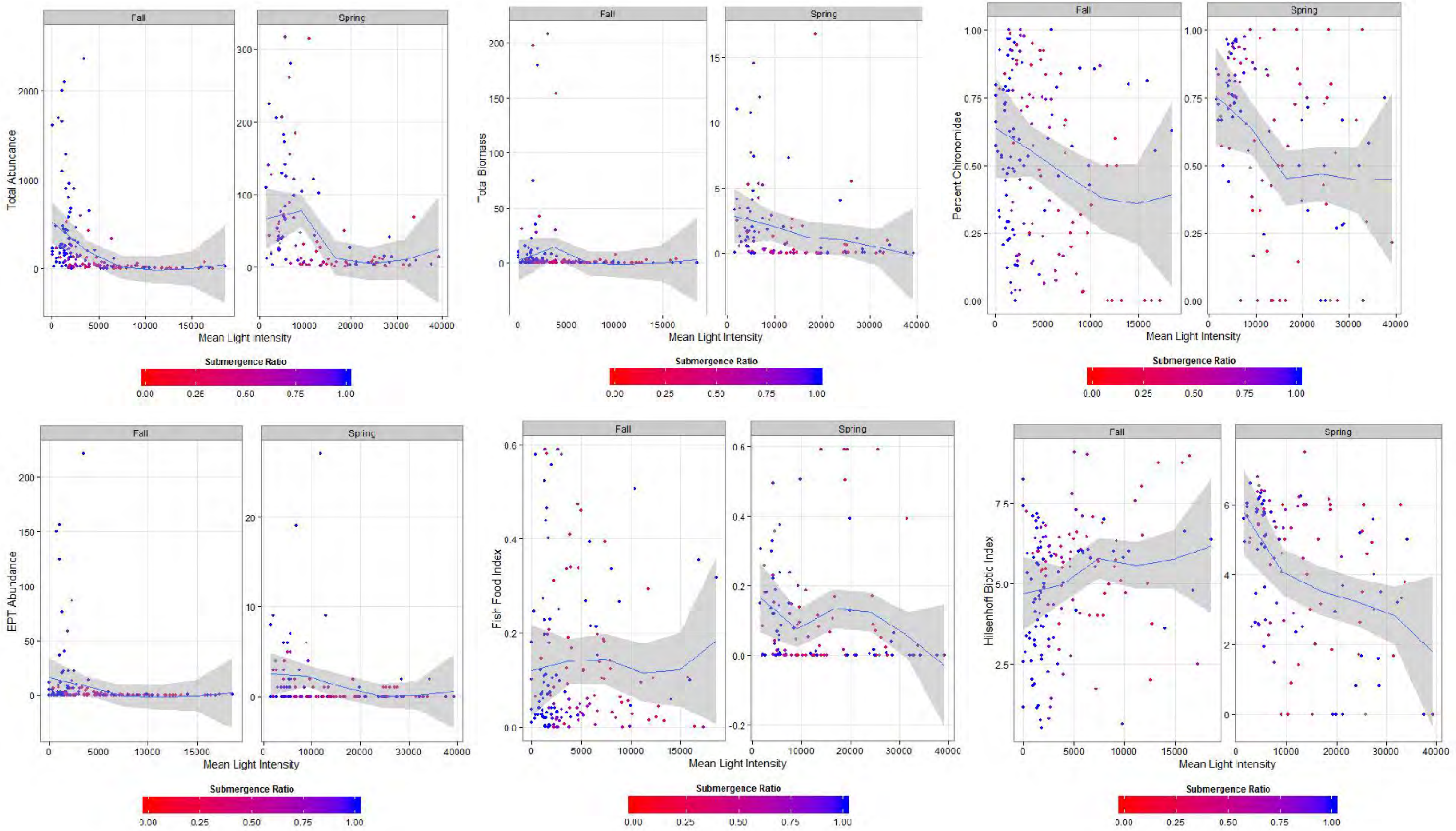


Figure A-5: Total abundance, total biomass, percent chironomidae, EPT abundance, fish food index, and Hilsenhoff Biotic Index production responses to mean light intensity (Lux) for spring and fall data. Sampler sites are coloured by submergence ratio to highlight the relationships between temperature and submergence. The submergence data explains the relationship between the response and predictor.

