Campbell River Project Water Use Plan

JHTMON-4 Upper and Lower Campbell Reservoirs Littoral Productivity Assessment

Implementation Year 2

Reference: JHTMON-4

JHTMON-4 Year 2 Monitoring Report

Study Period: March 1, 2015 to July 31, 2017

Laich-Kwil-Tach Environmental Assessment Ltd. Partnership and Ecofish Research Ltd.

October 23, 2017

JHTMON-4: Upper and Lower Campbell Reservoirs Littoral Productivity Assessment

Year 2 Annual Monitoring Report




Prepared for:

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EXECUTIVE SUMMARY

Water Use Plans (WUPs) were developed for all of BC Hydro's hydroelectric facilities through a consultative process involving local stakeholders, government agencies and First Nations. As the Campbell River WUP (BC Hydro 2012) process reached completion, a number of uncertainties remained with respect to the effects of BC Hydro operations on aquatic resources. In lakes and reservoirs, fish production is assumed to be proportional to overall aquatic productivity, but there is considerable uncertainty over the extent to which fish production is driven by littoral vs. pelagic production and whether this is influenced by operations. BC Hydro affects lake littoral production through drawdowns. The *Upper and Lower Campbell Littoral Productivity Assessment* (JHTMON-4) is part of wider monitoring of the Campbell River WUP. JHTMON-4 is designed to assess the effect of variation in water surface elevation on biological production in the littoral zone of the Upper and Lower Campbell reservoirs, and how this relates to BC Hydro operations.

The Terms of Reference for JHTMON-4 focused on the Effective Littoral Zone (ELZ) Performance Measure, with the assumption that increasing the primary productivity of the littoral zone would lead to increases in fish productivity. However, inherent uncertainties led to a first management question:

1. Does the ELZ performance measure adequately estimate the change in littoral productivity due to changes in reservoir operation, particularly in relation to changes implemented with the Campbell River WUP and potential future changes?

A second management question addressed ecological factors influencing ELZ:

2. To what extent does colonization rate, photosynthetically active radiation (PAR) penetration, growth rate and survival rate impact the utility and reliability of the ELZ performance measure for WUP decision-making purposes?

A third management question addressed changes to biological production in the littoral zone of the Upper and Lower Campbell reservoirs with application of water management rules under the WUP:

3. Following implementation of the Campbell River WUP, does littoral productivity increase as predicted by the ELZ performance measure?

Given ultimate interest in potential benefit to fish populations in the reservoirs from the WUP, a fourth management question asked:

4. How does littoral productivity translate into fish production in Campbell River reservoirs?

JHTMON-4 was completed following a two-year field program. Periphyton, benthic invertebrate, and fish sampling was completed in Lower Campbell Reservoir in Year 1 (2015) and in Upper Campbell Reservoir in Year 2 (2016).

Summary of the Main Method to Test Management Questions

A challenge with ELZ as it was defined in the original TOR is it does not quantitatively consider environmental factors other than light that are known to modify periphyton accrual over water depths spanning a littoral zone. We therefore revised the ELZ to include three environmental factors (photosynthetically active radiation (PAR), temperature, nutrient concentration) that are important determinants of algal growth rates. We then derived equations to express the relationship between periphyton accrual and those factors. This change was discussed with representatives of BC Hydro and incorporated into a revised Terms of Reference (BC Hydro 2015).

ELZ was defined as the amount of periphyton biomass (B) accrued on an area of substrata in a littoral zone with modification by light, temperature, and nutrient concentrations over time and space. This performance measure is now called L as described in Equation 1. L is conceptually the same as ELZ but it is named differently because its calculation includes more variables than we understand were included in ELZ. Accrual of periphyton was measured as change in biomass over time on standardized submerged substrata, similar to the approach used by Bothwell (1989) and Perrin *et al.* (1987) to examine growth of stream periphyton.

The definition of L can be stated as follows:

Equation 1

$$L_t = \sum_{i=1}^{n} A_{it} B_{it}$$

where;

L is accrued B that may be modified by habitat conditions and area of flooded littoral habitat at time t,

A is area of stratum i within the littoral habitat having n strata at time t, and

B is biomass of accrued periphyton at time t in littoral depth stratum i, defined as:

Equation 2

$$B_{it} = \beta_0 + \beta_1 x_{1it} + \beta_2 x_{2it} + \beta_3 x_{3it} + \varepsilon$$

is a multiple regression model explaining B at time t in depth stratum i as a function of x independent variables where β_0 is the regression intercept, x_1 is PAR, x_2 is concentration of a nutrient that limits growth of periphyton, x_3 is water temperature, $\beta_{1\ldots3}$ are regression coefficients, and ε is model error.

The combination of equations 1 and 2 was used to answer management questions 1 through 3. Management question 1 was tested using Equation 1, which is sensitive to change in water surface elevation. Management question 2 was answered by entering values for independent habitat

attributes (nutrient concentrations, temperature, PAR), to test different management scenarios. Management question 3 was answered by testing sensitivity of periphyton biomass accrual in the littoral zone to different timing and magnitude of surface water elevation changes.

Management question 4 was answered using multiple lines of evidence, including fish stomach contents and stable isotope analysis. Fish stomach data alone are not sufficient to determine sources of food for fish because they only relate to the time when samples were collected. JHTMON-4 therefore used stable isotope analysis of nitrogen and carbon of fish tissues and their potential diet items to assess relative energy flows to fish from the algal component of periphyton and from other basal nutrient sources in the littoral zone.

Digital Elevation Model

The extent of littoral area that can support periphyton biomass changes according to water surface elevation reflecting individual reservoir morphology. A digital elevation model (DEM) was developed following bathymetric surveys, and used to determine the relationship between littoral area and water surface elevation for each reservoir. The area of the littoral zone where attached algae grows is defined as the region where PAR in the overlying water column is greater than 1% of that at the water surface (the standard measure of euphotic zone depth, Wetzel 2001).

Periphyton Accrual and Habitat Attributes

Periphyton accrual was measured following sequential weekly collections at four sampling stations on Lower Campbell Reservoir, during two eight-week sampling periods in 2015 (summer and fall) and at four stations on Upper Campbell Reservoir, during two twelve-week periods in 2016 (summer and fall). A longer sampling duration was used in 2016 because the 2015 sampling showed that maximum biomass accrual takes longer than eight weeks in the Campbell Reservoirs. Peak biomass (PB) was defined as the highest concentration of chl-*a* attained on a substrate over time of measurement. PAR, water temperature, and nutrient concentrations were measured during the same sampling periods. The combined and relative contributions of these habitat attributes to periphyton biomass accrual were calculated via the multiple regression model (Equation 2).

Periphyton can vary in its composition, and includes living algae but also bacteria, protozoa, fungi and non-living organic detritus. To account for this potential variability, periphyton was collected for stable isotope analysis from three sources in 2015: 1) Four acrylic plates that were submerged in the water column for two months, 2) Periphyton biomass from the mooring line, collected as a backup in case acrylic plate samples had insufficient biomass for sampling, and 3) Periphyton scraped from rocks in the wadable reservoir margins near three of the periphyton sampling stations. Periphyton from acrylic plates did not accrue sufficient biomass to obtain a sample. Backup samples of periphyton from the mooring lines were mainly composed of living algal species and represented a portion of periphyton referred to hereafter as "attached algae". The shoreline samples contained living algal biomass, detritus from reservoir and potentially terrestrial sources, and the assemblage of heterotrophic decomposer organisms associated with the substrate. These shoreline samples are

referred to hereafter as "littoral periphyton". In 2016, the periphyton for stable isotope analysis was collected in Upper Campbell Reservoir from 5/8" lines suspended from the periphyton moorings. These suspension lines were separate from the mooring lines but made of the same material and were used mainly to provide sufficient area of substrata from which to collect the periphyton biomass for stable isotope analysis. To be consistent with terminology from 2015, the periphyton biomass from these suspension lines was called "attached algae". Shoreline samples were also collected in 2016 and were called "littoral periphyton", again to be consistent with terminology from 2015.

Performance Measure L

L (the performance measure defined as PB on substrate in the littoral zone and substituted for ELZ in the project terms of reference) was the sum of products of area of littoral strata and PB accrued on substrata. In both reservoirs, PB was influenced most by accumulated photosynthetically active radiation (PAR) and less by water temperature and TN, the latter being was used as a surrogate for nutrient concentrations, reflecting that dissolved inorganic nutrient forms could not be consistently detected.

Before calculating ***L***, the effect of the WUP on water surface elevation that drives littoral area was tested. This test examined a year effect on water surface elevation wherein pre-WUP years were 1998 to 2004 and the post-WUP years were 2006 to 2015 in Lower Campbell Reservoir and 2006 to 2016 in Upper Campbell Reservoir. Results showed no statistically significant change in water surface elevation due to implementation of the WUP.

Despite this finding, ***L*** was calculated for the range of water surface elevations that are normally encountered as part of the WUP in each reservoir during the productive summer period. Results showed that algal biomass over the whole littoral zone is relatively low at the maximum operational water surface elevation compared to lower elevations, even as littoral area declines. This counterintuitive finding reflects the bathymetry of the littoral zone, and that PAR accumulation increases exponentially with decreasing water depth. PAR is a major driver of algal accrual in the littoral zone and thus has great influence on PB as it changes at the substrata – water interface.

For each reservoir, peak biomass was then calculated for pre-WUP and post-WUP periods using a regression model that predicted peak biomass based on water elevation. This regression model was fitted based on the results of the modelling ***L*** and it accounted for the sum of algal accrual at different elevation strata. The results showed that, following implementation of the WUP, peak biomass decreased by 0.01% in Upper Campbell Reservoir and increased by 2.0% in Lower Campbell Reservoir. These predicted changes are within the range of model error and are deemed to be not ecologically significant.

Fish Stomach Contents Results

Fish stomach contents were used as a first step to examine links between periphyton production in the littoral zone and fish use of that habitat, thus addressing the fourth management question, "How

does littoral productivity translate into fish production in Campbell Reservoirs?" The stomach contents data for Lower Campbell Reservoir showed that the most common prey for Cutthroat Trout and Rainbow Trout were zooplankton and terrestrial taxa, with benthic insects that are common in littoral habitats making limited contribution to the diets of these fish species. Fish were a common diet item for Cutthroat Trout but not Rainbow Trout. In Upper Campbell Reservoir the Cutthroat Trout and Rainbow Trout ingested mostly zooplankton (based on abundance, not biomass). These findings show a disconnect between biological production of fish food organisms in littoral habitat where benthic insects are prevalent and food that is actually ingested by fish of management interest (Cutthroat Trout and Rainbow Trout). This evidence implies that the littorally-derived periphyton production is not important for supporting resident fish species and that food production in riparian areas and pelagic habitat is more important.

Stable Isotope Analysis Results

Stable isotope data, which represent an integrated signature of fish diet over a growing season, showed similar results to stomach content analyses, in that littoral-derived algal production was not very important. Terrestrial primary production contributed 58% to Cutthroat Trout diets and 46% to Rainbow Trout diets on average, illustrating the importance of allochthonous nutrient sources in the ultra-oligotrophic Upper and Lower Campbell reservoirs. Terrestrial vegetation (e.g., riparian leaf litter) was consumed directly by littoral invertebrates and is the basal carbon source for terrestrial invertebrates, which were heavily consumed themselves by littoral prey fish (e.g., juvenile trout and Sculpin spp.), stickleback, and larger Cutthroat and Rainbow Trout. The high importance of allochthonous carbon sources was major finding of this study. This finding undermines the rationale for the ELZ approach, which assumes that littoral autotrophic production is a major driver of fish productivity in the two study reservoirs.

Pelagic primary production was particularly important for Rainbow Trout in both Upper and Lower Campbell reservoirs: phytoplankton contributed approximately 40% to Rainbow Trout diets and 12% to Cutthroat Trout diets in both systems, largely through consumption by zooplankton. In contrast, the contribution of attached algae to Cutthroat Trout and Rainbow Trout is estimated to be only 9.5% and 4.1% respectively in Lower Campbell Reservoir, and 8.3% and 4.7%, respectively in Upper Campbell Reservoir.

The current data thus suggest that, while algal accrual can be used to make predictions regarding the functioning of ELZ as described above, the littoral food webs of both Upper Campbell Reservoir and Lower Campbell Reservoir are more complex than assumed under the ELZ model. The current ELZ approach is based on an incomplete conceptual model of the reservoir food webs that does not consider the primary driver of littoral fish production, which is terrestrial-derived carbon via sources such as leaf litter and terrestrial invertebrates. Further, periphyton in littoral areas does not solely comprise attached algae and is an assemblage of algae, protozoa, bacteria, fungi and detrital material. This is supported by analysis of two types of periphyton (attached algae and littoral), which were found to have distinct isotope signatures. The different signatures are likely due to several

factors. Terrestrial allochthonous carbon sources contribute to littoral periphyton closer to shore and enrich the carbon signature. The presence of heterotrophs such as bacteria will enrich the carbon signature further. The algal portion of periphyton grown on the mooring line grew slowly under ultra-oligotrophic conditions with carbon derived from autochthonous production.

In summary, the stable isotope techniques provided a powerful tool to quantify carbon fluxes within the reservoir food-webs and address management question 4: "How does littoral productivity translate into fish production in Campbell River reservoirs?" Of the basal nutrient sources, the contribution of attached algae (representative of autotrophic productivity by periphyton in the littoral zone) to Cutthroat Trout and Rainbow Trout diets in Upper and Lower Campbell Reservoirs is estimated to be only 8–10% and 4–5% respectively. These low contributions show that the current ELZ approach is based on an incomplete conceptual model of the reservoir food webs that does not consider the primary driver of littoral fish production, which is terrestrial-derived carbon via sources such as via leaf litter and terrestrial invertebrates. The importance of terrestrial (allochthonous) carbon subsidies to the reservoir food-webs means that other effect pathways that are in addition to impacts on periphyton accrual need to be considered to fully understand the ecological effects of water level management operations. There is uncertainty about how water level operations affect the terrestrial linkages to fish production.

Table 1. Status of JHTMON-4 Management Questions and Hypotheses.

Management Questions	Management Hypotheses	Year 2 (Final) Status
1. Does the ELZ performance measure adequately estimate the change in littoral productivity due to changes in reservoir operation, particularly in relation to changes implemented with the Campbell River WUP and potential future changes?	$H_0$1: The extent of littoral development in lakes, as governed by the magnitude and frequency of water level fluctuations, is not correlated with the ratio of littoral versus pelagic energy flows to reservoir fish populations.	ELZ was updated as the sum of products of littoral area and peak algal biomass (PB) within littoral strata wherein PB was a metric of algal accrual and a function of PAR, nutrient concentrations and temperature. The updated performance measure was sensitive to change in water surface elevation potentially encountered in Upper and Lower Campbell reservoirs as part of the WUP that affected area of littoral habitat and the habitat attributes that determine algal accrual. These findings show that the performance measure, renamed as L, is effective for showing change in periphyton accrual due to changes in reservoir water surface elevation and thus answers management question 1. However, a key finding of this study was that terrestrial allochthonous carbon sources are a major driver of fish productivity in the study reservoirs. This finding undermines the rationale for the ELZ approach, which assumes that littoral autotrophic production is a major driver of fish productivity in the two study reservoirs.
2. To what extent does colonization rate, PAR penetration, growth rate and survival rate impact the utility and reliability of the ELZ performance measure for WUP decision-making purposes?	$H_0$2: There is no significant correlation between the modified ELZ model (which includes depth-integrated periphyton production estimates based on differential growth and survival information) and empirically measured values from the field.	Colonization rate, growth rate and survival rate are integrated in the updated performance measure. The use of suspended substrata limited grazing effects and therefore the contribution of this loss process would have been underestimated, meaning that the periphyton accrual measurements were maximum values. Habitat attributes including PAR, water temperature, and nutrient concentrations that are determinants of periphyton accrual are predictors in the updated performance measure. These habitat attributes explained 56% of the variance in PB in Lower Campbell Reservoir and 89% of the variance in Upper Campbell Reservoir, instilling high confidence in the model with appropriate error for WUP decision-making purposes. Sensitivity analysis showed the performance measure is highly responsive to change in water surface elevation that is the main driver of littoral area and habitat attributes, most notably PAR that mainly determines PB under the ultraoligotrophic conditions of Upper and Lower Campbell Reservoirs.

Table 1. Continued.

Management Questions	Management Hypotheses	Year 2 (Final) Status
3. Following implementation of the Campbell River WUP, does littoral productivity increase as predicted by the ELZ performance measure?	$H_0$3: Primary production in the littoral zone of the Upper Reservoir does not increase following implementation of the Campbell River WUP.	Following consultation with BC Hydro, data from 1998–2004 were assumed representative of pre-WUP conditions, while 2006–2016 was assumed representative of post-WUP conditions. Model predictions for these periods showed that the WUP did not cause a biologically significant change in peak periphyton biomass, which was used as an indicator of littoral productivity Within the normal variation of water surface elevations in Upper and Lower Campbell reservoirs as defined in the WUP, littoral production defined by the performance measure, L, increases with declining water surface elevation due to increased PAR affecting shallower water depths in the littoral zone compared to conditions at the maximum operational water surface elevations. This effect of water surface elevation on periphyton accrual in the littoral zone was present before and after implementation of the WUP. Modelling peak biomass for pre-WUP and post-WUP periods showed that implementing the WUP did not result in ecologically significant changes to autotrophic periphyton production.
4. How does littoral productivity translate into fish production in Campbell River reservoirs?	$H_0$4: Following implementation of the Campbell River WUP abundance of adult trout is not correlated with littoral productivity during the cohort's first year.	A key finding of this study was that terrestrial allochthonous carbon sources are a major driver of fish productivity in the study reservoirs. Of the basal nutrient sources, the contribution of attached algae to Cutthroat Trout and Rainbow Trout diets in Upper and Lower Campbell Reservoirs is estimated to be only 8–10% and 5% respectively. The current data thus suggest that, while the ELZ model can be used to make predictions about periphyton accrual, the littoral food webs of the Lower and Upper Campbell reservoirs are more complex than assumed under the ELZ model. The importance of terrestrial (allochthonous) carbon subsidies to the reservoir food-webs means that other effect pathways that are in addition to impacts on periphyton accrual need to be considered to fully understand the ecological effects of water level management operations. As described in the Year 2 proposal, $H_0$4 cannot be tested with only two years of algal accrual data. There is an option to conduct analysis at the end of JHTMON-3 (ten year study, currently in Year 4) to examine the relationship between fish production (JHTMON-3) and ELZ predictions. The results of JHTMON-4 (low importance of littoral autotrophic productivity for fish production), indicate that these relationships are weak or absent. Models of additional effect pathways could be compared at the end of JHTMON-3 to examine potential links between drawdown operations and fish production.

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1. INTRODUCTION

1.1. Background to Water Use Planning

Water use planning exemplifies sustainable work in practice at BC Hydro. The goal is to provide a balance between the competing uses of water that include fish and wildlife, recreation, and power generation. Water Use Plans (WUPs) were developed for all of BC Hydro's hydroelectric facilities through a consultative process involving local stakeholders, government agencies and First Nations. The framework for water use planning requires that a WUP be reviewed on a periodic basis and there is expected to be monitoring to address outstanding management questions in the years following the implementation of a WUP.