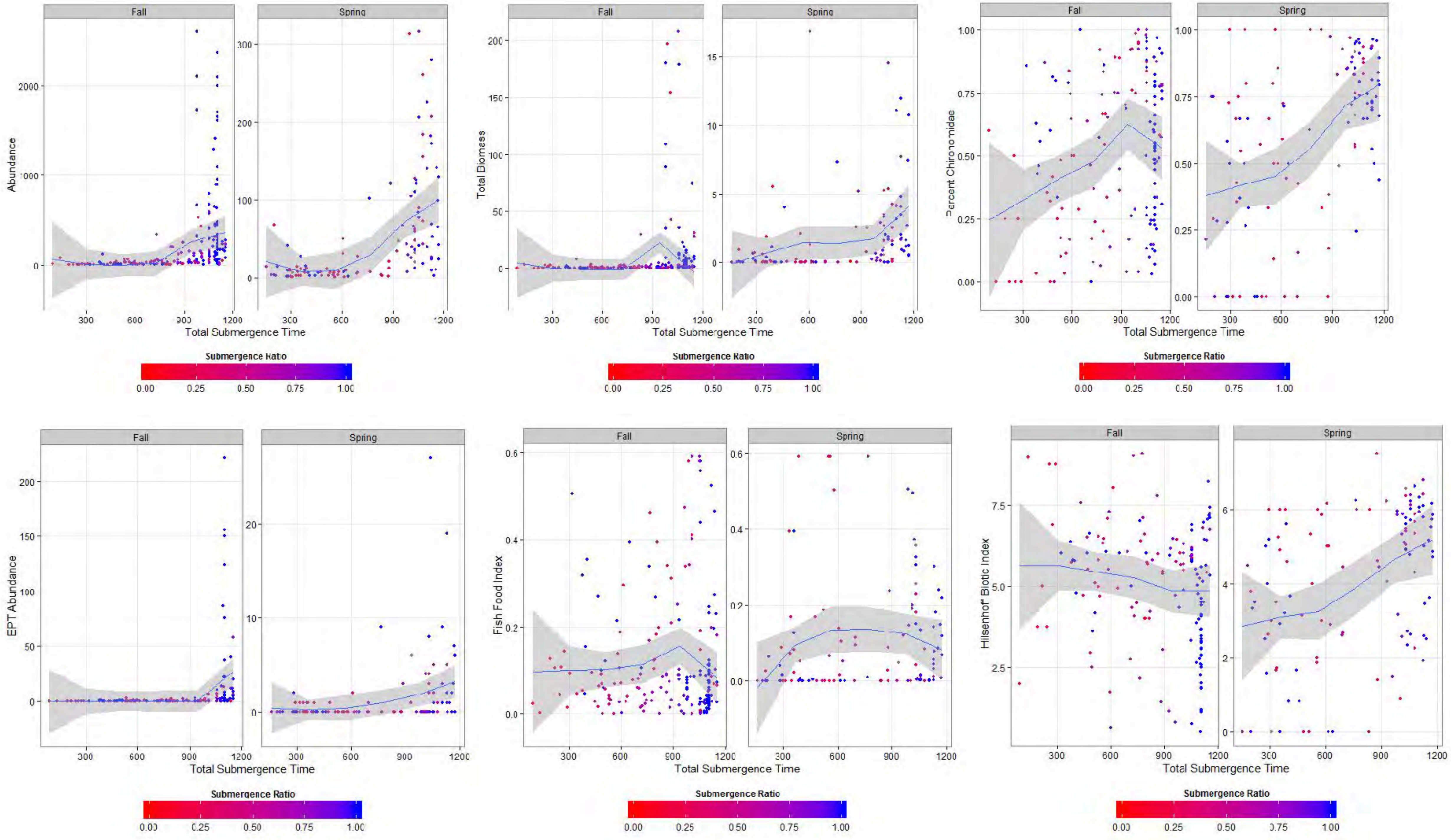


Figure A-6: Total abundance, total biomass, percent chironomidae, EPT abundance, fish food index, and Hilsenhoff Biotic Index production responses to total submergence time (hrs) for spring and fall data. Sampler sites are coloured by submergence ratio to highlight the relationships between temperature and submergence. The submergence data explains the relationship between the response and predictor.

Table A-1: Summary statistics for periphyton in the Mid Columbia River in the fall from 2007 to 2013.

		Pre				Post		
Diversity Measures	Statistics	2007	2008	2009	2010	2011	2012	2013
Abundance cells/cm^2	Sample Size	19	24	25	37	49	42	47
	Mean	1.25E+06	4.98E+05	7.05E+05	4.18E+05	5.88E+05	2.73E+05	4.61E+05
	Median	1.23E+06	4.87E+05	7.37E+05	4.17E+05	5.89E+05	2.21E+05	4.20E+05
	Minimum	2.51E+05	1.91E+05	9.86E+04	1.92E+04	1.13E+05	1.70E+04	1.71E+04
	Maximum	2.06E+06	8.38E+05	1.33E+06	1.20E+06	1.13E+06	8.23E+05	1.04E+06
Species Richness # of species	Sample Size	19	24	25	37	49	42	47
	Mean (±SD)	9.8 ± 2.1	18.3 ± 3.6	17.7 ± 3.3	20.8 ± 7.7	22.9 ± 6.1	19.3 ± 6.8	21.0 ± 4.5
	Median	9	18	18	23	23	19.5	21
	Minimum	7	13	11	3	10	4	10
	Maximum	15	25	25	35	37	30	29
Biovolume microns^3/cm^2	Sample Size				37	49	47	47
	Mean				3.78E+08	3.12E+08	9.80E+07	3.33E+08
	Median		NA		3.31E+08	2.80E+08	6.10E+07	2.55E+08
	Minimum				5.29E+06	1.55E+07	3.40E+05	2.27E+06
	Maximum				9.80E+08	7.86E+08	4.20E+08	1.48E+09
Simpson's Index	Sample Size	19	24	25	37	49	42	47
	Mean (±SD)	0.66 ± 0.11	0.81 ± 0.05	0.84 ± 0.02	0.82 ± 0.12	0.82 ± 0.07	0.80 ± 0.09	0.70 ± 0.02
	Median	0.69	0.82	0.85	0.84	0.84	0.82	0.71
	Minimum	0.35	0.63	0.81	0.31	0.58	0.39	0.64
	Maximum	0.78	0.86	0.89	0.92	0.91	0.9	0.72
Chlorophyll-a ug/cm^2	Sample Size	19	26	25	37	49	42	45
	Mean (±SD)	1.43 ± 0.75	0.86 ± 0.43	0.93 ± 80	1.03 ± 0.85	0.76 ± 0.42	0.49 ± 0.46	1.01 ± 0.94
	Median	1.32	0.84	0.59	0.79	0.68	0.4	0.76
	Minimum	0.79	0.02	0.05	0.04	0.09	0.003	0.23
	Maximum	4.1	1.8	2.87	2.96	1.68	2.06	6.29
Ash-free Dry weight mg/cm^2	Sample Size				37	49	39	44
	Mean (±SD)				4.89 ± 3.26	2.94 ± 3.85	1.82 ± 1.26	0.81 ± 3.23
	Median		NA		4.47	1.64	1.36	0.18
	Minimum				1.05	0.66	0.52	0.04
	Maximum				17.14	17.74	6.25	21.66

Table A-2: Summary statistics for periphyton in the Mid-Columbia River in the spring from 2011 to 2013

Diversity Measures	Statistics	2011	2012	2013
Abundance cells/cm^2	Sample Size	48	47	46
	Mean (±SD)	2.70E+05	2.54E+05	2.82E+05
	Median	2.03E+05	2.66E+05	2.49E+05
	Minimum	2.68E+04	2.16E+04	3.82E+04
	Maximum	1.23E+06	5.78E+05	6.37E+05
Species Richness # of species	Sample Size	48	47	46
	Mean (±SD)	12.5 ± 4.3	16.8 ± 5.7	20.2 ± 4.4
	Median	13	17	20
	Minimum	5	2	12
	Maximum	21	31	28
Biovolume microns^3/cm^2	Sample Size	48	47	46
	Mean (±SD)	1.18E+08	1.36E+08	1.25E+08
	Median	5.49E+07	1.08E+08	7.88E+07
	Minimum	1.22E+06	4.43E+06	1.13E+07
	Maximum	8.97E+08	8.70E+08	3.95E+08
Simpson's Index	Sample Size	48	47	46
	Mean (±SD)	0.76 ± 0.12	0.76 ± 0.14	0.71 ± 0.02
	Median	0.817244	0.79199	0.71
	Minimum	0.349091	0.036132	0.61
	Maximum	0.876339	0.905109	0.73
Chlorophyll-a ug/cm^2	Sample Size	48	47	44
	Mean (±SD)	0.16 ± 0.22	0.19 ± 0.21	0.53 ± 0.32
	Median	0.05	0.11	0.40
	Minimum	0.003	0.002	0.23
	Maximum	1.05	0.81	1.55
Ash-free Dry weight mg/cm^2	Sample Size	48	47	44
	Mean (±SD)	9.28 ± 12.11	4.70 ± 6.92	0.35 ± 0.20
	Median	4.44	2.58	0.35
	Minimum	1.16	0.88	0.16
	Maximum	62.24	44.44	1.06

Table A-3 Summary statistics for periphyton in the Mid Columbia River by reach and season from 2010 to 2013.