As the Campbell River Water Use Plan (BC Hydro 2012) process reached completion, a number of uncertainties remained with respect to the effects of BC Hydro operations on aquatic resources. A key question throughout the WUP process was "what limits fish abundance?" For example, are fish abundance and biomass in lakes limited by pelagic or littoral sources of production? Answering this question is an important step to better understanding how human activities in the watersheds affect fisheries, and to effectively manage water uses to protect and enhance aquatic resources. The Campbell River Water Use Plan Consultative Committee developed aquatic ecosystem objectives for the Campbell Lakes system that included efforts to maximize the abundance and diversity of fish populations while establishing flow controls for hydroelectric power generation, flood protection, water quality and supply, among other interests (BC Hydro 2012). Tradeoffs occurred in the water use planning, with some uncertainty among decisions to set water elevations in the Campbell system reservoirs, manage spills, and define flow releases from the Strathcona, Ladore and John Hart dams. The Consultative Committee was constrained in making unequivocal decisions by lack of information about the effects of change in water elevations and flows on fish populations and biological production that support those populations.

To address uncertainties and better inform decisions in future years, monitoring programs were designed to assess whether fish benefits are being realized under the WUP operating regime and to evaluate the extent to which fish production is related to operations.

In lakes and reservoirs, fish production is assumed to be proportional to overall aquatic productivity, but there is considerable uncertainty over the extent to which fish production is driven by littoral (near-shore) vs. pelagic (open water) production and whether this is influenced by operations. BC Hydro affects lake littoral production through drawdowns. The *Upper and Lower Campbell Littoral Productivity Assessment* (JHTMON-4) is part of a wider monitoring of the Campbell River WUP. JHTMON-4 is designed to assess the effect of variation in water surface elevation on biological production in the littoral zone. This is the final report for JHTMON-4 and presents methods, results and conclusions from the study, including answers to each of the management questions.

1.2. BC Hydro Infrastructure, Operations and the Monitoring Context

The Campbell River WUP project area is complex and includes facilities and operations in the Campbell, Quinsam and Salmon watersheds. Within this project area there are river mainstems, three large reservoirs, nine diversion lakes influenced by water diverted from the Quinsam and Salmon rivers, and many tributaries and small lakes that are not directly affected by operations (Map 1). Details of BC Hydro's Campbell River infrastructure and operations are provided in the Campbell River System WUP (BC Hydro 2012).

1.2.1. Reservoirs

Strathcona, Ladore and John Hart dams regulate reservoir water levels for Buttle/Upper Campbell, Lower Campbell, and John Hart reservoirs respectively. Buttle/Upper Campbell Reservoir experiences the greatest range in water levels fluctuations, whereas John Hart Reservoir water levels vary the least. During development of the Campbell River WUP, the Fish Technical Committee hypothesized that fish production in Upper and Lower Campbell reservoirs was negatively impacted by fluctuations in water level through effects on littoral production. This hypothesis is supported by research elsewhere that has shown that large water level fluctuations can cause a decrease in littoral primary productivity (Furey *et al.* 2004), and that such fluctuations have a disproportionately negative effect on productivity in the littoral zone, compared with other habitats (Turner *et al.* 2005). Stable reservoir levels were therefore assumed to have a positive influence on fish production.

Due to relatively large within-year water level fluctuations, the littoral zones of upper and lower Campbell reservoirs are spatially dynamic, moving up and down over substrata of the drawdown zone over the course of a year. These fluctuations depend on hydrological differences among years; however, in general, the reservoir is drawn down in late winter and early spring and recharges during late spring and early summer. A less-pronounced drawdown typically occurs in late summer and early fall, prior to recharge due to fall rainfall. These seasonal changes are much less pronounced in Lower Campbell Reservoir, which is operated within a narrower range of elevations. Evaluation of reservoir operations relied heavily on the Effective Littoral Zone (ELZ) performance measure (see Section 1.3), with the assumption that increasing littoral productivity as predicted by the ELZ performance measure would lead to increases in fish productivity. This assumes a strong link between littoral and fish production. JHTMON-4 is designed to investigate the effect of operations on littoral primary production, and JHTMON-5 is designed to test the assumption that improvements in littoral production lead to corresponding increases in fish production. This information will then be used to directly evaluate the impact of the Campbell River WUP on reservoir fish production, help refine reservoir-related performance measures and assess their relative importance for future WUP review processes. The understanding gained through the present monitoring program may help evaluate alternative management strategies for reservoir operations.

1.3. Management Questions and Hypotheses

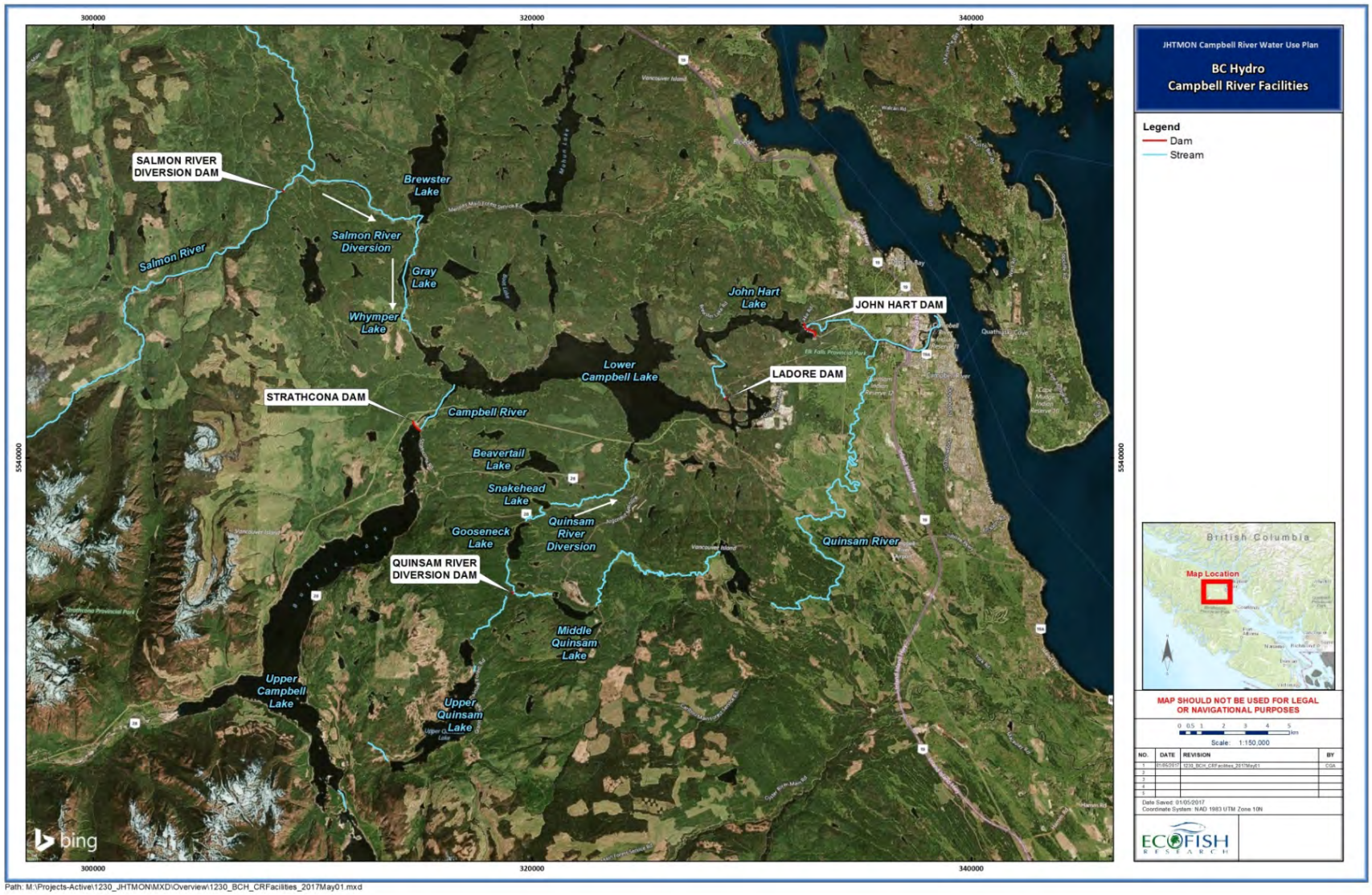
The present study (called JHTMON-4) was designed to reduce uncertainty about the effect of variation in water surface elevation on biological production in the littoral zones of Upper and Lower Campbell reservoirs. The littoral zone refers to shallow water habitat where macrophyte and non-macrophyte primary production occurs, determined at least in part by the vertical extent of light penetration associated with water clarity and change in water surface elevation (Wetzel 2001). Thus, the littoral zone is the shallow habitat of lake and reservoir shorelines extending to a water depth at which light is sufficient to support photosynthesis that produces biomass on substrata. The spatially dynamic nature of the reservoir littoral zones means that potential effects of change in reservoir operation on littoral processes must be considered in terms of change relative to the entire area of benthic production where addition of benthic biomass from photosynthesis (P) exceeds loss from respiration (R) (i.e., $P/R > 1$).

The approved operating strategy for each reservoir in the WUP (BC Hydro 2012) is presented in Table 2. The intent was to maintain Lower Campbell Reservoir within a narrow range of 176.5 – 177.5 m and maintain Upper Campbell Reservoir within a range of 217.0 – 220.5 m during the summer season, with different preferred operating ranges outside of the summer that reflect the seasonal pattern of drawdown and recharge described above. An additional objective for Upper Campbell was to maintain stable water surface elevations near 219 m where possible in the summer. These targets were expected to improve recreational opportunities and improve fish production within the littoral zone.

Table 2. Operating alternatives and expected benefits in Upper and Lower Campbell Reservoirs Water Use Plans (BC Hydro 2012).

Reservoir	Recommended operating alternative in the water use plan	Expected benefit
Lower Campbell Reservoir	Normal operating water surface elevation of 176.5 m (minimum) to 177.5 m (maximum) during the peak summer season of June 21 through September 10.	No change in erosion
		Improve access to the reservoir for recreation
		Increase fish productivity by improving littoral zone habitat and spawning conditions in tributary mouths.
Upper Campbell Reservoir	Normal operating water surface elevation of 217 m (minimum) to 220.5 m (maximum) during the peak summer season of June 21 through September 10.	Reduce erosion by reducing number of days when water surface elevation exceeds 220 m under normal operations
	Maintain more stable peak season operations near a target water surface elevation of 219 m during the peak summer season of June 21 through September 10.	Increase the number of days when the reservoir supports high quality recreation
		Improve access to the reservoir for recreation during shoulder seasons
		Improve aesthetics and terrestrial habitat when less variation in water surface elevation is combined with re-vegetation
		Increase fish productivity by improving littoral zone habitat and spawning conditions in tributary mouths.

Map 1. Overview of BC Hydro Campbell River facilities.



The Terms of Reference (TOR) for JHTMON-4 describe a term called the "effective littoral zone" (ELZ) that was a performance measure used during water use planning (BC Hydro 2012). ELZ was considered to be biomass of periphyton expressed as a function of rate of accrual of attached algae on substrata within a range of depths measured over a growing season in the littoral zone. The WUP used ELZ to assess change in productive potential of the littoral zone among scenarios of water level management but recognized uncertainty in the ELZ measure. This uncertainty led to a first management question as follows:

1. Does the ELZ performance measure adequately estimate the change in littoral productivity due to changes in reservoir operation, particularly in relation to changes implemented with the Campbell River WUP and potential future changes?

A second management question relates to the ecological factors that influence ELZ and was stated in the TOR as follows:

2. To what extent does colonization rate, PAR penetration, growth rate and survival rate impact the utility and reliability of the ELZ performance measure for WUP decision-making purposes?

PAR is photosynthetically active radiation that occurs within irradiance wavelengths of 400 – 700 nm (Wetzel 2001). Availability of PAR for photosynthesis in surface waters and lack of PAR in bottom waters is why lake and reservoir periphyton grows on shallow substrates but not at great depths. A general rule is that photosynthesis produces biomass where PAR occurs at intensities of more than 1% of irradiance found at the water surface (Wetzel 2001). PAR attenuation is affected by particles in water that contribute to turbidity. When turbidity is high, photosynthetic production occurs over a shallower depth than would occur if turbidity is lower.

A third management question relates to changes to biological production in the littoral zone of the Upper and Lower Campbell reservoirs with application of water management rules under the WUP as follows:

3. Following implementation of the Campbell River WUP, does littoral productivity increase as predicted by the ELZ performance measure?

Given ultimate interest in potential benefit to fish populations in the reservoirs from the WUP, a fourth management question asked:

4. How does littoral productivity translate into fish production in Campbell River reservoirs?

Each of these management questions were addressed in this study by analyzing data collected during 2015 (Lower Campbell Reservoir) and 2016 (Upper Campbell Reservoir).

1.4. Scope of the JHTMON4 Study

1.4.1. Overview

The JHTMON-4 schedule consisted of two years of field and lab work followed by analysis. Repeated measurements of periphyton accrual and sampling of benthic invertebrates and fish was completed in Lower Campbell Reservoir in 2015 and in Upper Campbell Reservoir in 2016. Bathymetric mapping and a digital elevation model (DEM) was completed for each reservoir as part of analytical tasks. Stable isotope techniques were applied to examine food webs and modelling was undertaken to examine scenarios of reservoir operations.

1.4.2. Summary of the Main Method to Test Management Questions

ELZ as it is defined in the TOR does not quantitatively consider environmental factors other than light that are known to modify periphyton accrual over water depths spanning a littoral zone. The second management question, in particular, suggests that physiological adaptation to habitat including algal colonization rate, growth rate, and survival upon desiccation determine ELZ. It also suggests that only one environmental factor (PAR) is important in determining ELZ. Physiological responses to environmental conditions (e.g., colonization and growth rate) are lumped in with an environmental condition (light) as predictor variables but the reality is that the two are correlated (physiological adaptation is a response to environmental condition) and thus cannot be used together as predictor variables. A resulting equation would be unstable because one independent variable depends upon another. Algal biomass accrues according to environmental conditions of which light is a part and so we suggest that question 2 is really asking about what the relative importance is of several environmental factors that potentially determine growth and biomass of periphyton. Where PAR is sufficient to support photosynthesis (Krause-Jensen and Sand-Jensen 1998, Dodds *et al.* 1999, Wetzel 2001, Karlsson *et al.* 2009), production of algae may be limited by nutrient supply (Bothwell 1989, Biggs 2000, Guildford and Hecky 2000, Wetzel 2001) or temperature (Goldman and Carpenter 1974, Bothwell 1988) within available habitat that is influenced by reservoir filling and drawdown. The TOR included tasks to measure irradiance and temperature but did not suggest application of the data to the measurement of ELZ.

We revised the ELZ as defined in the TOR to include three environmental attributes (PAR, temperature, nutrient concentration) that can affect the accrual of periphyton biomass in a littoral zone and we derived equations to express the relationship between periphyton accrual and those attributes. That relationship can be linked to the area of the littoral zone and used to explore potential change in algal accrual with change in water surface elevation that can be affected by management actions. This change was discussed with representatives of BC Hydro and it was incorporated into the revised Terms of Reference (BC Hydro 2015.).

ELZ was defined as the amount of periphytic algal biomass (B) accrued on an area of substrata in a littoral zone with modification by light, temperature, and nutrient concentrations over time and space. This performance measure is called L as described in Equation 1 below. L is conceptually the same as ELZ but it is named differently because its calculation includes more variables having

ecological relevance than we understand were conceived for ELZ. B is in units of µg chl-*a*·cm^{-2} where chl-*a* is chlorophyll-*a*, a primary plant pigment that is commonly used as a measure of biomass in algae (Wetzel 2001, Behrenfeld *et al.* 2005). Chlorophyll-*a* can be approximately converted to carbon (e.g., Riemann *et al.* 1989, Cloern *et al.* 1995, Behrenfeld *et al.* 2005, Li *et al.* 2010) to yield units of mg C·m^{-2} for carbon budgeting if needed later, or to support other WUP studies of Upper Campbell and Lower Campbell reservoirs. These measurements represent the amount of carbon fixed per unit area that corresponds to a set of defined environmental conditions found at some time. The area of the littoral zone where periphyton grows is defined as the area of the reservoir bed that is shallower than the depth where PAR in the overlying water column is greater than 1% of that at the water surface (the standard measure of euphotic zone depth, Wetzel 2001). Area of a littoral zone can therefore be modified by processes that change PAR attenuation. Within the littoral zone, periphyton biomass can be vary for individual depth strata (i.e., bands at varying depths) depending on variability in environmental conditions. Summing the biomass of periphyton in each stratum provides an estimate of the periphyton biomass in the entire littoral zone.

The definition of L can be stated as follows:

Equation 1

$$L_t = \sum_{i=1}^{n} A_{it} B_{it}$$

where;

L is accrued B that may be modified by habitat conditions and area of flooded littoral habitat at time t,

A is area of stratum i within the littoral habitat having n strata at time t; and

B is biomass of accrued periphyton at time t in littoral depth stratum i, defined as:

Equation 2.

$$B_{it} = \beta_0 + \beta_1 x_{1it} + \beta_2 x_{2it} + \beta_3 x_{3it} + \varepsilon$$

is a multiple regression model explaining B at time t in depth stratum i as a function of x independent variables where β_0 is the regression intercept, x_1 is concentration of a nutrient that limits growth of periphyton, x_2 is PAR, x_3 is water temperature, $\beta_{1\ldots3}$ are regression coefficients, and ε is model error.

The combination of equations 1 and 2 will be used to answer management questions 1 through 3. The WUP is designed to keep water surface elevation within agreed ranges (Table 2). Equation 1 is sensitive to change in water surface elevation. The littoral area that can support periphyton biomass changes according to water surface elevation due to variability in the gradient of the beds of the

reservoirs (i.e., their bathymetry). Applying Equation 1 can answer management question 1. The littoral area for any water surface elevation was defined using a DEM that was developed in 2015 by Ecofish Research Ltd for each of Lower Campbell Reservoir and Upper Campbell Reservoir. Also in 2015, periphyton biomasses and various habitat attributes were measured at replicate stations in the summer and fall in Lower Campbell Reservoir. The same measurements were made in 2016 in Upper Campbell Reservoir. Resulting data were used to develop the regression model in Equation 2 to predict periphyton biomass as a function of the three main habitat conditions: nutrient concentrations, temperature, and PAR. One model was developed for Lower Campbell Reservoir and another was developed for Upper Campbell Reservoir. In 2015, all sampling was done in Lower Campbell Reservoir to coordinate activities between the present study and JHTMON-5 that was occurring at the same place and time. These two studies have elements that are closely linked, as will be explained below in relation to management question 4. In 2016, all sampling was done in Upper Campbell Reservoir. Values for the independent habitat attributes from each reservoir can be entered into the respective models to show sensitivity of algal biomass to change in the habitat attributes (nutrient concentrations, temperature, PAR) and thus answer management question 2. Once finalized, the models can be used to test different management scenarios, as might be required during consideration of changes to reservoir operations. They can be used to test sensitivity of periphyton biomass accrual in the littoral zone to decisions on change to the timing and magnitude of change of different water surface elevations and thus answer management question 3. A change to water surface elevation at a given time of year changes littoral area and potentially physical and chemical attributes that drive periphyton accrual as shown in Equations 1 and 2.