Diversity Measures	Statistics	Fall		Spring	
		R3	R4	R3	R4
Abundance cells/cm^2	Sample Size	120	123	69	72
	Mean	5.40E+05	5.09E+05	2.74E+05	2.38E+05
	Median	5.03E+05	4.63E+05	2.49E+05	2.01E+05
	Minimum	2.63E+03	1.71E+04	1.72E+04	1.19E+04
	Maximum	1.97E+06	2.04E+06	8.27E+05	1.01E+06
Species Richness # of species	Sample Size	120	123	69	72
	Mean (±SD)	20 ± 6	19 ± 6	17 ± 5	16 ± 5
	Median	20	20	18	16
	Minimum	4	5	3	6
	Maximum	35	33	28	29
Biovolume microns^3/cm^2	Sample Size	84	91	69	72
	Mean	2.52E+08	3.03E+08	1.30E+08	1.22E+08
	Median	1.59E+08	2.06E+08	8.84E+07	6.93E+07
	Minimum	6.97E+04	2.27E+06	3.37E+06	1.13E+06
	Maximum	9.29E+08	1.48E+09	8.70E+08	8.96E+08
Simpson's Index	Sample Size	120	123	69	72
	Mean (±SD)	0.70 ± 0.024	0.70 ± 0.023	0.69 ± 0.033	0.69 ± 0.029
	Median	0.705	0.708	0.704	0.700
	Minimum	0.589	0.577	0.500	0.574
	Maximum	0.729	0.725	0.727	0.726
Chlorophyll-a ug/cm^2	Sample Size	105	106	66	71
	Mean (±SD)	1.05 ± 0.84	0.64 ± 0.47	0.42 ± 0.35	0.17 ± 0.18
	Median	1.017	0.541	0.367	0.111
	Minimum	0.003	0.040	0.007	0.002
	Maximum	6.288	2.130	1.545	0.848
Ash-free Dry weight mg/cm^2	Sample Size	79	91	66	71
	Mean (±SD)	0.49 ± 0.43	0.60 ± 2.25	0.60 ± 0.66	0.49 ± 0.34
	Median	0.529	0.350	0.529	0.352
	Minimum	0.000	0.044	0.123	0.159
	Maximum	3.520	21.660	5.290	1.762

Table A-4: Relative abundance and relative biomass of benthic invertebrates in the fall of each year from 2007 to 2013.

Species	2007		Species
	Relative Abundance (%)	Relative Biomass (%)	
Heterotrissocladius sp.	46.2%	49.1%	*Hydra sp.*
Hydra sp.	34.3%	23.1%	*Orthocladius complex*
Chaetogaster sp.	6.7%	10.6%	*Nais sp.*
Enchytraeidae	2.9%	3.9%	Chironomidae
Torrenticolidae	2.4%	3.1%	Enchytraeus
Diamesa sp.	1.9%	1.7%	*Simulium sp.*
Drunella sp.	1.2%	1.6%	*Ecclisomyia sp.*
Procladius sp.	0.9%	1.5%	Hymenoptera (Adults)
Hydrozetes sp.	0.9%	1.5%	*Lymnaea sp.*
Ecclisomyia sp.	0.5%	1.2%	*Thienemannimyia group*

Species	2008		Species
	Relative Abundance (%)	Relative Biomass (%)	
Hydra sp.	65.1%	78.5%	*Hydra sp.*
Orthocladiinae	16.6%	6.1%	Enchytraeus
Chaetogaster sp.	4.3%	3.4%	Orthocladiinae
Enchytraeidae	2.8%	3.3%	*Lymnaea sp.*
Procladius sp.	2.5%	2.8%	*Nais sp.*
Torrenticolidae	2.2%	1.7%	*Drunella grandis*
Tanytarsus sp.	1.3%	0.7%	Pseudocaeciliidae
Rheotanytarsus sp.	0.9%	0.6%	*Tanytarsus sp.*
Cricotopus sp.	0.9%	0.6%	*Thienemannimyia group*
Epeorus sp.	0.6%	0.4%	*Polycelis coronata*

Species	2009		Species
	Relative Abundance (%)	Relative Biomass (%)	
Hydra sp.	82.1%	82.5%	*Hydra sp.*
Orthocladiinae	5.6%	9.4%	Enchytraeus
Enchytraeidae	4.7%	3.3%	Orthocladiinae
Torrenticolidae	4.6%	1.8%	Diamesini
Diptera (Adults)	1.3%	1.0%	Tanytarsini
Eisenella sp.	1.0%	0.8%	Diptera (Adults)
Hymenoptera (Adults)	0.3%	0.4%	Hymenoptera (Adults)
Frontipedia sp.	0.2%	0.3%	*Ecclisomyia sp.*
Ecclisomyia sp.	0.2%	0.3%	*Eisenella sp.*
Diamesini	0.1%	0.1%	*Frontipedia sp.*

Species	2010		Species
	Relative Abundance (%)	Relative Biomass (%)	
Hydra sp.	40.8%	59.7%	*Hydra sp.*
Orthocladiinae	31.9%	19.1%	Enchytraeus
Naididae	9.5%	6.1%	*Diamesa sp.*
Tubificidae	3.7%	3.4%	*Orthocladius complex*
Nemata	3.4%	3.3%	*Pseudosmittia sp.*
Oligochaeta	2.7%	2.6%	Diamesini
Pseudosmittia sp.	2.0%	2.0%	Tubificidae
Diamesa sp.	1.5%	1.3%	Apatania
Orthocladius complex	1.3%	0.6%	Lumbriculidae
Enchytraeidae	0.8%	0.4%	*Brillia sp.*

Table 3-11 Con't:

Species	2011		Species
	Relative Abundance (%)	Relative Biomass (%)	
Hydra sp.	40.0%	26.8%	Orthocladiinae
Orthocladiinae	34.4%	21.9%	Enchytraeus
Naididae	6.9%	12.8%	*Hydra sp.*
Orthocladius complex	4.9%	7.7%	Lumbriculidae
Oligophlebodes sp.	1.6%	4.3%	Ephemerellidae
Ephemerellidae	1.5%	4.0%	Tanypodinae
Harpacticoida	1.5%	3.2%	*Chironomus sp.*
Cyclopoida	1.4%	2.9%	*Eukiefferiella sp.*
Diamesa sp.	1.2%	2.3%	*Diamesa sp.*
Calanoida	1.0%	2.0%	*Suwallia sp.*

Species	2012		Species
	Relative Abundance (%)	Relative Biomass (%)	
Orthocladius complex	54.8%	51.5%	*Orthocladius complex*
Tanypodinae	9.1%	10.0%	Tanypodinae
Hydra sp.	8.8%	5.2%	Ephemerellidae
Orthocladiinae	3.2%	4.4%	*Simulium sp.*
Eukiefferiella sp.	2.9%	3.9%	Chironomidae
Nais sp.	2.8%	3.9%	*Orthocladiinae*
Ephemerellidae	2.2%	2.6%	*Eukiefferiella sp.*
Chironominae	1.8%	2.6%	*Hydra sp.*
Daphnia	1.5%	2.4%	Nemouridae
Mesenchytraeus	1.2%	2.3%	Mesenchytraeus

Species	2013		Species
	Relative Abundance (%)	Relative Biomass (%)	
Eukiefferiella sp.	28.8%	33.0%	*Eukiefferiella sp.*
Hydra sp.	24.0%	24.6%	*Orthocladius complex*
Orthocladius complex	23.4%	5.7%	*Nais sp.*
Copepoda	3.9%	4.8%	*Potthastia longimana group*
Nais sp.	3.3%	4.4%	*Thienemannimyia group*
Naididae	2.2%	3.5%	Ephemerellidae
Thienemannimyia group	1.9%	3.4%	Lumbriculidae
Psectrocladius sp.	1.4%	3.4%	*Simulium sp.*
Ephemerellidae	1.2%	2.6%	*Hydra sp.*
Tanytarsus sp.	1.2%	2.1%	*Cryptochia sp.*

Table A-5: Relative abundance and relative biomass of benthic invertebrates in the spring of each year from 2011 to 2012.

Species	2011		Species
	Relative Abundance (%)	Relative Biomass (%)	
Orthocladius complex	39.9%	41.2%	Diamesa sp.
Cyclopoida	17.5%	11.2%	Micropsectra sp.
Hydra sp.	10.6%	7.7%	Sperchon sp.
Orthocladiinae	9.7%	6.6%	Stictochironomus sp.
Eukiefferiella sp.	8.6%	5.0%	Hydra sp.
Nais sp.	3.4%	4.7%	Copepoda
Nemata	2.6%	3.1%	Turbellaria
Micropsectra sp.	1.6%	2.9%	Cyclopoida
Daphnia	1.1%	2.4%	Enchytraeus
Diamesa sp.	1.0%	1.9%	Poduridae

Species	2012		Species
	Relative Abundance (%)	Relative Biomass (%)	
Orthocladius complex	29.2%	33.8%	*Orthocladius complex*
Cyclopoida	24.6%	16.1%	Hydra sp.
Orthocladiinae	12.4%	13.9%	*Orthocladiinae*
Hydra sp.	11.3%	4.3%	*Eukiefferiella sp.*
Eukiefferiella sp.	4.1%	4.2%	Lumbriculidae
Calanoida	1.9%	4.1%	*Ephemerella dorothea/excrucians*
Daphnia	1.5%	3.5%	Chironomidae
Pagastia sp.	1.5%	3.5%	Ephemerellidae
Cardiocladius sp.	1.4%	2.4%	Heptageniidae
Ephemerellidae	1.1%	2.3%	Suwallia sp.