Accrual of periphyton biomass must be measured under a wide range of PAR, nutrient concentrations, and temperature (independent variables) for an informative regression model to be developed that can be effectively used to tease apart the relative influence of each environmental factor. In 2015, this range of conditions was captured by completing measurements of periphyton biomass and habitat attributes in the fall (low temperature, low PAR) and summer (high temperature, high PAR). The same temporal layout was used for sampling in Upper Campbell Reservoir in 2016. In addition, a gradient in nutrient concentrations was expected between the fall when mobile nutrients were likely flushed from forest soils and the summer, when there was expected to be lower flux of nutrients from the watershed to the reservoir. In each season, four sampling stations distributed throughout each reservoir were used to capture the variability of physical and chemical conditions that were needed for model development. At each station, periphyton biomass was measured on substrata at six depths covering potential ranges of PAR and temperature. Within a season, little to no variation in nutrient concentrations was expected between the surface and bottom of the littoral zone because water will be well mixed according to density gradients. This condition means that nutrient concentration may not be a good predictor of B within a given season. The influence of nutrient concentrations was hypothesized to be apparent based on comparison between data from summer and fall (mainly reflecting differences in nutrient mobility from forest soils).

A part of management question 2 that is not captured in equations 1 and 2, relates to the physiological adaptation of an algal mat to ambient conditions including cell colonization, growth, and survival, all of which contribute to biomass accrual on substrata. Colonization can be defined as the time for algal cells to become established on a substratum (a linear process) before growth determines change in algal biomass (a logarithmic process) (Bothwell 1989). Algal survival in question 2 is related to senescence as substrata become exposed to air when water surface elevation declines during drawdown of a reservoir. For practical purposes, algae exposed to air will not survive and will decay from living algae to detrital matter.

Accrual of periphyton was measured as change in biomass over time on standardized submerged substrata, similar to the approach used by Bothwell (1989) and Perrin *et al.* (1987) to examine growth of stream periphyton. Colonization period was the linear part of the accrual curve before logarithmic growth was detected. That period showed the time required for a rudimentary community to become established on newly flooded substrata (e.g., after rising of water surface elevation over previously dewatered substrata in a reservoir). Growth was considered the logarithmic phase of biomass accrual, reaching a maximum or peak biomass (PB; see Section 2.3) over time as determined by ambient habitat conditions (PAR, temperature, nutrient concentrations). Measurements in 2015 allowed two months for colonization and growth to PB to be achieved. Results showed no clear evidence of PB so the sampling duration was extended to three months in Upper Campbell Reservoir in 2016. These durations were more than double the time reported for periphyton to achieve PB in running waters (Bothwell 1989, Perrin *et al.* 1987).

Question 4 will be answered using multiple lines of evidence. There are few studies showing direct links between littoral periphyton production and littoral fish production in lakes, the one by Hecky and Hesslein (1995) being particularly noteworthy, and none in reservoirs that we are aware of. In contrast, there is well known evidence of fish feeding on invertebrates of different origin (e.g., Mehner *et al.* 2005, Vadeboncoeur *et al.* 2002, Weidel *et al.* 2008) and of littoral invertebrates feeding on detrital matter of different aquatic and terrestrial origins (France 1995, Solomon *et al.* 2008). Part of the challenge in quantifying links between algae and fish is that valued fish species using littoral habitat are commonly opportunistic in their foraging behaviour, targeting invertebrates produced from many sources. This behaviour is particularly true in Rainbow Trout (*Oncorhynchus mykiss*) and Cutthroat Trout (*O. clarkii*) (Nilsson and Northcote 1981, Perrin *et al.* 2006), which are the species of primary management interest. Hence, there may be some disconnect between production of algae and benthic invertebrates within a littoral zone and fish using that habitat in Upper and Lower Campbell reservoirs. Juvenile trout in particular might be expected to use the littoral habitat but the carbon present in the assemblage of ingested food may not be fixed there and instead be derived from terrestrial sources. This food web structure is different from pelagic habitats, where growth of obligate planktivores like Sockeye Salmon juveniles, for example, can be predicted from rates of pelagic primary production (Shortreed *et al.* 2001). That pelagic food web is much simpler and easier to model than littoral habitats.

Some insight for answering question 4 was provided in this study by analysing fish stomach content data from fish sampled with gill nets in Lower Campbell Reservoir in 2015 and in Upper Campbell Reservoir in 2016 as part of JHTMON-3 and JHTMON-5. Lab work to enumerate stomach contents, by taxon, was part of the present JHTMON-4 project. Analysis of these data involved examining whether food ingested by fish was typical of littoral benthos (e.g., benthic aquatic invertebrates), which would indicate that changes in production of littoral periphyton may influence availability of food for those fish. Conversely, if analysis showed that most food ingested by fish was not derived from littoral benthos (e.g., insects from the forest canopy), then changes in production of littoral periphyton may not strongly influence food availability for those fish.

Fish stomach data alone are not sufficient to unequivocally determine sources of food for fish because they only relate to the time when samples were collected and fish diets may vary. This problem can be resolved by collecting fish stomachs at several times and conditions, but that option was not available in this study because fish stomachs were only collected at a single time during either JHTMON-3 or JHTMON-5. A method was therefore needed that integrated the relative contributions of different food sources to fish diets over a wide temporal scale. Furthermore, stomach contents analysis does not necessarily provide clear information about the basal source of the carbon present in food sources. Fish may ingest littoral invertebrates that gain energy from living periphyton or from benthic detrital matter (e.g., small particulate organic matter (SPOM)) that is not related to periphyton production, or from a mixture of the two. They may feed on zooplankton (which predominantly derive energy from pelagic production) at some times and benthos at other times (Nilsson and Northcote 1981). Periphyton itself can also vary in composition, as it includes a living algal component, but also bacteria, fungi and non-living organic material (Schroeder *et al.* 2013). Even organic matter in different places of the littoral zone may come from different sources, including: terrestrial leaf litter, organic matter from the original forest floor that was flooded at the time of reservoir formation, macrophyte decay, or detritus from senesced periphyton. Analysis of sediment in John Hart Reservoir (immediately downstream of Lower Campbell Reservoir) found that the flooded forest floor remains intact and represents a large pool of labile organic matter (Perrin *et al.* 2012, Abell *et al.* 2017). Given the potentially different sources of food for fish, other lines of evidence were needed to examine links between periphyton and fish using littoral habitat.

Stable isotope techniques were applied to fill this void. Stable isotopes of nitrogen and carbon were measured in samples from fish, invertebrates (benthic invertebrates, littoral invertebrates, terrestrial invertebrates, zooplankton), and basal nutrient sources in littoral areas, including small particulate organic matter (SPOM), terrestrial vegetation, attached algae, and littoral periphyton that includes non-algal material. Samples were collected from Lower Campbell Reservoir in 2015 and Upper Campbell Reservoir in 2016. Isotopic signatures were then used in mixing models to isolate the relative contribution of periphyton to fish diets in Upper Campbell and Lower Campbell reservoirs.

1.4.3.Stable Isotope Techniques

Substantial information regarding the structure and functioning of lake food webs can be gained by using stable isotopes to reconstruct the diets of lake biota (Vander Zanden and Vadeboncoeur 2002, McIntyre *et al.* 2006). JHTMON-4 used stable isotope analysis (SIA) of nitrogen and carbon of fish tissues and their potential diet items to quantify energy flow to fish from the algal component of periphyton, and from other basal nutrient sources in the littoral zone. Nitrogen isotope ratios ($\delta^{15}N$) are commonly used to assess the trophic position of species in a food web (DeNiro and Epstein 1981, Peterson and Fry 1987), whereas carbon isotope ratios ($\delta^{13}C$) are commonly used to indicate the sources of primary production (DeNiro and Epstein 1978, Peterson and Fry 1987). The main premise is that the isotopic ratios in the tissues of consumers represent the isotopic ratios of their diet. In other words, you are what you eat. In lakes, fish that are high in the lake food web tend to have the highest $\delta^{15}N$ signatures. In contrast, fish that have higher $\delta^{13}C$ signatures tend to have a greater reliance on terrestrial sources of carbon than zooplankton.

Using both $\delta^{15}N$ and $\delta^{13}C$ together allows for the development of stable isotope mixing models, which can estimate the contributions of different prey sources to a consumer's diet (Semmens *et al.* 2009, Parnell *et al.* 2010). The primary species of interest in JHTMON-4 are Cutthroat Trout and Rainbow Trout. Sampling was designed to understand the relative contribution of periphyton to these two fish species, which are the resident fish species of primary management concern in reservoirs and lakes of the Campbell River system. Primary diet items for Cutthroat Trout and Rainbow Trout include zooplankton, benthic/littoral invertebrates, terrestrial invertebrates that fall into littoral areas (allochthonous source), and, for Cutthroat Trout, other fish, including Threespine Stickleback (*Gasterosteus aculeatus*), Sculpin spp. (*Cottus* spp.), and juvenile trout (*Oncorhynchus* spp.). Attached algae is one of several primary nutrient sources for the littoral prey of Cutthroat Trout and Rainbow Trout. Thus, the JHTMON-4 study was designed to obtain representative samples of Cutthroat Trout and Rainbow Trout, their potential diet items and basal nutrient sources in littoral habitats. Stable isotope data can be obtained from tissue samples of individuals (e.g., fin clips, muscle samples), from whole organisms (e.g., whole insects), or from composite samples (e.g., periphyton, zooplankton and SPOM samples).

2. METHODS

2.1. Study Area

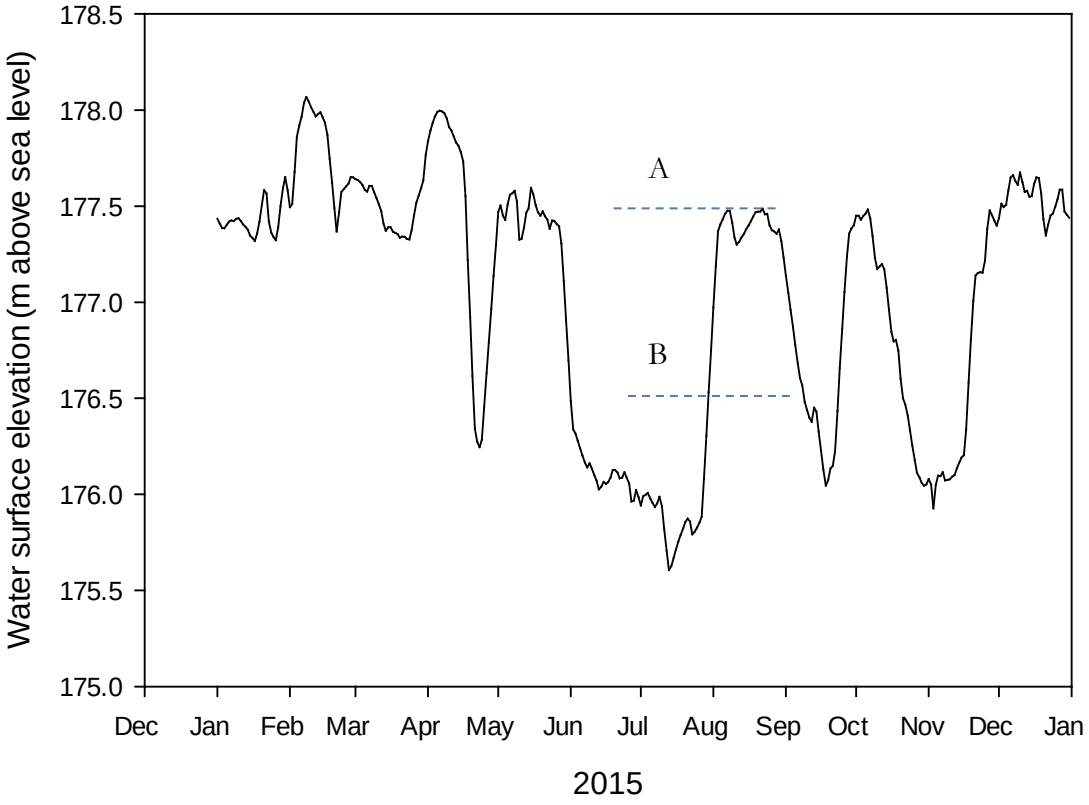
The study reservoirs are within the Campbell River watershed, which originates in the Vancouver Island Mountain Range at elevations up to 1,900 m (Map 1). Headwaters flow north from Strathcona Park into Buttle Lake and then into Upper Campbell Reservoir that supplies most storage for the Campbell River hydroelectric generating system. From Upper Campbell Reservoir, water flows through the 65 MW Strathcona generating station into Lower Campbell Reservoir, where water flows through the 47 MW Ladore generating station and into John Hart Reservoir, which supplies water for the 126 MW John Hart generating station via three wood stave penstocks

and surge towers. The John Hart water intake, penstocks, and power generating station are being replaced as part of upgrades to infrastructure in the Campbell power generating system.

Lower Campbell Reservoir has a length of 15 km. It is <0.5 km wide near the inflow from Upper Campbell Reservoir, it broadens to 2 km wide in the central basin and narrows to small channels of 0.1 to 0.2 km at the east end where water is released to John Hart Reservoir. There is typically no regular seasonal drawdown, but the water surface elevation can vary within seasons according to water and power production management within the whole Campbell system. In 2015, the elevation ranged over 2 m (177.6 – 175.6 m) during the biologically active period of May through October in 2015 and over 3 m for all of calendar 2015 (Figure 1). During the "peak summer season" defined in the WUP as June 21 to September 10, the water surface elevations were 175.6 – 177.5 m, which was about double the target range in the WUP (Table 2). The exceedance was 1m below the target low elevation of 176.5 m. At water elevation of 178.0 m (approximately full supply), the reservoir surface area is 26.4 km^2, total volume is 460.6 x 10^6 m^3, mean depth is 17.5 m, and maximum water depth is 71.3 m[1].

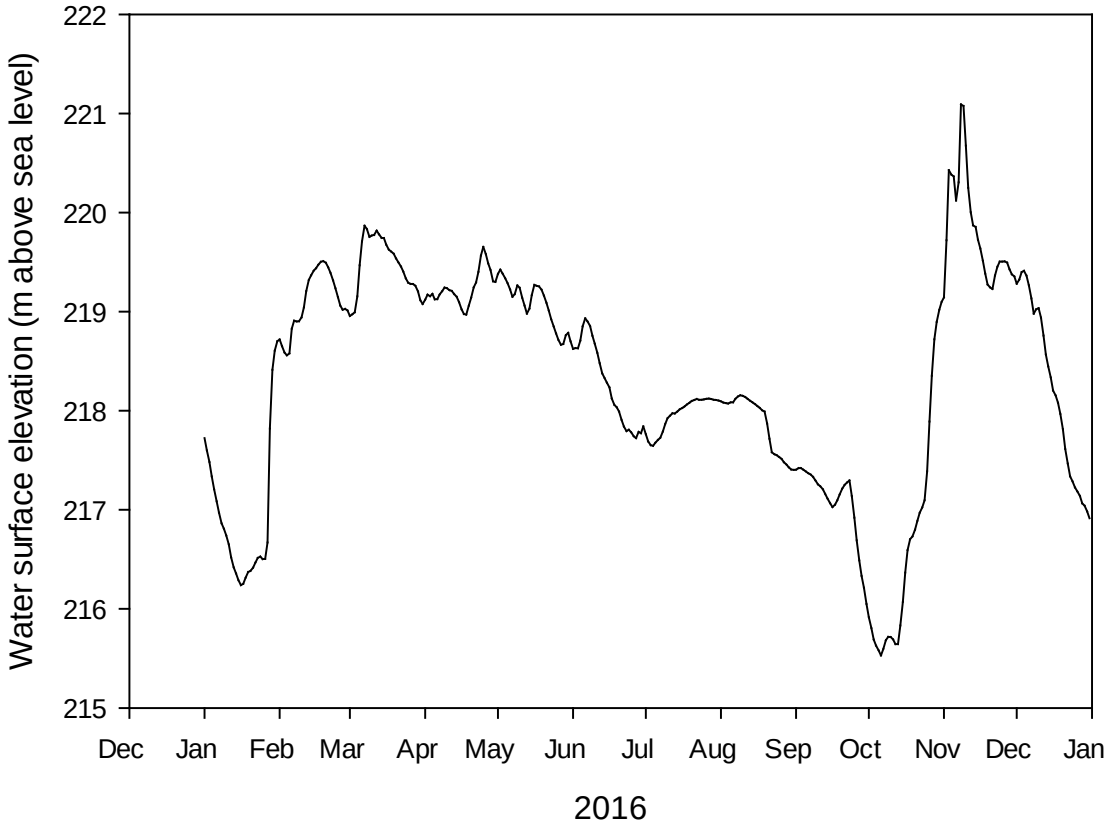
[1] Morphometric data are from a DEM developed by Ecofish Research Ltd. 2015.

Figure 1. **Mean daily water surface elevation in Lower Campbell Reservoir, 2015. Horizontal line A shows the "peak summer season" preferred maximum water surface elevation as defined in the Water Use Plan and line B shows the preferred minimum elevation.**



Upper Campbell Reservoir is operated with seasonal drawdown. It has a length of 19.6 km along its central north to south axis and a 5 km long arm extending from the Elk River that flows into the reservoir from the west (Map 1). Near the inflow from Buttle Lake the reservoir is 600 – 800 m wide, it broadens to 1,800 m downstream of the Elk River arm and then narrows to 600 m near the Strathcona Dam. The water surface elevation is low in winter, it increases with rising storage in spring, it declines in summer, and rises again in the fall according to water and power production management within the whole Campbell system. In 2016, the elevation ranged over 6 m (215.5 – 221 m) (Figure 2). During the "peak summer season" defined in the WUP as June 21 to September 10, the water surface elevations were 217.3 – 218.2 m, which was within the target range in the WUP (Table 2). At water elevation of 221 m (approximately full supply), the reservoir surface area is 30.8 km^2, total volume is 688 x 10^6 m^3, mean depth is 22.3 m, and maximum water depth is 66 m.

Figure 2. Mean daily water surface elevation in Upper Campbell Reservoir, 2016.



2.2. Bathymetric Survey and Digital Elevation Model (DEM)

2.2.1. Field

A bathymetry survey of Lower Campbell Reservoir was completed during October 20 – 24, 2015 and a survey of Upper Campbell Reservoir was completed during August 17 – 21, 2014 as part of JHTMON-3 (Hatfield *et al.* 2015). Data from the surveys were then used to develop a digital elevation model (DEM) for each reservoir to derive a relationship between littoral area and water surface elevation.