Species	2013		Species
	Relative Abundance (%)	Relative Biomass (%)	
Orthocladius complex	40.4%	35.2%	*Orthocladius complex*
Orthocladiinae	18.5%	8.5%	Orthocladiinae
Hydra sp.	15.5%	8.0%	*Ephemerella dorothea/excrucians*
Eukiefferiella sp.	2.9%	5.8%	*Hydropsyche sp.*
Cardiocladius sp.	2.9%	5.1%	Hydra sp.
Ceraclea sp.	2.4%	4.8%	*Lumbriculidae*
Nais sp.	1.6%	3.9%	Caudatella sp.
Lumbriculidae	1.5%	3.3%	Helodon sp.
Tanytarsus sp.	1.4%	2.4%	Eukiefferiella sp.
Helodon sp.	1.4%	2.4%	Ceraclea sp.

Table A-6: Summary statistics for benthic invertebrates in the Mid Columbia River in the fall from 2007 to 2013.

		Pre				Post		
Diversity Measures	Statistics	2007	2008	2009	2010	2011	2012	2013
Abundanc (#/basket)e	Sample Size	21	26	25	37	49	41	45
	Mean (±SD)	213.62 ± 319.41	511.23 ± 770.09	67.56 ± 81.94	201.19 ± 351.11	518.12 ± 617.11	156.63 ± 406.86	164.29 ± 150.8
	Median	76.0	94.0	29.0	39.0	268.0	26.0	111.0
	Minimum	21.0	5.0	3.0	1.0	8.0	1.0	3.0
	Maximum	1407.0	2611.0	305.0	1615.0	2356.0	2516.0	507.0
Biomass (mg/basket)	Sample Size	21	26	25	36	49	40	42
	Mean (±SD)	3.78 ± 4.96	30.53 ± 54.19	2.11 ± 2.35	3.8 ± 6.51	5.38 ± 24.5	18.04 ± 51.63	18.74 ± 44.26
	Range	1.3	2.4	1.2	1.6	0.7	0.3	1.2
	Minimum	0.4	0.1	0.1	0.1	0.0	0.0	0.0
	Maximum	18.2	179.9	9.0	29.7	171.1	207.8	229.3
Species Richness	Sample Size	21	26	25	37	49	41	45
	Mean (±SD)	9.43 ± 3.92	9.88 ± 5.34	4.16 ± 1.14	5.32 ± 2.25	10.45 ± 4.21	7.68 ± 5.25	10.76 ± 6.38
	Range	9.0	9.5	4.0	5.0	10.0	5.0	9.0
	Minimum	5.0	3.0	3.0	2.0	3.0	2.0	3.0
	Maximum	18.0	23.0	7.0	10.0	21.0	21.0	31.0
Percent EPT	Sample Size	NA			37	49	41	45
	Mean (±SD)				0 ± 0.01	0.02 ± 0.03	0.04 ± 0.09	0.02 ± 0.05
	Range				0.00	0.01	0.00	0.01
	Minimum				0.00	0.00	0.00	0.00
	Maximum				0.05	0.14	0.50	0.24
Percent Chironomidae	Sample Size	NA			37	49	41	45
	Mean (±SD)				0.34 ± 0.29	0.4 ± 0.22	0.73 ± 0.26	0.64 ± 0.26
	Range				0.3	0.4	0.8	0.7
	Minimum				0.0	0.0	0.0	0.1
	Maximum				0.9	0.9	1.0	1.0
Simpson's Index	Sample Size	21	26	25	37	49	41	45
	Mean (±SD)	0.67 ± 0.04	0.65 ± 0.06	0.62 ± 0.07	0.66 ± 0.06	0.67 ± 0.05	0.67 ± 0.07	0.69 ± 0.05
	Range	0.68	0.65	0.60	0.66	0.67	0.70	0.69
	Minimum	0.60	0.55	0.52	0.52	0.54	0.51	0.57
	Maximum	0.73	0.75	0.73	0.77	0.75	0.77	0.77
Hilsenhoff Biotic Index	Sample Size	NA			37	49	41	45
	Mean (±SD)				4.63 ± 2.42	3.71 ± 1.47	5.55 ± 1.27	6.41 ± 0.9
	Range				4.71	3.66	5.92	6.42
	Minimum				0.75	0.51	0.62	4.50
	Maximum				9.06	6.88	8.00	8.24

Table A-7: Summary statistics for benthic invertebrates in the Mid Columbia River in the spring from 2011 to 2013, after implementation of minimum flows.

Diversity Measures	Statistics	2011	2012	2013
Abundance (#/basket)	Sample Size	47	38	42
	Mean (±SD)	74.36 ± 100.06	50.92 ± 69.78	55.62 ± 87.74
	Range	22.0	23.5	26.0
	Minimum	1.0	2.0	1.0
	Maximum	403.0	312.0	497.0
Biomass (mg/basket)	Sample Size	45	32	42
	Mean (±SD)	2.11 ± 3.39	2.3 ± 6.27	6.88 ± 23.37
	Range	0.7	0.3	0.9
	Minimum	0.0	0.0	0.0
	Maximum	16.7	33.5	141.6
Species Richness	Sample Size	47	38	42
	Mean (±SD)	6.77 ± 4.73	7.42 ± 5.5	6.33 ± 4.43
	Range	5.0	5.5	5.5
	Minimum	2.0	2.0	2.0
	Maximum	21.0	28.0	18.0
Percent EPT	Sample Size	47	38	42
	Mean (±SD)	0.02 ± 0.04	0.04 ± 0.07	0.05 ± 0.16
	Range	0.00	0.00	0.00
	Minimum	0.00	0.00	0.00
	Maximum	0.20	0.33	1.00
Percent Chironomidae	Sample Size	47	38	42
	Mean (±SD)	0.6 ± 0.31	0.53 ± 0.32	0.7 ± 0.29
	Range	0.71	0.57	0.80
	Minimum	0.00	0.00	0.00
	Maximum	1.00	1.00	1.00
Simpson's Index	Sample Size	47	38	42
	Mean (±SD)	0.68 ± 0.05	0.7 ± 0.05	0.68 ± 0.05
	Range	0.70	0.72	0.69
	Minimum	0.55	0.56	0.59
	Maximum	0.77	0.76	0.77
Hilsenhoff Biotic Index	Sample Size	47	38	40
	Mean (±SD)	4.32 ± 2.33	3.65 ± 1.97	4.67 ± 1.47
	Range	5.36	3.83	5.00
	Minimum	0.00	0.00	1.49
	Maximum	8.00	6.56	6.84

Table A-8: Summary statistics for benthic invertebrates in the Mid Columbia River in the fall from 2007 to 2013. Sampler positions occur from the thalweg (T1) to infrequently wetted areas at T7.

Diversity Measures	Statistics	T1	T2	T3	T4	T5	T6	T7
Abundance (#/basket)	Sample Size	59	37	58	32	30	25	3
	Mean	483.46 ± 646.74	342.27 ± 422.14	267.16 ± 383.59	137.25 ± 351.65	72.63 ± 142.59	112.64 ± 468.98	14.67 ± 9.87
	Median	240.00	219.00	82.00	43.00	28.50	8.00	10.00
	Minimum	2.00	16.00	6.00	1.00	1.00	1.00	8.00
	Maximum	2611.00	2100.00	1807.00	2001.00	622.00	2356.00	26.00
Biomass (mg/basket)	Sample Size	59	34	57	32	29	25	3
	Mean (±SD)	13.93 ± 30.31	31 ± 64.94	11.23 ± 34.44	3.12 ± 9.62	6.76 ± 31.75	0.72 ± 1.14	1.6 ± 1.7
	Median	2.2	2.6	1.4	0.4	0.4	0.3	1.3
	Minimum	0.1	0.0	0.0	0.0	0.0	0.0	0.1
	Maximum	179.9	229.3	169.2	47.6	171.6	4.9	3.4
Species Richness	Sample Size	59	37	58	32	30	25	3
	Mean (±SD)	9.66 ± 5.22	9.78 ± 6.01	9.02 ± 5.32	7.41 ± 4.61	7.5 ± 3.91	5.36 ± 3.08	5.33 ± 1.53
	Median	9.0	8.0	8.0	6.0	7.0	4.0	5.0
	Minimum	3	3	3	2	2	2	4
	Maximum	23	24	31	18	20	14	7
Percent EPT	Sample Size	31	32	28	26	27	25	3
	Mean	0.02 ± 0.03	0.02 ± 0.04	0.03 ± 0.05	0.01 ± 0.02	0.03 ± 0.05	0.04 ± 0.1	0 ± 0
	Median	0.000	0.010	0.010	0.000	0.000	0.000	0.000
	Minimum	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	Maximum	0.110	0.240	0.170	0.060	0.200	0.500	0.000
Percent Chironomidae	Sample Size	31	32	28	26	27	25	3
	Mean (±SD)	0.69 ± 0.23	0.57 ± 0.31	0.54 ± 0.3	0.49 ± 0.27	0.46 ± 0.27	0.4 ± 0.33	0.21 ± 0.34
	Median	0.78	0.58	0.59	0.52	0.42	0.43	0.03
	Minimum	0.16	0.04	0.03	0.00	0.03	0.00	0.00
	Maximum	0.97	1.00	0.95	0.92	0.93	1.00	0.60
Simpson's Index	Sample Size	59	37	58	32	30	25	3
	Mean (±SD)	0.64 ± 0.05	0.64 ± 0.07	0.66 ± 0.06	0.69 ± 0.04	0.7 ± 0.05	0.71 ± 0.04	0.7 ± 0.03
	Median	0.64	0.65	0.67	0.69	0.71	0.71	0.70
	Minimum	0.52	0.51	0.54	0.59	0.57	0.62	0.66
	Maximum	0.75	0.75	0.77	0.77	0.77	0.76	0.73
Hilsenhoff Biotic Index	Sample Size	31	32	28	26	27	25	3
	Mean (±SD)	4.31 ± 2.13	5.44 ± 1.6	4.99 ± 1.68	4.85 ± 1.88	5.27 ± 1.9	5.49 ± 1.77	5.56 ± 3.48
	Median	4.35	5.85	5.32	5.35	5.01	5.90	5.72
	Minimum	0.75	0.79	0.51	1.15	0.62	1.71	2.00
	Maximum	7.23	8.22	8.24	9.01	9.06	8.75	8.95