The survey of Lower Campbell Reservoir was completed using a Lowrance LCX-27C depth sonar and GPS rover system. Bathymetric data collection was completed following standard data collection guidelines (OMNR 2004, Wilson and Richards 2006, MOE 2009). The depth sonar uses a single frequency transducer of 200 kHz to measure the distance from sensor to the lake bottom with a stated vertical accuracy of ±0.10 m. The GPS system of the sonar unit has a horizontal accuracy of +/- 3 m, depending on satellite coverage (Lowrance 2006), which will be about 3% of a 100 m spacing between two transects. The GPS system collected data in a proprietary coordinate system owned by Lowrance, the data were then converted to the WGS 1984 coordinate system following

the standard methodology (MOE 2009). Further details about field conditions and data quality assurance are presented in the Year 1 Annual Report (Perrin *et al.* 2016).

The survey of Upper Campbell Reservoir was undertaken using an echo sounding system that consisted of a BioSonics DTX echo sounder and two split-beam transducers paired with a Garmin model 546 differential GPS. Further details about the methods used to survey Upper Campbell Reservoir are presented in Hatfield *et al.* (2015).

2.2.2. Bathymetric Mapping

DEMs were developed for both reservoirs based on the bathymetry surveys. Individual bathymetric data points (depths) collected in the field were converted into elevations by subtracting the depths from the hourly average reservoir elevations observed at the time of the surveys.

During the bathymetry survey of Lower Campbell Reservoir, the maximum observed average daily water surface elevation was 176.6 m. This was less than the 2015 annual maximum average daily water surface elevation of 178.068 m observed on February 8, 2015. To generate a DEM that reflected the maximum average daily water surface elevation observed in 2015, the 2015 data were added to existing shoreline bathymetric data provided by BC Hydro for elevations from 176.6 m to 178.068 m.

The DEM of Upper Campbell Reservoir was developed by combining the field data collected in 2014 with an existing bathymetry map provided by BC Hydro (Kaulback, pers. comm. 2014). This map was prepared with data from: pre-flooding maps (1949 and 1951); a multi-beam bathymetry survey conducted within 200 m upstream of Strathcona Dam (2009), and; nearshore (EL. > 211.90 m) stereo DEM data collected during an undated survey (Kaulback, pers. comm. 2014). The maximum elevation of the DEM was 217.1 m, which was the water surface elevation at time of the 2014 survey. The maximum water elevation in 2016 was 221.1 m and therefore it was necessary to extend the stage–area relationship to this higher elevation. This was done by interpolating data from a DEM that included elevations up to 231 m (Kaulback, pers. comm. 2014).

For both reservoirs, DEMs were generated with the ArcGIS commercial mapping software. The Inverse Distance Weighted (IDW) method of interpolation was used to generate an elevation surface, with 5 m horizontal resolution, from the elevations data inputs. The surface area and volume calculations were completed using the ArcGIS Surface Volume tool with 0.1 m depth intervals. The littoral zone was classified as the areas where the reservoir beds received >1% of surface irradiance, based on PAR measurements collected in the field (Section 2.4). The pelagic zone included all other areas that were in deeper waters.

2.3. Periphyton Biomass Accrual

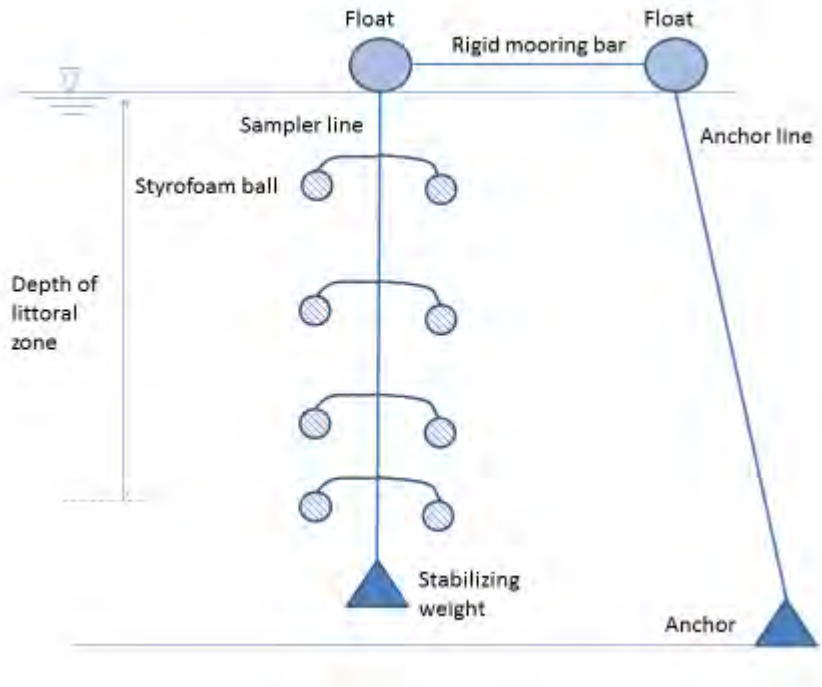
An increase in periphyton biomass on substrata over time is called algal accrual, which is a function of cell colonisation, cell growth, and losses associated with senescence, invertebrate grazing, and sloughing. There can be differences in the amount of biomass accruing on different natural littoral substrata because of variation in surface texture. To avoid that surface effect, a standard artificial

substratum was used for measurements of biomass accrual. Styrofoam was selected, following its successful application by Bothwell (1989). Styrofoam balls were suspended on lines from surface floats at different water depths, thus removing the accrued periphyton from exposure to grazing by benthic invertebrates. This standardization was needed because of the need to examine variability in algal accrual associated with PAR, temperature, and nutrient concentrations, and minimize variance associated with other factors.

A periphyton sampler consisted of an array of Styrofoam balls, each having a diameter of 2.5 cm, attached to a 5/16 inch nylon double braid mooring line that extended over the depth of the euphotic zone (Figure 4). Each Styrofoam ball was attached to a halibut setline clip using a cable tie that was threaded through the ball and around one end of the clip (Figure 3). In Lower Campbell Reservoir during 2015, 8 balls were clipped onto the mooring line at each of 1 m, 7 m, and 14 m depths, 1 other ball was clipped to the line at each of 4 m, 10 m, and 18 m depths, and another ball was clipped at the 1 m depth (28 balls on each line). In Upper Campbell Reservoir during 2016, 8 balls were clipped onto the line at each of 1 m, 4 m, 7 m, 10 m, 14 m, and 18 m depths and another ball was clipped onto the line at the 1 m depth (49 balls on each line). The larger number of balls was used in 2016 to increase sample size for analysis of periphyton accrual. The depth range of 18 m extended over the depth of the euphotic zone where PAR exceeded 1% of that immediately under the water surface. This range of sampling depths provided a range in PAR and temperature. The vertical line with Styrofoam balls was suspended from a float and held in position using a rigid mooring bar that was connected to a separate float, anchor line, and anchor as shown in Figure 4. By being suspended from a float on the water surface, the balls remained at a fixed depth regardless of change in water surface elevation.

Figure 3. **Image of Styrofoam balls clipped on to a mooring line. The balls provided substrata for colonization and growth of attached algae.**

Figure 4. Schematic image of rigging used to deploy attached algae sampling apparatus.



One mooring line (each configured as shown in Figure 4) was placed at each of four sampling stations in each reservoir. Sampling occurred in summer (July 24 through September 25, 2015) and fall (September 25 through November 27, 2015) in Lower Campbell Reservoir and during summer (June 17 through September 27, 2016) and fall (September 9 through December 13, 2016) in Upper Campbell Reservoir (Map 2 and Map 3, respectively). Based on the results from 2015, the duration of the sampling periods was increased in 2016 to allow greater time for algal biomass to reach maxima. Map 2 shows five sampling stations in Lower Campbell Reservoir but hardware at the LCR-PERWQ1 station was vandalized within the first week after installation on July 31, 2015 and was replaced with LCR-PERWQ1A. In Upper Campbell Reservoir, station UCR-PERWQ2 was lost after day 33 during the fall sampling in 2016 due to the station being submerged during a period of high reservoir elevation that reflected exceptional flood conditions. The mooring was not found after the water surface elevation declined, which suggests that the mooring was subsequently removed by people not involved in the project. The mooring was not replaced. In each reservoir, the stations were widely distributed and placed where water depths were at least 20 m to allow unobstructed suspension of the mooring lines (Figure 3 and Figure 4) that extended to a depth of 18 m and included most of the euphotic zone (depths where PAR is >1% of that at the water surface) (Section 3.1).

Periphyton accrual was measured following sequential collection of the eight Styrofoam balls at each depth (1 m, 7 m, and 14 m at each site in Lower Campbell Reservoir and 1 m, 4 m, 7 m, 10 m, 14 m, and 18 m at each site in Upper Campbell Reservoir) over the duration of the summer and fall sampling periods. Samples were collected once per week during the two eight-week sampling periods in Lower Campbell Reservoir and once every 11-12 days during the two twelve-week sampling periods in Upper Campbell Reservoir. A ball was unclipped from the mooring line and placed into a plastic vial that was labelled with date, station, and position on the vertical line. The vials were capped and packed on ice for delivery to Campbell River where the samples were stored at -15ºC until shipment to the lab. On the final sampling date of each series in Lower Campbell Reservoir, the final ball was removed from the 1 m, 7 m, and 14 m depths and the single ball at each of the 4 m, 10 m, and 18 m depths was removed and processed the same way for measurement of biomass at all six depths. Once all samples were collected for a sampling series (summer or fall), they were packed on dry ice and shipped frozen to the lab for analysis of chl-*a* concentration using extractions in acetone followed by analysis of chl-*a* concentration by fluorometry (Arar and Collins 1997). Units of concentration were μg chl-a·sample^{-1}. Values were corrected to areal units (μg chl-a·cm^{-2}), where the sampling area was the surface area of the Styrofoam ball (38.5 cm^2). Three replicate blanks that were not deployed at sampling sites were processed the same way to test for contamination: none was found. The extra ball that was attached at the 1 m depth on each line was also removed on the final sampling date of each series for enumeration of algal species composition. Each of those balls was placed in a vial with enough deionized water to cover the ball and preserved in Lugol's solution for later identification and enumeration of cells by species. In the lab, cells were removed from the Styrofoam using a fine spray of deionized water from a dental cleaning instrument inside the sample vial. Contents were dispensed into an Utermöhl chamber to settle over 24 hours. Cell counts were made at 500× magnification under an inverted microscope. Only cells containing cytoplasm were enumerated. A minimum of 100 cells of the most abundant species and a minimum of 300 cells in total were counted per sample. Diversity metrics, including species richness (number of unique species per sample) and Simpson's Diversity Index were calculated from the cell counts.

Curves were produced from the biomass accrual measurements to present chl-*a* concentration as a function of time (days). Each of the four stations in each reservoir was considered an independent replicate for the calculation of mean chl-*a* concentration ± standard deviation at each of the three depths at which weekly samples were collected (1 m, 7 m, and 14 m in Lower Campbell Reservoir and 1 m, 4 m, 7 m, 10 m, 14 m, and 18 m in Upper Campbell Reservoir). Peak biomass (PB) was the highest concentration of chl-*a* attained on a Styrofoam ball over the time of measurement. A general linear model for analysis of covariance (ANCOVA) was used to test for homogeneity of slopes of the regression lines wherein the dependent variable was $\log_{10}$ of 1+chl-a concentration (a $\log_{10}$ transformation was applied to produce a straight line that is required for ANCOVA and 1 was added to each value to avoid negative numbers), the independent covariate was days of incubation, and the independent variable was depth (m) as follows:

Equation 3.

$$\boldsymbol{log_{10}(1 + [chla]) = Constant + Depth + Days + (Depth * Days)}$$

If the interaction term $(Depth * Days)$ was significant (p<0.05), slopes of the regression lines were considered different because it indicated that algal biomass, measured as chl-*a* concentration, differed over time between the three depths (hence a difference in slope of the regression line).

2.4. Periphyton Habitat Attributes

PAR, temperature, and nutrient concentrations (predictor variables in Equation 2) were measured during the sampler incubations at both reservoirs (Table 4, Table 5) to correspond with the measurements of chl-*a* concentration. Temperature was recorded in 30-minute intervals using a Tidbit temperature logger attached to each of the six periphyton sampling positions on each mooring line. PAR was measured weekly at 1 m intervals over a vertical profile from surface to the bottom of each sampler at each station using a LiCor LI250A irradiance meter equipped with a spherical quantum sensor (LiCor Inc. Lincoln, Nebraska). The instantaneous PAR data was correlated with PAR that was continuously logged at a base station (Onset pyranometer sensor and microstation logger, Onset Computer Corporation, Bourne Massachusetts) located on the Strathcona Dam, allowing the continuous measurements to be corrected for attenuation in water to provide a continuous record of PAR at each position on the mooring line during incubation.

One water sample was collected from the surface and one 2 m off bottom at the start and finish of the summer and fall sampling series in each reservoir for analysis of total nitrogen (TN), ammonium (NH_4-N), nitrate (NO_3-N), soluble reactive phosphorus (SRP), total dissolved phosphorus (TDP), and total phosphorus (TP). The end-of-summer sample was the same as the beginning-of-fall sample. One field duplicate and a field blank (deionized water from the lab) were processed using the same procedures used for the regular samples as part of QA procedures on each sampling day. Samples for analysis of dissolved fractions (SRP, TDP, NO_3-N, NH_4-N) were filtered in the field through Waterra 0.45 µm FHT-45 polyethersulphone filters[2] using an Alexis peristaltic pump[3]. The TN and TP samples were preserved with H_2SO_4. The NH_4-N samples were also preserved with H_2SO_4 following filtration. The samples were packed on ice and submitted for analysis within 24 hours of sampling to ALS Environmental in Burnaby using standard methods (APHA *et al.* 2014, Table 3).

[2] http://www.waterra.com/pages/Product_Line/filters/filters_2011.html

[3] http://pegasuspumpcompany.com/alexis-peristaltic-pumps

Table 3. Methods and detection limits for laboratory nutrient analysis.

Variable	Method	Detection Limit ($\mu g\ L^{-1}$)
SRP	Colorimetry following field filtration (0.45 µm).	1.0
TDP	Colorimetry following field filtration (0.45 µm) and digestion by persulphate oxidation.	2.0
TP	Colorimetry following digestion by persulphate oxidation.	2.0
NO_3-N	Ion chromatography with conductivity and/or UV detection following field filtration (0.45 µm).	5.0
NH_4-N	Fluorescence following field filtration (0.45 µm).	5.0
TN	Colorimetry following digestion by persulphate oxidation.	30.0

Table 4. Sampling undertaken at Lower Campbell Reservoir in 2015. Data collected for JHTMON-5 (zooplankton and fish) were also analyzed (see text).

Component	Site	Method	Sampling Date	UTM (Zone = 10U)	
				Easting	Northing
Water chemistry and physicochemical vertical profiles	LCR-PERWQ1	Van Dorn grabs and YSI seabird	31-Jul-15	327193	5542199
	LCR-PERWQ1A		25-Sept-15, 27-Nov-15	323326	5543836
	LCR-PERWQ2		31-July-15, 25-Sept-15, 27-Nov-15	326070	5545145
	LCR-PERWQ3		31-July-15, 25-Sept-15, 27-Nov-15	324154	5544652
	LCR-PERWQ4		31-July-15, 25-Sept-15, 27-Nov-15	327221	5542559
Benthic invertebrates	LCR-LKIV01	Rock Baskets	07-Aug to 25-Sep, 2015	327212	5542144
	LCR-LKIV02		07-Aug to 25-Sep, 2015	326127	5545273
	LCR-LKIV03		07-Aug to 25-Sep, 2015	324185	5544832
	LCR-LKIV04		07-Aug to 25-Sep, 2015	327250	5542638
	LCR-PERWQ1A	Ponar grabs	13-Oct-15, 13-Nov-15	323086	5543498
	LCR-PERWQ2		13-Oct-15, 13-Nov-15	326134	5545255
	LCR-PERWQ3		13-Oct-15, 13-Nov-15	324136	5544823
	LCR-PERWQ4		13-Oct-15, 13-Nov-15	327243	5542624
Carbon sources	LCR-PERWQ3	Rock scrapings	25-Sep-15	324185	5544832
	LCR-PERWQ1	Leaf litter, and macrophyte biomass	02-Oct-15	327212	5542144
	LCR-PERWQ2		02-Oct-15	326127	5545273
	LCR-PERWQ3		02-Oct-15	324185	5544832
	LCR-PERWQ4		02-Oct-15	327250	5542638
	LCR-PERWQ1A	Mooring line scraping	02-Oct-15	323326	5543836
	LCR-PERWQ2		02-Oct-15	326070	5545145
	LCR-PERWQ3		03-Oct-15	324154	5544652
	LCR-PERWQ4		04-Oct-15	327221	5542559
	LCR-PERWQ1A	Scraping of 4 acrylic plates on periphyton mooring lines	25-Sept-15, 27-Nov-15	323326	5543836
	LCR-PERWQ2		25-Sept-15, 27-Nov-15	326070	5545145
	LCR-PERWQ3		25-Sept-15, 27-Nov-15	324154	5544652
	LCR-PERWQ4		25-Sept-15, 27-Nov-15	327221	5542559
PAR at surface[1]	LCR-LKPAR	Land PAR station download	23-Oct-15, 30-Nov-15	314729	5541619

[1] Collected at Strathcona Dam

Table 5. Sampling undertaken at Upper Campbell Reservoir in 2016. Data collected for JHTMON-5 (zooplankton and fish) were also analyzed (see text).

Component	Site	Method	Sampling Date	UTM (Zone = 10U)	
				Easting	Northing
Water chemistry and physicochemical vertical profiles	UCR-PERWQ1	Van Dorn grabs and YSI seabird	28-June-16, 27-Sept-16, 13-Dec-16	307740	5531389
	UCR-PERWQ2		28-June-16, 27-Sept-16, 13-Dec-16	311231	5536329
	UCR-PERWQ3		28-June-16, 27-Sept-16, 13-Dec-16	313184	5537707
	UCR-PERWQ4		28-June-16, 27-Sept-16, 13-Dec-16	314838	5539808
Benthic invertebrates	UCR-PERWQ1	Rock baskets	17-June to 19-Oct, 2016	307740	5531389
	UCR-PERWQ2		17-June to 19-Oct, 2016	311231	5536329
	UCR-PERWQ3		17-June to 19-Oct, 2016	313184	5537707
	UCR-PERWQ4		17-June to 19-Oct, 2016	314838	5539808
	UCR-PERWQ01	Ponar grabs	02-Aug-16, 19-Oct-16	307740	5531389
	UCR-PERWQ02		02-Aug-16, 19-Oct-16	311231	5536329
	UCR-PERWQ03		02-Aug-16, 19-Oct-16	313184	5537707
	UCR-PERWQ04		02-Aug-16, 19-Oct-16	314838	5539808
Carbon sources	UCR-PERWQ01	Rock scrapings	19-Jul-16, 26-Aug-16, 27-Sep-16, 19-Oct-16	307740	5531389
	UCR-PERWQ02		19-Jul-16, 26-Aug-16, 27-Sep-16, 19-Oct-16	311231	5536329
	UCR-PERWQ03		19-Jul-16, 26-Aug-16, 27-Sep-16, 19-Oct-16	313184	5537707
	UCR-PERWQ04		19-Jul-16, 27-Sep-16, 19-Oct-16	314838	5539808
	UCR-PERWQ01	Grab sampling of leaf litter and macrophytes	19-Jul-16, 19-Oct-16	307740	5531389
	UCR-PERWQ02		19-Jul-16, 19-Oct-16	311231	5536329
	UCR-PERWQ03		19-Jul-16, 19-Oct-16	313184	5537707
	UCR-PERWQ04		19-Jul-16, 19-Oct-16	314838	5539808
	UCR-PERWQ01	Mooring line scraping	15-Aug-16, 19-Oct-16	307740	5531389
	UCR-PERWQ02		19-Oct-16	311231	5536329
	UCR-PERWQ03		19-Oct-16	313184	5537707
	UCR-PERWQ04		19-Oct-16	314838	5539808
PAR at surface[1]	LCR-LKPAR	Land PAR station download	27-Sep-16, 13-Dec-16	314729	5541619

[1] Collected at Strathcona Dam

The nutrient variable to be used in Equation 2 was identified based on molar N:P ratios. The molar ratio of bioavailable nitrogen: phosphorus in water can indicate whether nitrogen (N) or phosphorus

(P) potentially limits algal production, given that N or P, or a combination of N and P, are growth-limiting nutrients in coastal lakes and reservoirs (Johnston *et al.* 1999, Perrin *et al.* 2006, Hyatt and Stockner 1985). The ratio was calculated based on bioavailable forms of N, represented by dissolved inorganic nitrogen (called DIN and includes NH_4-N plus NO_3-N and NO_2-N), and P, which is best represented by SRP when it can be detected. If DIN could not be detected using standard low level wet chemistry techniques, total nitrogen (TN) was used. If SRP was not detected (SRP < 1 $\mu g \cdot L^{-1}$), TDP was used. If TDP could not be detected (TDP < 2 $\mu g \cdot L^{-1}$), TP was used. If TP could not be detected (TP < 2 $\mu g \cdot L^{-1}$), extreme limitation of algal growth by phosphorus was assumed. Rhee (1978) showed that for a given species of algae, there is a sharp transition between P-limited and N-limited growth. The particular N:P ratio (using bioavailable forms of N and P) at which the transition between N and P-limitation occurs is species dependent, varying from as low as 7:1 for some diatoms (Rhee and Gotham 1980) to as high as 45:1 for some blue-green algae (Healey 1985). In aquatic ecosystems that support many algal species, the growth of most species will be N-limited at low supply ratios and P-limited at high supply ratios. Guildford and Hecky (2000) found that among lakes from wide ranging regions, N-deficient growth of microalgae occurs at molar nitrogen: phosphorus <20 while P-deficient growth occurs at nitrogen: phosphorus >50. At intermediate ratios, either N or P can be deficient among the algal species within an assemblage. To determine the nutrient and form of nutrient to be used in the Equation 2, the molar N:P was calculated from results of the nutrient sampling described above. If the molar N:P for any site was >50, the concentration of SRP was used. If molar N:P for any site was <20, the concentration of DIN was used. If the molar N:P was between 20 and 50, the concentration of SRP and DIN was used in Equation 2, each nutrient being an independent predictor variable.

Other measurements were made for descriptive purposes. Depth profiles of turbidity, conductivity, temperature, and dissolved oxygen were measured with a YSI Model 6920 Sonde (YSI Inc. Yellow Springs, Ohio) or Sea-Bird Electronics SBE19plusV2 CTD (Sea-Bird Electronics, Bellevue, Washington) on each water sampling date. The temperature data from these profiles were used to examine temperature stratification differences among stations on the sampling dates. Time course change in water surface elevation, reservoir volume, inflow, and outflow, in daily time steps for each sampling series, was accessed from Power Records at BC Hydro.

2.5. Linking Periphyton with Habitat Attributes

A separate multiple regression model (Equation 2) was developed to examine links between peak biomass (PB) and the three habitat attributes (PAR, temperature, nutrient concentrations) for each reservoir. The model was used to examine:

1. The *combined* contribution of the three habitat attributes (PAR, temperature, nutrient concentrations) to determining periphyton biomass accrual.

2. The relative contribution of each of the three habitat attributes (PAR, temperature, nutrient concentrations) to determining periphyton biomass accrual.

The regression yielded an equation (a model) that retained original units of measurement and allowed quantitative prediction of the dependent variable with estimated error. The dependent variable was PB (maximum chl-*a* concentration during the sampling time series). PB in Lower Campbell Reservoir was recorded on the final sampling day of each series (day 42-56, mean ± SD = 55 days ± 4.7) because chl-*a* concentration did not peak during the incubation periods in any of the series in 2015. In Upper Campbell Reservoir, PB was the highest concentration observed within each series up to 60 days of incubation (53.8 days ± 9.7) so that results could be compared between the two reservoirs. The independent variables were PAR, temperature, and nutrient concentration. Temperature was the mean temperature over a sampling series as logged by the Tidbit logger at the same depth as the respective Styrofoam ball on a mooring line. Thus, the temperature data were specific to each mooring line and depth of periphyton sample. Nutrient concentrations were average concentrations in samples collected in the euphotic zone at the start and finish of each sampling series. PAR was accumulated PAR ($mol \cdot m^{-2}$) specific to a given depth over the duration of a sampling series calculated as follows. The proportion of PAR in water at a specific depth relative to PAR measured in the air immediately above the water surface and also to PAR measured in water just below the surface was calculated for each of the weekly PAR profiles. A logarithmic model was fit to the data from each week (PAR attenuates logarithmically in water). Each equation was back transformed and used to predict the proportion of PAR in water relative to the surface PAR at each depth where a Styrofoam ball was located. These depth-specific predicted proportions of surface PAR were used as correction factors to calculate PAR at a specific sampler depth from the continuous record of PAR in air that was logged on the Strathcona Dam. Each weekly correction factor was employed for the period beginning on the day of one PAR profile and ending on the day before the next PAR profile. Those predicted PAR values were in units of $\mu mol \cdot m^{-2} \cdot sec^{-1}$. The predicted PAR values were multiplied by the number of seconds in each 15 min logging time interval (900 s). The sum of those 15-minute depth-corrected PAR values over each weekly calculation period resulted in units of $mol \cdot m^{-2}$ for the period of incubation of the periphyton samplers. This approach resulted in a single value of accumulated PAR to which each Styrofoam ball was exposed during the time of incubation.

In 2015, the air PAR data from the Strathcona Dam were missing for two periods: July 31 to Aug 8, and Oct 23 to Oct 28. Accumulated PAR on August 9 was substituted for each day in the first period based on the assumption that PAR on August 9 was close to that on each day of the preceding week. In the case of the October 23 to 28 missing data, the data from October 22 and 23 were used to fill in the missing values. For practical purposes, these substitutions were considered preferable to loss of corresponding observations of PB for solving Equation 2.

Regression analysis proceeded in the following steps. First, scatterplots were examined and Pearson correlation coefficients were calculated between pairs of the three independent variables to determine if any relationships existed between them and to determine whether the variables provided unique information. If any two of the independent variables were found to be statistically

redundant, the variable with the most direct and explainable relationship to algal biomass was retained and the other variable was deleted. The selected independent variables (three or less) were tested for normality using the Shapiro-Wilk normality test (α=0.05) and they were examined for both skewness and kurtosis of the sampling distribution. PAR was $\log_{10}(x+1)$ transformed to improve normality and reduce skew because it changes logarithmically with water depth. All variables were used in a complete regression analysis (no backward or forward selection), and models with and without an interaction between $\log_{10}$PAR and water temperature were tested. The interaction between two or more independent variables tested for a non-additive effect on the dependent variable, in this case PB. Goodness of fit of the model to the data was determined from the value of the multiple correlation coefficient (R^2) and the standard error of the estimate. The absolute value of standardized regression coefficients (subtracting the sample mean from a measured value and then dividing these new values by the standard deviation of the variable) indicated the relative importance of the predictor variables in determining change in algal biomass. Use of standardized regression coefficients removed bias due to different scales of measurement when comparing coefficients. Non-standardized coefficients were used in the regression equation used to predict PB to derive predictions based on the correct units of measurement of each independent variable

2.6. The Performance Measure Called ***L***

The performance measure, ***L*** (Equation 1) was calculated as iterative sums of products of periphyton biomass (Equation 2) and areas of submerged littoral strata. For Lower Campbell Reservoir, Equation 1 was solved for the maximum operating level[4] of 178.0 m, in addition to elevations of 177.0 m, 176.0 m, and 175.0 m, which covered the range of elevations recorded in 2015. For Upper Campbell Reservoir, Equation 1 was solved for the maximum operating level of 221 m and in 1 m intervals down to 215 m that was close to the lowest elevation recorded in 2016 (Figure 2). For each elevation, values of the independent variables were changed within ranges that were measured in 2015 and 2016 to show percent change in periphyton biomass extending throughout the littoral zone (depths extending from the surface to that corresponding with 1% of surface irradiance). For example, in Lower Campbell Reservoir, during a decline in water surface elevation from the maximum operating elevation of 178 m down to 177 m, ***L*** will show the amount by which algal biomass is expected to change. That value can be expressed as a percent change from the maximum operating elevation. This simulation accounts for the death of periphyton due to dewatering at the upper part of the littoral zone, in addition to change in periphyton accrual in the lower part of the littoral zone due to changes in the depth that PAR penetrates into the water column.

[4] Precisely, the maximum operating elevation defined in the WUP is 178.3 m (BC Hydro 2012). This was rounded to 178.0 m in this study.

Further, modelled peak biomass was compared between pre- and post WUP periods for both reservoirs to examine whether implementation of the WUP affected littoral productivity. Mean modelled peak biomass was compared between both periods using a *t*-test to determine whether differences were statistically-significant.

2.7. Fish Sampling

Fish sampling was undertaken to obtain representative stable isotope samples of the target fish species of Cutthroat Trout and Rainbow Trout and potential fish prey items including Threespine Stickleback, Sculpin spp., and juvenile trout. Several fishing methods were used to maximize catch of these food web components: gill netting, minnow trapping and trap netting. Tissue and stomach samples for diet analysis were obtained. This work was completed as part of JHTMON-3 and JHTMON-5 and is briefly summarized below. Further details about this work are presented in Hocking *et al.* (2017).

2.7.1. Gill Netting

Gill netting was undertaken on August 23 and October 4, 2015 in Lower Campbell Reservoir, at three littoral and three pelagic sites (Map 2) and on 29–31 August 2016 in Upper Campbell Reservoir, at six littoral sites (Map 3). Sinking gill nets were used to target different depths within the water column. At the littoral sites, nets were set on the bed, perpendicular to shore. At pelagic sites on Lower Campbell Reservoir, nets were set perpendicular to depth contours, with sinking nets suspended in the water column at a depth of 10 m below the surface, close to the assumed thermocline depth. RISC standard gill nets were used; the nets consist of six panels, each 15.2 m long and of different mesh sizes, strung together in a "gang" to form a net 91.2 m long and 2.4 m deep. The mesh sizes were as follows: 25 mm, 76 mm, 51 mm, 89 mm, 38 mm, and 64 mm. This sequence of mesh sizes captures a range of size classes of fish, although gill netting was primarily used to sample Cutthroat Trout and Rainbow Trout.

When setting a net, the boat operator ensured the proper location and depth of the site using a GPS and depth sounder, and positioned the net according to depth contours and wind conditions. The net was held in place with a net anchor at each end of the net. Nets were set overnight with soak times of 19–26 hours. Floating lights were attached to each net to mark their location overnight for boater safety.

2.7.2. Trap Netting

Trap netting was undertaken on October 4, 2015 in Lower Campbell Reservoir at two sites: LCR-LKTN01 and LCR-LKTN02 (Map 2) and on September 1, 2016 in Upper Campbell Reservoir at two sites: UCR-LKTN09 and UCR-LKTN10 (Map 3). Trap netting was primarily used to sample Threespine Stickleback. Traps were set overnight in littoral areas with a target soak time of 24 hours. Sites were selected for suitability for trap netting based on site depths and absence of underwater hazards. When setting a net, the boat operator ensured the proper location and depth of the site using a GPS and depth sounder and positioned the net according to depth contours and wind

conditions. The net was held in place with a net anchor. Nets were set overnight with soak times of 19–29 hours.

2.7.3.Minnow Trapping

Minnow trapping was undertaken on June 25 and August 23, 2015 in Lower Campbell Reservoir at three littoral and three pelagic sites (Map 2). In Upper Campbell Reservoir, minnow trapping was undertaken at two littoral sites (UCR-LKMT09 and UCR-LKMT10) on September 1, 2016. Target species were Sculpin spp., juvenile trout and Threespine Stickleback. Traps were either deployed on the bed and secured to the shoreline or suspended at a range of depths (0.5–10 m beneath a buoy). Each trap was baited with a small amount of fish roe placed in a perforated photographic film container, which allowed the scent to escape but prevented the attractant from being consumed. Traps were marked with a float, and UTM co–ordinates, depth, time, and mesh size of trap were recorded. Traps were fished overnight, with soak times ranging from 20–26 hours. Captured fish were separated by site and trap number and then brought back to shore for processing.

2.7.4.Individual Fish Analysis

All fish captured by gill netting, trap netting, or minnow trapping were processed as soon as possible after capture. In total, 32 Cutthroat Trout and 70 Rainbow Trout were collected from Lower Campbell Reservoir in 2015, while 56 Cutthroat Trout and 210 Rainbow Trout were collected from Upper Campbell Reservoir in 2016. Further details are presented in the JHTMON-5 Year 3 annual report (Hocking *et al.* 2017).

2.7.5.Stomach Content Analysis

For comparison to isotope results, fish stomachs were extracted from 23 Cutthroat Trout, 61 Rainbow Trout, and 12 Sculpin from Lower Campbell Reservoir in 2015. Fish stomachs were also extracted from 26 Cutthroat Trout and 29 Rainbow Trout from Upper Campbell Reservoir in 2016. At the time of capture, the body cavities were opened and each fish stomach was removed. The stomach was opened by longitudinal incision, the contents extracted, and placed in a 100 mL plastic sample bottle. Each sample was individually labelled and preserved with 60% denatured ethanol.

Stomach contents were identified to the lowest taxon that could be accurately identified and counted. Head counts were used for the enumeration of partly digested animals. Each identifiable fish retrieved from stomach contents was counted. Fish parts in advanced stages of digestion that could not be discriminated (e.g., muscle tissue) were counted together as a single fish. The data were compiled as counts per stomach for each fish species, i.e., abundance, not biomass, of prey was measured. The prey were grouped into eight categories: Ephemeroptera (mayflies), Plecoptera (stoneflies), Trichoptera (caddisflies), chironomids, other aquatic invertebrates, terrestrial invertebrates, zooplankton, and fish.

Note that this analysis is separate from stomach contents analysis conducted for JHTMON-5 (Hocking *et al.* 2017). Different methods were used for JHTMON-5, which involved broadly estimating the relative composition of stomach contents based on the following prey groups: fish, littoral invertebrates, terrestrial invertebrates, and zooplankton. The laboratory analysis conducted

for JHTMON-4 provided more precise data regarding fish diet composition although, unlike prey biomass, prey abundance is not necessarily correlated with the magnitude of energy flows to fish when there are large differences in prey size. Biomass of stomach contents was not measured directly (i.e., weighed) in this study because prey items showed variable levels of partial digestion. Further, biomass was not estimated indirectly (e.g., based on literature values for the mass of prey items) because it was deemed that the accuracy would have been too low to have warranted the additional effort. Instead, the stomach contents data were used to understand the taxonomic composition of trout diets in details, and also to provide a high-level "check" of the stable isotope results. For the purpose of quantifying energy fluxes to fish, we place greatest weight on the stable isotope data (discussed further in Section 4.3).

2.8. Stable Isotopes

The stable isotope work for JHTMON-4, which was used to predict the periphyton contribution to fish diet, was undertaken through coordinated sampling between JHTMON-3, JHTMON-4, and JHTMON-5 in Lower Campbell Reservoir and Upper Campbell Reservoir (Map 2 and Map 3, respectively). Sampling for periphyton, benthic invertebrates and basal nutrient sources occurred in JHTMON-4 and is described further below. Sampling for Cutthroat Trout, Rainbow Trout and their diet items including zooplankton, terrestrial invertebrates, littoral invertebrates, and prey fish (Threespine Stickleback, Sculpin spp., and juvenile trout) were sampled as a part of JHTMON-3 (Upper Campbell Reservoir gill net sampling) and JHTMON-5. Fish sampling methods are summarized in Section 2.7, and can be viewed in detail in the JHTMON-5 Year 3 annual report (Hocking *et al.* 2017).

2.8.1. Periphyton

Periphyton communities have a varied composition, and include the living algal component, but also protozoa, bacteria, fungi and dead organic detritus. To account for this variable composition, periphyton was collected for stable isotope analysis from two sources[5]. The first source was periphyton biomass that accumulated on the nylon mooring line at each station. A razor blade was used to scrape algal biomass from the line within the top 2 m from the water column following the fall incubation period at Lower Campbell Reservoir (56 days; Sep 25 – Nov 27), and the summer (92 days; Jun 17 – Sep 27 and fall (95 days; Sep 9 – Dec 13) incubation periods at Upper Campbell Reservoir. Biomass was collected from each line, resulting in four samples per reservoir for stable isotope analysis. These samples reflect the isotopic composition of the living algal component of periphyton communities that inhabit the littoral zone. The second source of periphyton was rock scrapings from the wadable reservoir margins near each of the periphyton sampling stations. At

[5] Acrylic plates were also trialled in Year 1 to sample periphyton but this method yielded insufficient sample volume, resulting in periphyton being collected from the mooring line instead. Further details of this are provided in the Year 1 report (Perrin *et al.* 2016).

Lower Campbell Reservoir, three samples were collected on September 25, 2015 at the shoreline near site LCR-PERWQ3. At Upper Campbell Reservoir, four samples were collected at the shoreline at each of the four periphyton sampling stations, yielding 16 samples in total. The sampling dates were 19 July, 26 August, 27 September and October 19, 2017. For each sample, 10 rocks were collected and individually hand scrubbed in a bucket. Water was decanted and the remaining contents placed in one sample jar. These shoreline samples contained living algal biomass, detritus from reservoir and, potentially, terrestrial sources, and the assemblage of heterotrophic decomposer organisms associated with the substrata. These shoreline samples are referred to hereafter as "littoral periphyton".

2.8.2.Benthic and Littoral Invertebrates

Invertebrates were collected from soft sediment and stony material in the littoral zone to optimize the diversity and biomass for SIA. Samples were collected from eight sites at Lower Campbell Reservoir (Table 4, Map 2) and four sites at Upper Campbell Reservoir (Table 5, Map 3). A mini-Ponar sampler (Wildlife Supply Company, Yulee, Florida) was used to collect grabs from soft sediment (benthic invertebrates) and a basket sampling technique was used to collect invertebrates that graze on stony substrata. Invertebrate counts and biomass by taxon were measured for both types of sampler prior to stable isotope analysis.