Table A-9: Summary statistics for benthic invertebrates in the Mid Columbia River in the spring from 2011 to 2013. Sampler positions occur from the thalweg (T1) to infrequently wetted areas at T7.

Diversity Measures	Statistics	T1	T2	T3	T4	T5	T6
Abundance (#/basket)	Sample Size	26	23	21	20	19	18
	Mean (±SD)	86.69 ± 87.85	133.04 ± 127.19	65.62 ± 78.77	32.3 ± 48.51	10.79 ± 13.89	12.39 ± 16.65
	Median	64.00	75.00	36.00	6.50	6.00	8.00
	Minimum	3.00	12.00	1.00	1.00	1.00	1.00
	Maximum	403.00	497.00	314.00	134.00	57.00	68.00
Biomass (mg/basket)	Sample Size	26	22	18	20	16	17
	Mean (±SD)	2.76 ± 3.65	10.68 ± 30.17	4.95 ± 14.19	1.37 ± 2.15	1.54 ± 4.28	0.58 ± 1.35
	Median	1.8	2.0	0.5	0.1	0.1	0.1
	Minimum	0.0	0.0	0.0	0.0	0.0	0.0
	Maximum	16.7	141.6	60.5	7.2	17.4	5.6
Species Richness	Sample Size	26	23	21	20	19	18
	Mean (±SD)	8.19 ± 4.4	9 ± 6.02	7.38 ± 5.39	6.2 ± 5.14	3.95 ± 2.09	5.11 ± 3.03
	Median	7.0	7.0	5.0	4.0	3.0	3.5
	Minimum	2	4	2	2	2	2
	Maximum	17	28	18	17	10	12
Percent EPT	Sample Size	26	23	21	20	19	18
	Mean (±SD)	0.03 ± 0.06	0.03 ± 0.06	0.03 ± 0.05	0.03 ± 0.08	0.01 ± 0.02	0.08 ± 0.23
	Median	0.010	0.000	0.000	0.000	0.000	0.000
	Minimum	0.000	0.000	0.000	0.000	0.000	0.000
	Maximum	0.250	0.250	0.200	0.330	0.070	1.000
Percent Chironomidae	Sample Size	26	23	21	20	19	18
	Mean (±SD)	0.73 ± 0.22	0.83 ± 0.15	0.58 ± 0.34	0.52 ± 0.32	0.45 ± 0.36	0.47 ± 0.3
	Median	0.76	0.89	0.68	0.54	0.42	0.52
	Minimum	0.00	0.36	0.00	0.00	0.00	0.00
	Maximum	1.00	0.96	1.00	1.00	1.00	1.00
Simpson's Index	Sample Size	26	23	21	20	19	18
	Mean (±SD)	0.68 ± 0.04	0.67 ± 0.06	0.68 ± 0.05	0.7 ± 0.05	0.69 ± 0.05	0.71 ± 0.05
	Median	0.68	0.68	0.70	0.71	0.72	0.72
	Minimum	0.60	0.55	0.58	0.60	0.57	0.61
	Maximum	0.74	0.76	0.75	0.76	0.75	0.77
Hilsenhoff Biotic Index	Sample Size	25	23	21	19	19	18
	Mean (±SD)	5.13 ± 1.48	5.08 ± 1.4	4.26 ± 2.14	3.55 ± 2.13	3.76 ± 2.29	3.08 ± 1.89
	Median	5.67	5.52	5.00	4.06	3.50	3.42
	Minimum	1.25	1.93	0.00	0.00	0.00	0.00
	Maximum	6.81	6.84	7.50	6.25	8.00	6.00