One composite sample was collected by undertaking four or more casts with the mini-Ponar sampler along a transect that extended between the shore and each periphyton station. The sampler was deployed by hand from the boat. Jaws of the Ponar sampler bucket collected material from an area of 0.023 m^2 to a substratum depth of 10 cm. Where hard substrate was encountered, the boat was moved and the cast was repeated until softer material was found that could be effectively grabbed. Grab contents from each cast were washed into a plastic bin from which the contents were passed through a 250 μm mesh sieve to remove excess water and transferred to plastic sample containers. The samples were preserved in 90% ethanol. The ethanol was thoroughly mixed and the containers were sealed for shipment to Limnotek in Vancouver for analysis of invertebrate density and biomass. All individuals picked from detrital material in those samples were sent to the Stable Isotopes in Nature Laboratory at the University of New Brunswick for SIA.

Figure 5. Deploying Ponar grab at UCR-PERWQ04 on October 19, 2016 to sample benthic invertebrates.

One composite invertebrate sample was collected from each reservoir at the end of the summer sampling period from three wire baskets that contained stones. The baskets were incubated for installed shoreward of each periphyton sampling station during the summer sampling periods (Map 2, Map 3). Each basket was made of heavy gauge wire measuring 32 cm × 12 cm × 17 cm (planar area of 0.038 m^2), similar to one described by Merritt *et al.* (1996). Each basket was filled with dry and clean stones with a size range of 2.5– 3.5 cm that were collected from the beaches above the reservoir water surface elevation, near each sampling station. The baskets were locked closed with cable ties and placed in water depths of 2–4 m using 5/16 inch nylon double braid Samson line to tether the samplers to a tree on shore. The baskets were deployed in Lower Campbell Reservoir Reservoir for 49 days (Table 4) and Upper Campbell Reservoir for 124 days (Table 5). These incubation times were considered adequate for development of a benthic invertebrate community, based on colonization times reported by Mackay (1992). At the end of the incubation period, a 250 µm mesh Nitex scoop net was used to place each basket into a plastic bucket. The basket was opened in its bucket by clipping the closure ties. The basket and stones were brushed clean and removed. Sample contents in the bucket were passed back through the scoop net to remove excess water and concentrate the sample in the cod end. The sample was washed from the cod end into one or more sample jars, preserved in 90% ethanol, and labelled for delivery to the laboratory in Vancouver. The three basket samples from a given station were composited to one sample for

analysis in the lab, resulting in a total of four samples (one composite from each of the four stations).

In the laboratory, each invertebrate sample (basket or Ponar) was washed through 1 mm and 250 µm mesh sieves to yield a macrobenthos fraction (>1 mm) and a microbenthos fraction (<1 mm and >250 µm). In this process, animals were picked from twigs, grasses, clumps of algae, and other debris and were returned to the 1 mm sieve. Microbenthos was passed through a large plankton splitter to produce 16 subsamples. Animals were enumerated from successive sub-samples until 200 animals were counted. If 200 animals were counted part way through the sorting of a sub-sample, that sub-sample was sorted in its entirety. If the estimated abundance of animals in the macrobenthos fraction was less than 200 animals, that fraction was enumerated in its entirety. If there were more than 200 animals, the subsample was partitioned in a level tray into four equal parts. Animals were enumerated from successive macrobenthos sub-samples until 200 animals were counted. Sub-sample counts were extrapolated to the total sample. The sample count was the sum of microbenthos and macrobenthos in the complete sample. The animals were identified to genus or lowest reliable taxonomic level using keys from Edmondson (1959), Merritt and Cummins (1996), and Pennak (1978). One in 10 samples was sorted twice to test efficiency of the first sort. A target for acceptable sorting was that 90% of the sample must be enumerated on the first sort. If efficiency was <90%, samples in the group to which the test applied were re-sorted. Sorting efficiency was >90% on the first sort of all samples.

Biomass of individuals was estimated from established length-to-weight regressions (Smock 1980, Benke *et al.* 1999) using the Zoobbiom Version 1.3 (Hopcroft 1991) digitizing system. Up to 25 random length measurements per taxon were taken per sample, and the final biomass was expressed as mg per sample.

2.8.3.Primary Nutrient Sources

Littoral invertebrates and, ultimately, fish may derive some energy from periphyton, but may also derive energy from detritus, living plants and other terrestrial material. Samples of small particulate organic matter (SPOM), macrophytes and leaf litter were collected in the wadable shoreline areas near to the periphyton sampling stations (Table 4, Map 2, Map 3) to represent these potential additional food sources to fish.

Fish can also obtain energy derived from phytoplankton production in pelagic areas by consuming zooplankton. Zooplankton samples were collected as part of JHTMON-5 in Lower Campbell Reservoir in June, July and September of 2015, and in Upper Campbell Reservoir in June, August and September of 2016. Further details of sampling and analytical methods are presented in the JHTMON-5 Year 3 report (Hocking *et al.* 2017).

2.8.4.Stable Isotope Processing

Littoral detritus, macrophytes, invertebrates, and fish samples were processed for nitrogen and carbon stable isotopes at the Stable Isotope in Nature Laboratory (SINLAB[6]) located within the Canadian Rivers Institute at the University of New Brunswick in Fredericton, New Brunswick. Dr. Brian Hayden, the Science Manager of SINLAB, was the primary contact.

A total of 318 samples of basal nutrient sources, zooplankton, invertebrates and fish were sent for analysis (Table 6). Basal nutrient sources (SPOM, leaf litter, and periphyton), zooplankton, littoral/benthic invertebrates and terrestrial invertebrates were sent as composite samples, while fish were sent as fin clip samples. Invertebrates were separated into benthic and littoral groups. 'Benthic invertebrates' were collected using a Ponar grab sampler (Section 2.8.2). The isotopic signatures of 'littoral invertebrates' were based on invertebrates collected using the rock basket samplers (Section 2.8.2), and additional individuals collected in the littoral zone of both reservoirs as part of JHTMON-5 (see Hocking *et al.* 2017).

All samples were rinsed with distilled water, dried for 48 hours at 60°C and ground into a fine homogeneous powder using a pestle and mortar. Samples were then weighed into tin capsules and loaded into either a PN150 or Costech Zeroblank autosampler. Samples were converted to gases by combustion by a Carlo Erba NC2500 or Costech 4010 Elemental Analyzer (EA) and then analyzed for $\delta^{15}N$ and $\delta^{13}C$ using a Delta Plus or a Delta XP continuous flow isotope-ratio mass spectrometer (CF-IRMS) (ThermoFinnigan; Bremen, Germany) (see SINLAB website).

Isotopic signatures are expressed in delta notation (δ) as ratios relative to known isotopic standards of atmospheric N_2 and Vienna Pee Dee Belemnite (V-PDB) carbon. This is expressed in parts per thousand (‰) according to:

$$\delta^{15}N \text{ or } \delta^{13}C \text{ (‰)} = (R_{sample}/R_{standard} - 1) * 1000$$

where R is the ratio of the heavy isotope (^{15}N or ^{13}C)/ light isotope (^{14}N or ^{12}C).

Thirteen samples were run in duplicate to test repeatability of the stable isotope results. The absolute mean difference in $\delta^{15}N$ between repeats was 0.19±0.15‰. The absolute mean difference in $\delta^{13}C$ between repeats was 0.22±0.16‰.

[6] http://www.unb.ca/research/institutes/cri/sinlab/

Table 6. Primary producers, invertebrate, and fish samples analyzed for nitrogen and carbon stable isotopes at SINLAB, 2014 to 2016.

Trophic Level	Taxa	2014 Upper Campbell Reservoir	2015 Lower Campbell Reservoir	2016 Upper Campbell Reservoir	Total
Primary Producers	Periphytic Algae		3	4	**7**
	Littoral Periphyton		3	16	**19**
	Leaf Litter		4	8	**12**
	SPOM		4	8	**12**
Primary Consumers	Zooplankton	8	9	9	**26**
	Littoral Invertebrates	3	8	3	**14**
	Benthic Invertebrates		4	4	**8**
	Stream Invertebrates	2	1		**3**
s	Terrestrial Invertebrates	1	3		**4**
Secondary Consumers	Sculpin spp.	6	12	9	**27**
	Threespine Stickleback	10	10	9	**29**
	Juvenile Trout	12	5	4	**21**
	Rainbow Trout	18	27	20	**65**
Tertiary Consumers	Cutthroat Trout	20	29	21	**70**
Sum		**80**	**122**	**115**	**317**

2.8.5. Assessing Fish Diet Using Mixing Models

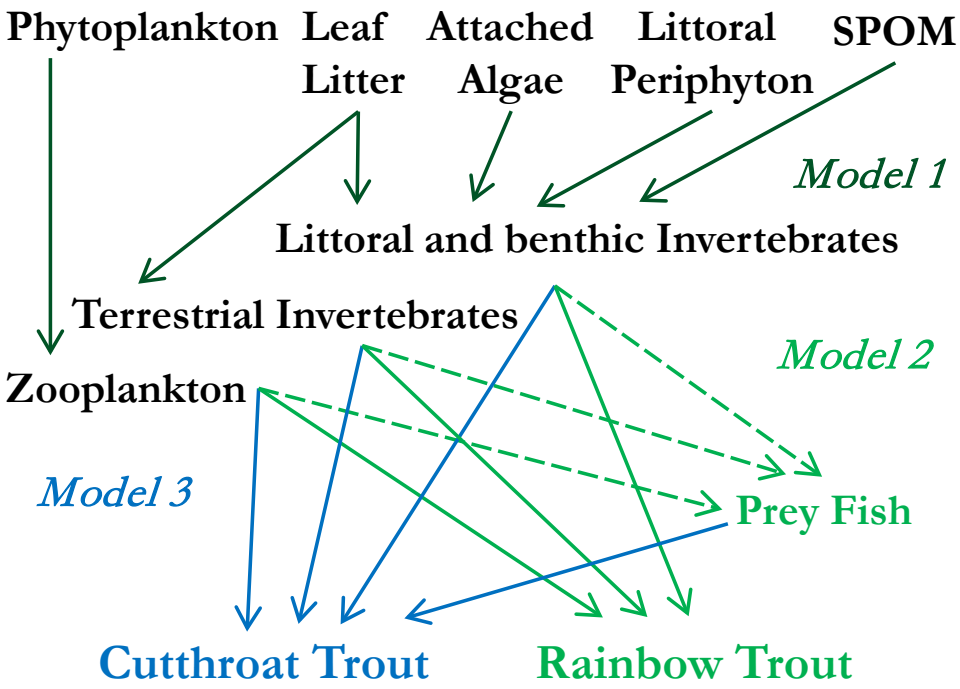
The relative contributions of pelagic and littoral primary production sources to Cutthroat Trout and Rainbow Trout diets were assessed through a series of dual isotope ($\delta^{13}C$ and $\delta^{15}N$), three to five-source Bayesian isotopic mixing models implemented in the program SIAR (Stable Isotope Analysis in R, Parnell and Jackson 2013). SIAR takes isotope data from consumers (littoral invertebrates and fish) and sources (diet items) along with estimates of diet-tissue isotopic fractionation, and fits Bayesian models based on Gaussian likelihoods with a Dirichlet prior mixture on the mean, which provide posterior distribution estimates of source contributions to diet (Parnell *et al.* 2010). The diet-tissue fractionation values used in the models were 0.40 ± 1.20 for $\delta^{13}C$ and 2.30 ± 1.60 for $\delta^{15}N$ for littoral invertebrate consumers and 1.50 ± 1.16 for $\delta^{13}C$ and 2.79 ± 1.46 for $\delta^{15}N$ for fish consumers. The former values are averaged diet-tissue fractionation rates for aquatic food webs (McCutchan *et al.* 2003), while the latter are average diet-tissue fractionation rates across several fish species and tissue types (Sweeting *et al.* 2007a, b).

A separate model was run for each of the three consumer groups within each reservoir (Figure 6). The first model estimated diet contributions of the four primary nutrient sources (SPOM, leaf litter, littoral periphyton, and attached algae) to littoral invertebrates. The second model estimated diet contributions of four invertebrate diet sources (zooplankton, benthic invertebrates, littoral invertebrates, and terrestrial invertebrates) to small bodied prey fish (Threespine Stickleback, Sculpin

spp., and juvenile trout) and larger Rainbow Trout. The third model estimated the diet contributions of potential diet items to large Cutthroat Trout (age >2+, FL ≥ 158 mm). Five potential diet sources (mean $\delta^{13}C$ and $\delta^{15}N$ ± SD) for large Cutthroat Trout were included in the third model: 1) zooplankton, 2) benthic invertebrates, 3) littoral invertebrates, 4) terrestrial invertebrates, 5) prey fish (juvenile trout (age ≤ 2, FL ≤ 143 mm), Sculpin spp. (FL ≤ 170 mm), and Threespine Stickleback (FL ≤ 64 mm)).

The three models were run to assess the total relative contributions of pelagic vs. littoral primary sources of production to large Cutthroat Trout and Rainbow Trout via indirect pathways. These total littoral vs. pelagic contributions to diets were derived through a series of steps: for prey fish and large Rainbow Trout we multiplied the relative contributions of the four primary nutrient sources to littoral and benthic invertebrates in model one by the contributions of littoral and benthic invertebrates to prey fish and large Rainbow Trout in model two, to calculate the total primary nutrient contributions to their diets. For large Cutthroat Trout, an additional pathway through the consumption of prey fish needed to be considered. Therefore, we multiplied the indirect relative contribution of primary nutrient sources to prey fish diets through both invertebrate groups by the contribution of prey fish to the diets of large Cutthroat Trout from model three, and then summed the indirect contributions of primary nutrient sources to Cutthroat Trout via littoral and benthic invertebrates and prey fish. For simplicity, we assumed that zooplankton and terrestrial invertebrates do not directly consume these littoral and pelagic primary nutrient sources, and therefore do not represent indirect pathways of these nutrient sources to fish diets.

Figure 6. **Schematic of trophic pathways by which littoral and benthic primary nutrient sources contribute to large trout diets in Lower Campbell and Upper Campbell reservoirs.**



3. RESULTS

3.1. Habitat Attributes

Temperature profiles for both reservoirs showed stratification in summer followed by de-stratification in the fall (Figure 7). The June 28, 2016 sampling in Upper Campbell Reservoir showed incomplete stratification while a month later in 2015 in Lower Campbell Reservoir, stratification was well-established. In late summer (September), the epilimnion (surface mixed layer) extended to a depth of 19 m in Lower Campbell Reservoir and to 15 m in Upper Campbell Reservoir, having a temperature of approximately 16°C. Both reservoirs were isothermal (7–8°C) in the late fall months.

The mean concentration of all forms of nitrogen and phosphorus (Table 7) were less than or close to method detection limits (Table 3). Concentrations of all forms of phosphorus were less than the method detection limits in all samples in Lower Campbell Reservoir in 2015. This was also the case for NO_3-N and NH_4-N at the surface in July and September. NH_4-N was not detected at the surface or bottom in the fall. NO_3-N was detected at ≤40 $\mu g \cdot L^{-1}$ near the bottom in summer and fall and it was 21 $\mu g \cdot L^{-1}$ in surface water in the fall. Given that NH_4-N can be readily oxidized to NO_3-N via nitrification, the low NH_4-N concentrations compared to NO_3-N were expected. Detection of

NO_3-N in November potentially indicates flushing from forest soils (nitrate is mobile in saturated soils) following a summer dry period (Verseveld *et al.* 2008) and mixing of the water column that occurred in November (Figure 7).

Similar chemistry was found in Upper Campbell Reservoir (Table 8). SRP and TDP concentrations were less than the method detection limit in all samples. TP concentrations were near the method detection limit in the June and September sampling but less than detection in the December samples. NH_4-N concentrations were less than or close to 5 $\mu g \cdot L^{-1}$ in all samples. NO_3-N concentrations were undetectable at the surface in June and September but they were >25 $\mu g \cdot L^{-1}$ at the bottom in all samples and were an average of 26.2 $\mu g \cdot L^{-1}$ at the surface in December.

Absence of measurable phosphorus of any form in most samples meant that molar N:P could not be reliably calculated and it indicates that algal growth in Lower Campbell and Upper Campbell reservoirs is potentially limited by availability of phosphorus. The undetectable or low concentrations of NH_4-N and NO_3-N reflect low availability of N, indicating that N was also potentially limiting or co-limiting algal growth. This finding is typical of lakes and reservoirs on northern Vancouver Island, which are generally ultra-oligotrophic (Stockner and MacIsaac 1996, Perrin and Harris 2006, Perrin *et al.* 2012, Suttle and Harrison 1988).

Figure 7. **Temperature profiles from the four sampling stations in Lower Campbell Reservoir in 2015 (left side) and in Upper Campbell Reservoir in 2016 (right side).**

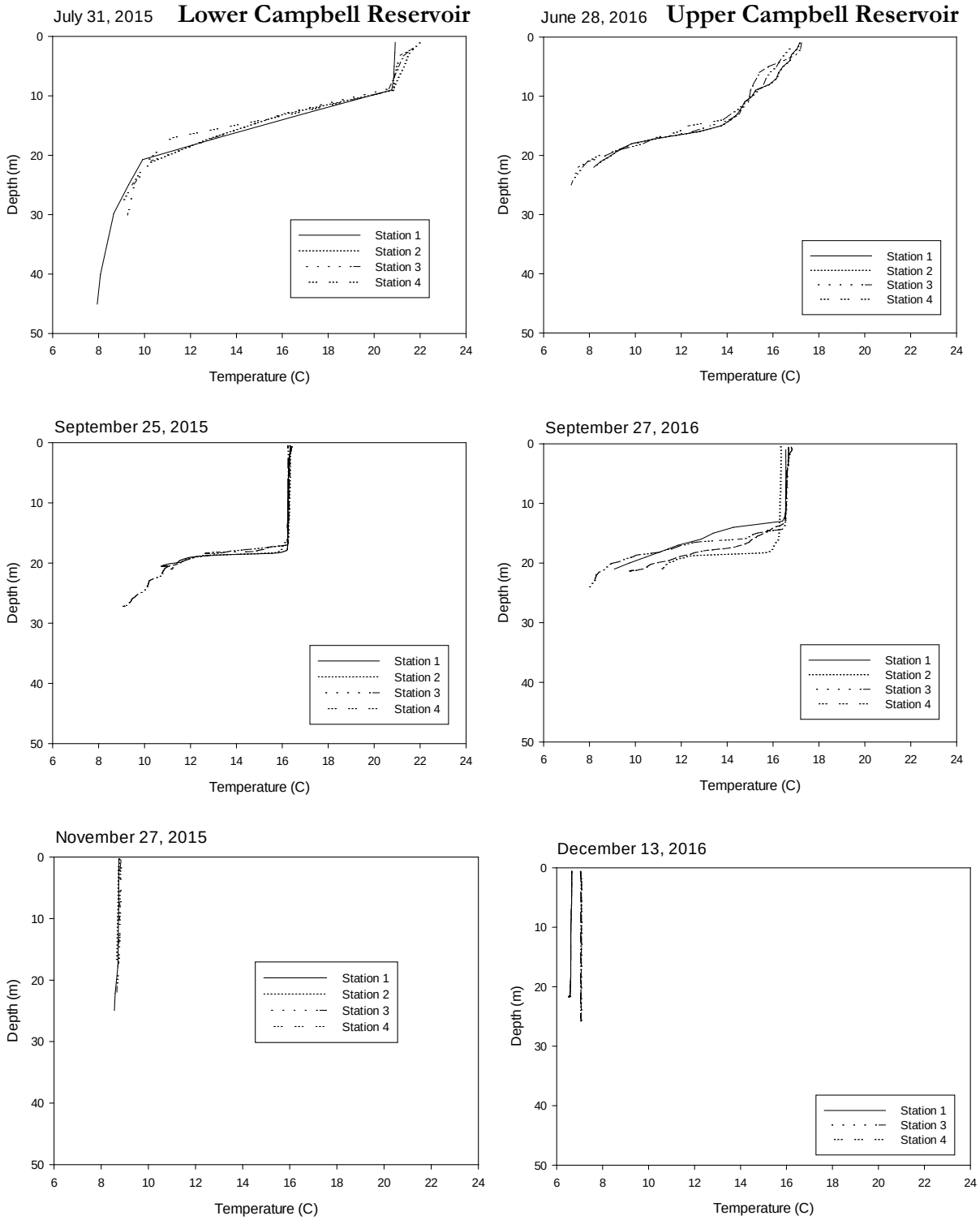


Table 7. Mean concentrations or values of the various forms of N and P and other chemical analytes in surface and bottom waters among the four stations in Lower Campbell Reservoir in 2015.

Date	Location	NH_4-N ($\mu g \cdot N\ L^{-1}$)	NO3-N ($\mu g \cdot N\ L^{-1}$)	Total Nitrogen ($\mu g \cdot L^{-1}$)	Soluble Reactive Phosphorus ($\mu g \cdot L^{-1}$)	Total Dissolved Phosphorus ($\mu g \cdot L^{-1}$)	Total Phosphorus ($\mu g \cdot L^{-1}$)	pH	Turbidity (NTU)	Conductivity ($\mu S \cdot cm^{-1}$)	Dissolved Oxygen ($mg \cdot L^{-1}$)
31-Jul-15	Surface	<5	<5	41	<1	<2	<2	7.6	0.48	48.8	9.1
	2 m off bottom	7.1	35.0	71	<1	<2	<2	7.5	0.65	48.8	10.8
25-Sep-15	Surface	<5	<5	Not measured	<1	<2	Not measured	7.6	0.36	43.5	8.9
	2 m off bottom	8	25.7	Not measured	<1	<2	Not measured	7.4	0.35	39.4	9.4
27-Dec-15	Surface	<5	20.6	76	<1	<2	<2	7.4	0.08	42	11.0
	2 m off bottom	<5	21.2	69	<1	<2	<2	7.4	0.08	42	10.6

Table 8. Mean concentrations or values of the various forms of N and P and other chemical analytes in surface and bottom waters among the four stations in Upper Campbell Reservoir in 2016.

Date	Location	NH_4-N ($\mu g\ N \cdot L^{-1}$)	NO_3-N ($\mu g \cdot N\ L^{-1}$)	Total Nitrogen ($\mu g \cdot L^{-1}$)	Soluble Reactive Phosphorus ($\mu g \cdot L^{-1}$)	Total Dissolved Phosphorus ($\mu g \cdot L^{-1}$)	Total Phosphorus ($\mu g \cdot L^{-1}$)	pH	Turbidity (NTU)	Conductivity ($\mu S \cdot cm^{-1}$)	Dissolved Oxygen ($mg \cdot L^{-1}$)
28-Jun-16	Surface	<5	<5	< 3	<1	<2	2.1	No data	0.7	42.8	9.6
	2 m off bottom	<5	33.3	61.0	<1	<2	2.5	No data	0.6	32.8	10.8
27-Sep-16	Surface	<5	<5	< 3	<1	<2	2	7.6	0.2	42.9	7.1
	2 m off bottom	5.5	31	50.3	<1	<2	<2	7.6	0.4	36	7.7
13-Dec-16	Surface	<5	26.2	61.7	<1	<2	<2	7.5	0.6	30.8	7.2
	2 m off bottom	<5	26	58.0	<1	<2	<2	7.5	0.3	30.9	6.3

Measurements of other chemical variables showed conditions typical of coastal lakes and reservoirs in BC. The pH was slightly alkaline, with no change with depth, indicating no effect of respiration in the sediments on the overlying water column (in richer reservoirs, pH can be relatively low near the sediments due to CO_2 release from decomposition in sediments). Low conductivity (31 – 49 $\mu S \cdot cm^{-1}$) was consistent with the low nutrient concentrations. Turbidity was consistently ≤0.7 NTU, which shows that few particles causing light scattering were present. The water column was well oxygenated (7 – 11 $mg \cdot L^{-1}$) at all times, with no evidence of oxygen demand from sediments.

PAR profiles showed logarithmic attenuation of light through the water column during the summer and fall sampling periods in each reservoir (Figure 8 and Figure 9). Using summer and fall regression equations shown in Figure 8, the depth at which PAR was 1% of that at the surface was 22.3 m in the summer series and 19.5 m in the fall in Lower Campbell Reservoir. These depths define the depth of the euphotic zone. For practical purposes it was rounded to 20 m. In Upper Campbell Reservoir, the euphotic zone depth was found to be 25 m using the equations in Figure 9.

Figure 8. **Percent of surface PAR over the depth profile among periphyton sampling stations in Lower Campbell reservoir in summer (top) and fall (bottom), 2015. The equations each show a logarithmic line of best fit (%SI is percent of PAR immediately under the water surface and depth is water depth). The r^2 is the correlation coefficient for the regression line.**

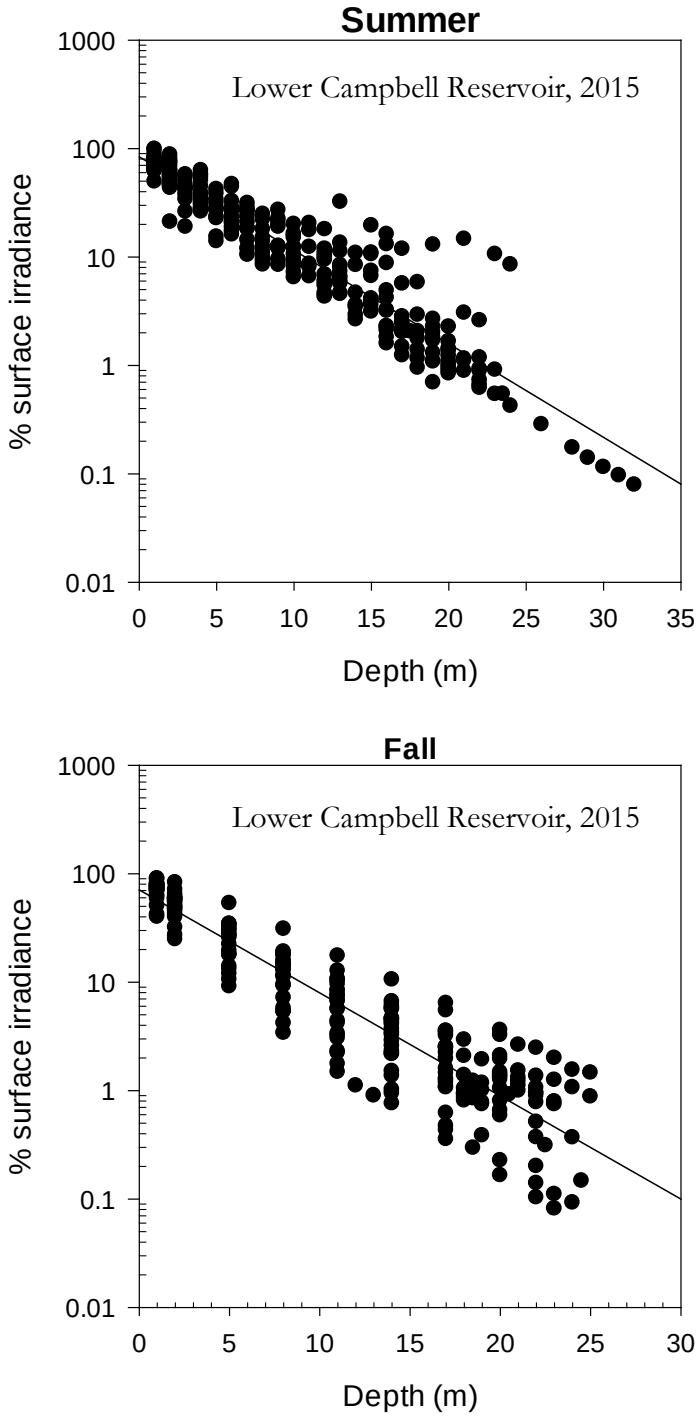
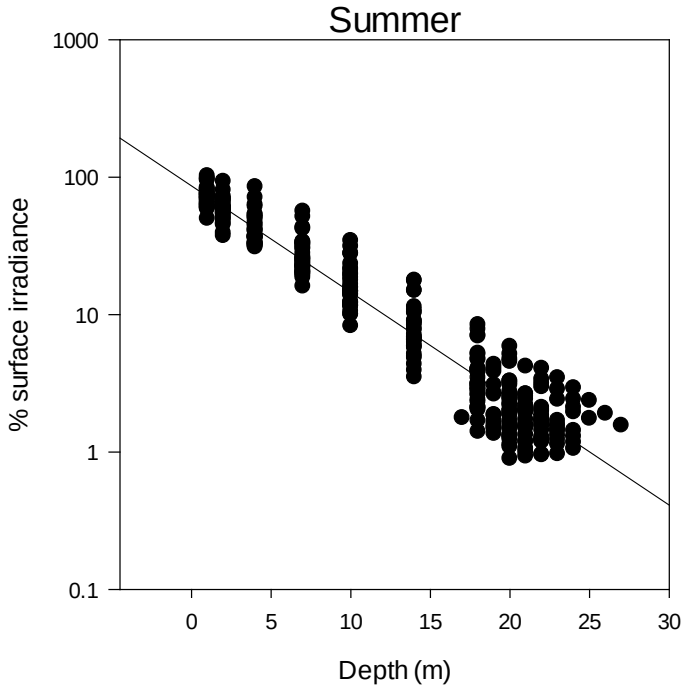
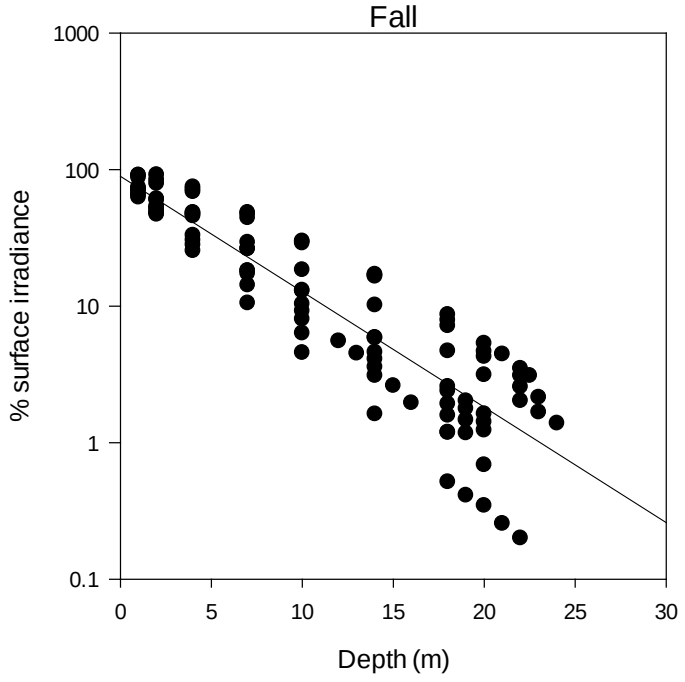


Figure 9. **Percent of surface PAR over the depth profile among periphyton sampling stations in Upper Campbell reservoir in summer (top) and fall (bottom), 2016. The equations each show a logarithmic line of best fit (%SI is percent of PAR immediately under the water surface and depth is water depth). The r^2 is the correlation coefficient for the regression line.**



$$\%SI = e^{(-1.783*depth)+4.457}$$

$r^2 = 0.94$



$$\%SI = e^{(-0.19*depth)+4.49}$$

$r^2 = 0.82$

3.2. Bathymetric Survey and Digital Elevation Mapping

Using a euphotic zone depth of 20 m in Lower Campbell Reservoir and 25 m in Upper Campbell Reservoir (Section 3.1), change in area of littoral and pelagic habitats across the annual range of water surface elevations in each reservoir is shown in Figure 10 for Lower Campbell Reservoir and Figure 11 for Upper Campbell Reservoir. These figures are based on the DEMs (Section 2.2). In Lower Campbell Reservoir, littoral areas are present throughout the west arm of the reservoir, within a southern embayment and along shorelines (Map 4). Pelagic habitat is present in mid-basin areas and in central portions of a northern embayment. Littoral area is more than twice the pelagic area over the range of water surface elevations that were observed in 2015 (Figure 10). In Upper Campbell Reservoir, littoral areas occur throughout the south and west arms, at an alluvial fan on the north shore of the main basin, and along shorelines (Map 5). Pelagic habitat is present within central areas of the main basin. Pelagic area is lower than littoral area and is about 70% of littoral area at full pool. As water surface elevation declines from full pool (221 m elevation) to the minimum elevation in 2016 of 215.5 m, the littoral area stays approximately constant while the pelagic area declines (Figure 11).

Figure 10. Change in littoral (water depths <20 m) and pelagic (water depths >20 m) areas over the range of water surface elevations in 2015 in Lower Campbell Reservoir.

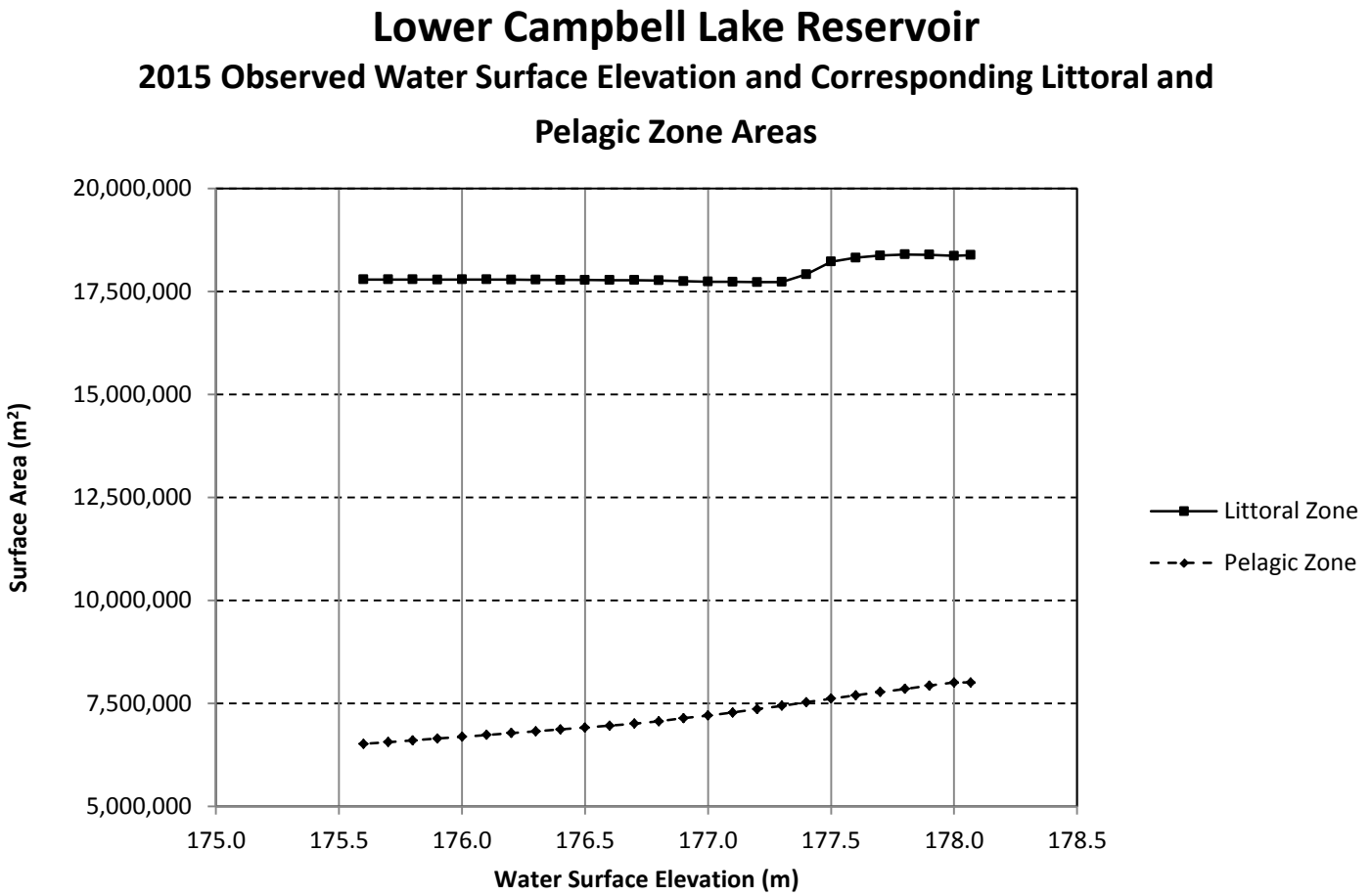
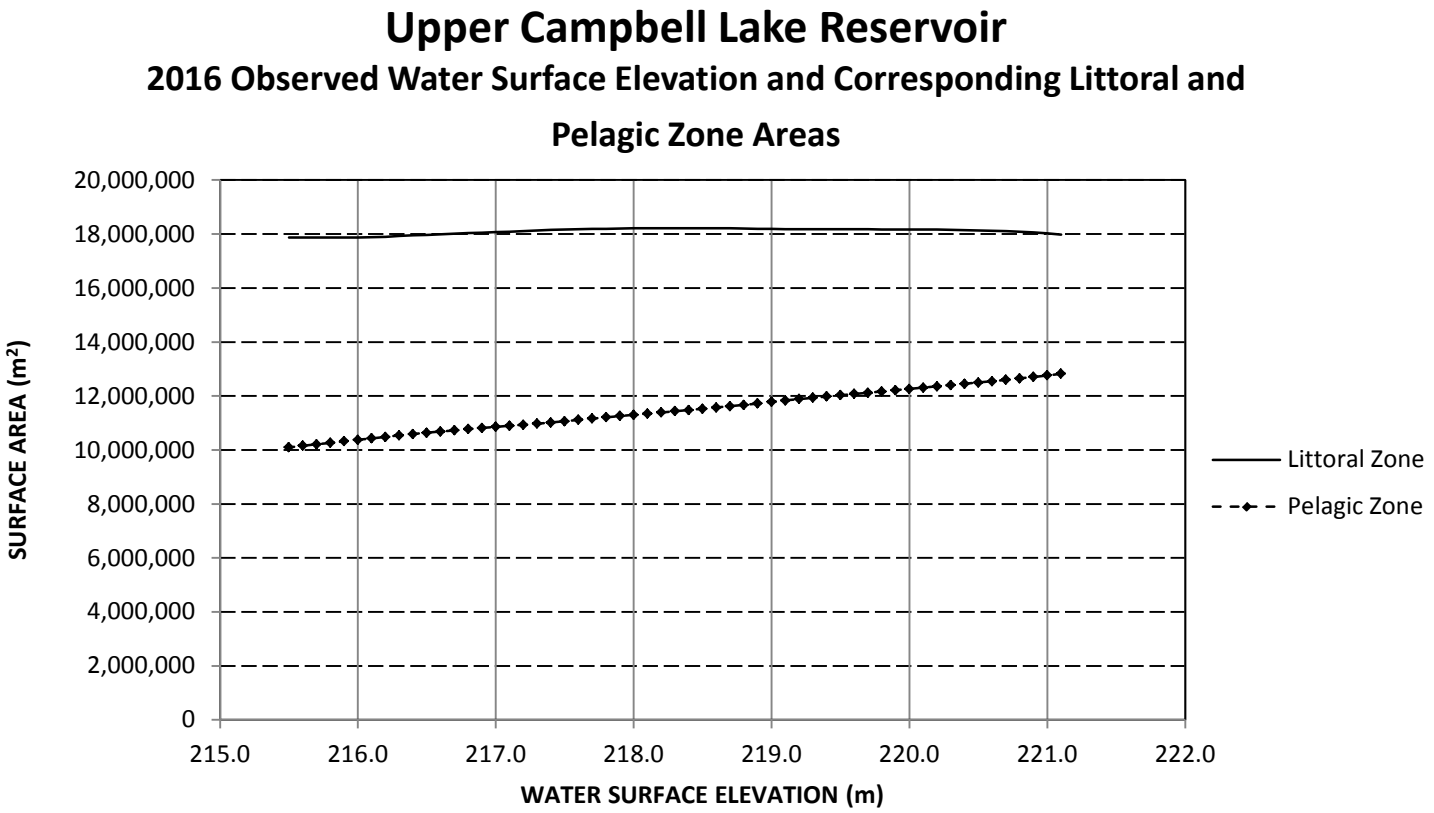


Figure 11. Change in littoral (water depths <25 m) and pelagic (water depths >25 m) areas over the range of water surface elevations in 2016 in Upper Campbell Reservoir.



3.3. Periphyton Biomass Accrual

3.3.1. Biomass

Periphyton biomass, measured as chl-*a* concentration, increased logarithmically at all depths in both seasons in Lower Campbell Reservoir (Figure 12) and Upper Campbell Reservoir (Figure 13). The slope of the accrual curves was significantly greater near the top of the littoral zone than near the bottom in summer (p=0.002) and fall (p<0.001) in Lower Campbell Reservoir and in both seasons in Upper Campbell Reservoir (p<0.001) (ANCOVA significance test for interaction term), i.e., algae grew at a faster rate at the surface than closer to the bottom of the euphotic zone.

To compare PB between reservoirs wherein sampling duration differed, PB was determined in Upper Campbell Reservoir for a period of 57 days to match the sampling duration in Lower Campbell Reservoir (Table 9). Based on this standard metric, PB in summer in Lower Campbell Reservoir was markedly higher than in Upper Campbell Reservoir (Table 9). At depths of 1–14 m during the summer, PB was 0.18–0.36 µg chl-*a*·cm^{-2} in Lower Campbell Reservoir and 0.02–0.03 µg chl-*a*·cm^{-2} in Upper Campbell Reservoir. In both reservoirs, PB was substantially lower at a depth of 18 m than at depths of 1–14 m (Table 9). In the fall, the difference in PB between reservoirs was smaller than in summer, although it was still greater in Lower Campbell Reservoir than in Upper Campbell Reservoir at five of the six depths sampled.

After 60 days during summer in Upper Campbell Reservoir, algal biomass continued to increase on substrata without evidence of a peak (Figure 13), showing that mat development did not exceed surficial capacity of the Styrofoam balls to retain algal biomass even at the three-month incubation period. During the fall in Upper Campbell Reservoir, a plateau of algal biomass was evident at depths ≥10 m after 45 days but no biomass peak was clear at shallower depths after three months. In Lower Campbell Reservoir, there was no clear peak in biomass over the 60-day accrual periods. The highest PB of 0.38 µg chl-a·cm^{-2} occurred at a depth of 4 m while the lowest PB of 0.02 µg chl-a·cm^{-2} occurred at the bottom of the euphotic zone at a water depth of 18 m. The lower PB with increasing water depth was statistically significant among all combinations of reservoir and season (p≤0.003, Table 9) except in Lower Campbell Reservoir in the fall when variation among PB samples was particularly large.

Figure 12. **Mean periphyton biomass (chlorophyll-*a* concentration) (±sd) over time of incubation of installed Styrofoam substrata at three depths in the euphotic zone of Lower Campbell Reservoir during summer (top panel) and fall (bottom panel).**

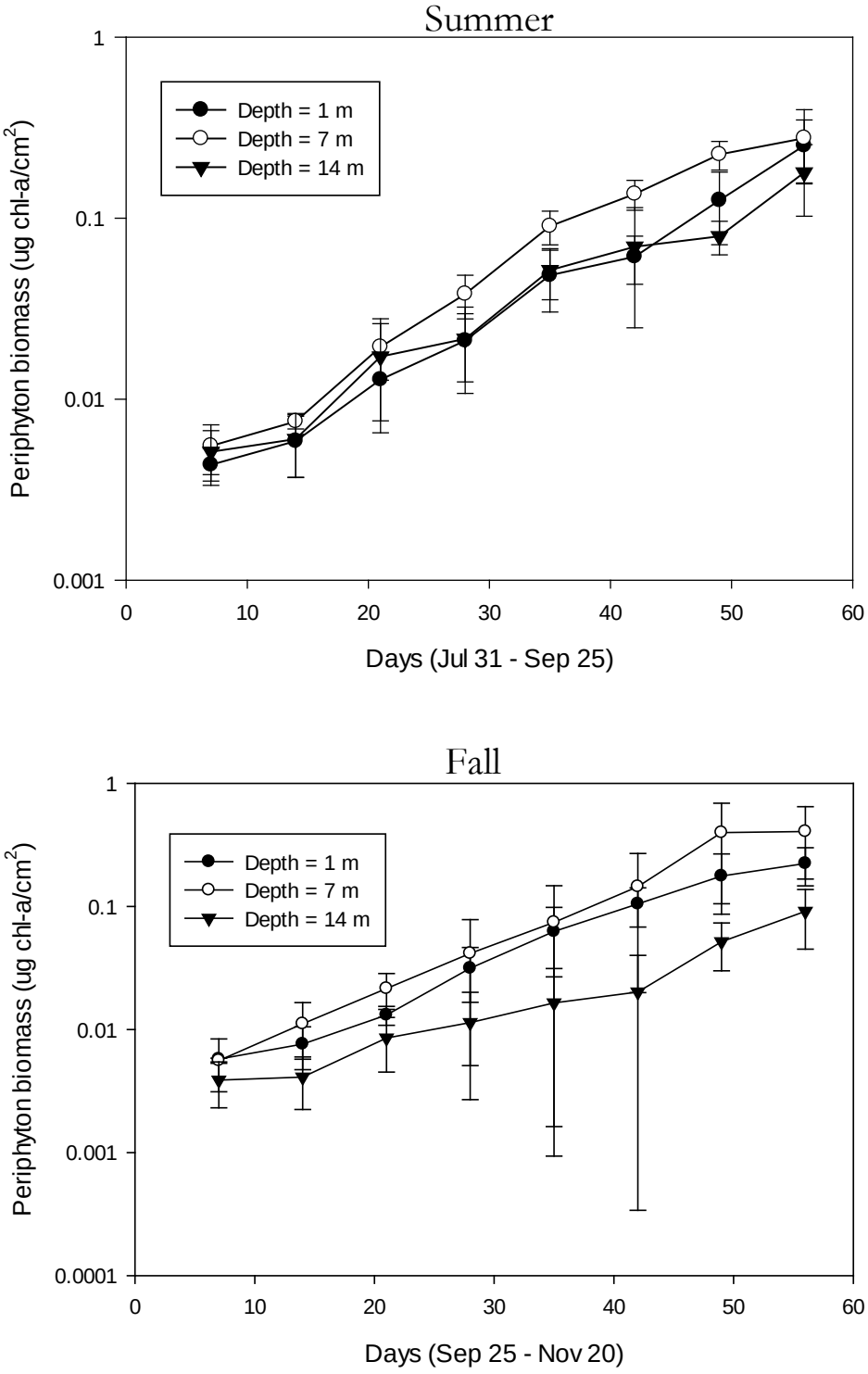


Figure 13. **Mean periphyton biomass (chlorophyll-*a* concentration) (±sd) over time of incubation of installed Styrofoam substrata at six depths in the euphotic zone of Upper Campbell Reservoir during summer (top panel) and fall (bottom panel).**

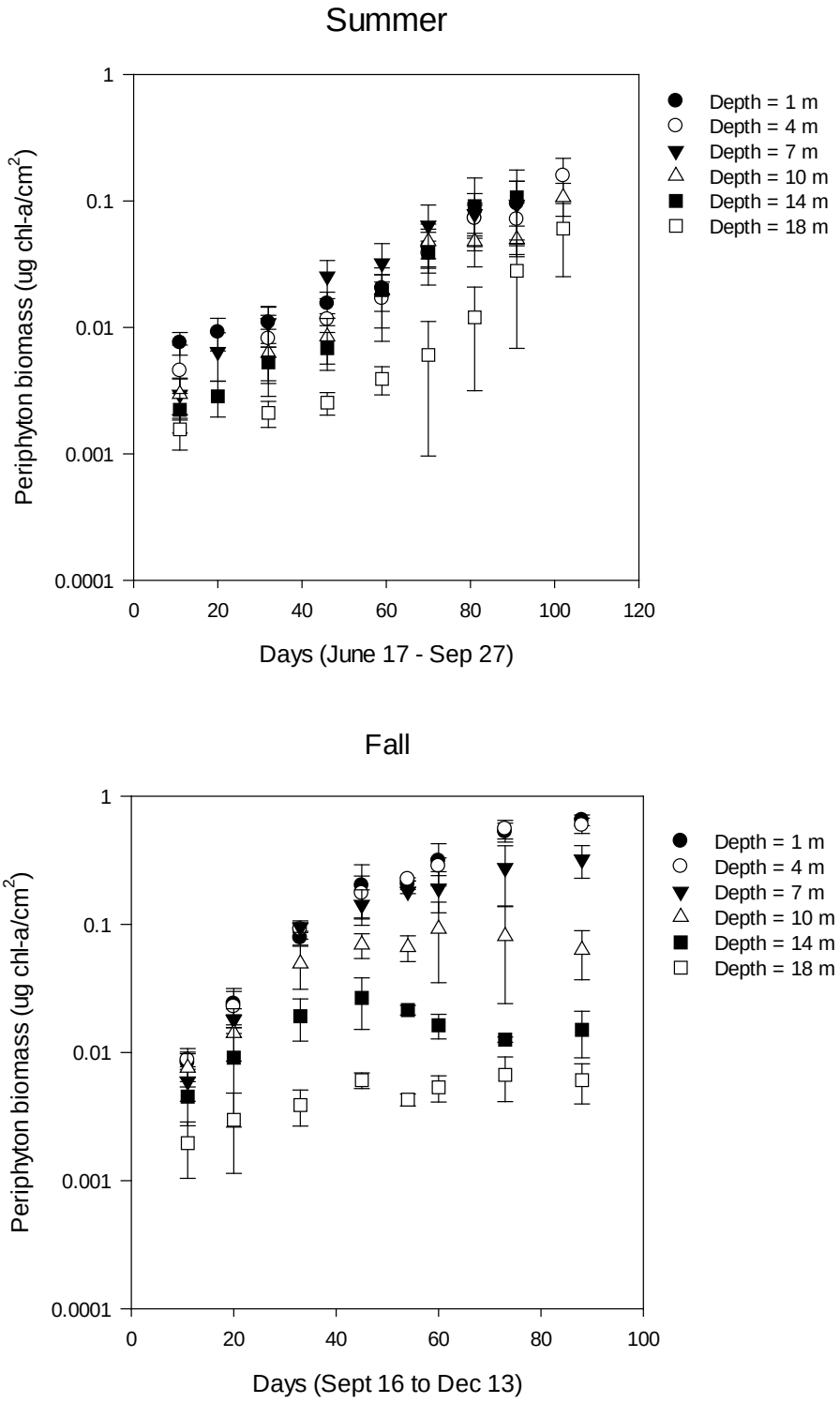


Table 9. **Mean periphyton peak biomass (PB) (± sd) by depth in the euphotic zone of Lower and Upper Campbell Reservoirs, standardized to 60-day sampling periods during the summer and fall.**

Season	Reservoir	Period	Mean peak periphyton biomass ± sd by depth in the littoral zone standardized to 60-day sampling periods (µg chl-*a* ·cm^{-2})						Depth effect (*p*)
			1 m	4 m	7 m	10 m	14 m	18 m	
Summer	Lower Campbell	Jul 31 – Sep 25, 2015	0.25 ± 0.1	0.36 ± 0.1	0.28 ± 0.12	0.23 ± 0.11	0.18 ± 0.08	0.02 ± 0.002	0.003
	Upper Campbell	Jun 17 – Aug 15, 2016	0.02 ± 0.002	0.02 ±0.01	0.03 ±0.01	0.02 ±0.01	0.02 ±0.01	0.004 ±0.001	<0.001
Fall	Lower Campbell	Sep 25 – Nov 20, 2015	0.18 ± 0.1	0.38 ± 0.29	0.31 ± 0.27	0.19 ± 0.18	0.07 ± 0.06	0.02 ± 0.02	0.08
	Upper Campbell	Sep 16 – Nov 15, 2016	0.29 ±0.13	0.28 ±0.04	0.20 ±0.06	0.11 ±0.04	0.03 ±0.01	0.006 ±0.001	0.002

3.3.2.Taxonomy

The periphyton assemblage on the Styrofoam balls mainly comprised diatoms and green algae, with lower density of blue-green algae (Figure 14 and Figure 15). Mean summertime periphyton cell density (8,251 x 10^6 cells·m^{-2}) was double that in the fall (3,508 x 10^9 cells·m^{-2}). Diatoms included *Tabellaria fenestrata*, *Achnanthes* sp., *Eunotia* sp., *Fragilaria* sp., *Nitzschia* sp., *Rhopalodia gibba*, *Gomphonema olivaceum*, and *Melosira* sp. *Spirogyra* sp. was the main chlorophyte. Trace numbers of blue greens (*Aphanizomenon* sp. and *Anabaena* sp.), Euglenoids, and Chryso-cryptophytes were found. In Upper Campbell Reservoir, the diatoms accounted for most cells in summer and fall. Trace numbers were represented by chlorophytes and blue greens. Diatom taxa in Upper Campbell Reservoir mainly included *Achnanthes* sp., *Nitzschia* sp., *Eunotia* sp., *Amphipleura pellucida, Stauroneis sp., Fragilaria* sp., and *Tabellaria fenestrata.* Cell density was also higher in summer than fall in Upper Campbell Reservoir, despite the markedly higher peak biomass in fall (Table 9).

Figure 14. Mean algal cell density by class in summer and fall in Lower Campbell Reservoir, 2015. Error bars are standard deviations.

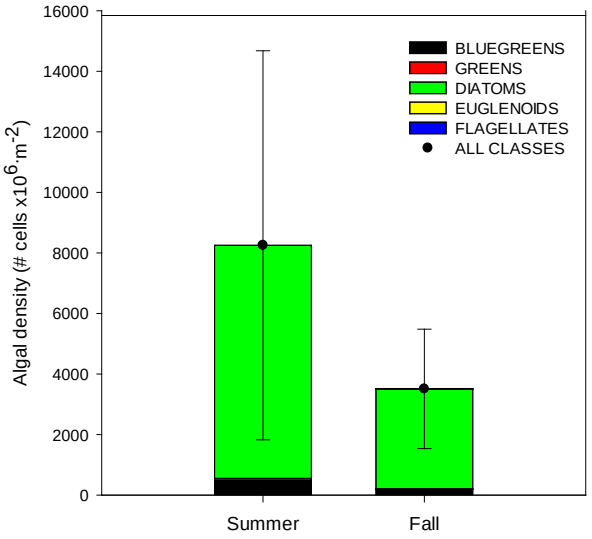
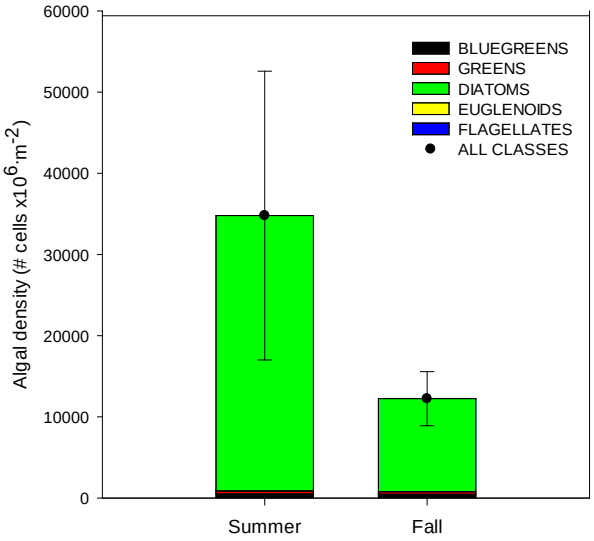


Figure 15. Mean algal cell density by class in summer and fall in Upper Campbell Reservoir, 2016. Error bars are standard deviations.



3.4. Linking Periphyton Accrual with Habitat Attributes

3.4.1. Lower Campbell Reservoir

As explained in Section 2.5, three different habitat variables were used in a regression model to explain variation in PB. They were: nutrient concentration, water temperature, and PAR. Nutrient samples were collected at the surface and near the bottom of the reservoir. Data from the surface samples were used in the regression model, based on the assumption that nutrient concentrations were the same throughout the euphotic zone due to mixing of the surface layer. It was not feasible to use any form of phosphorus as an independent variable in the regression models because none of the phosphorus fractions could be detected and, therefore, there was no variance in the values. Concentrations of NH_4-N were also below the method detection limit (Table 7). NO_3-N was not detectable in some samples. It was therefore necessary to use TN as a predictor variable. We did not regard TN as a specific nutrient that limited algal growth because it contains forms of N that are not biologically available and concentrations of bioavailable forms of inorganic N (NH_4-N and NO_3-N) and P (mainly SRP) are more likely to directly limit algal growth rates. Instead, we regarded TN as a surrogate for growth-limiting nutrient concentrations based on the assumption that the concentrations of bio-available forms of N and P would be correlated with TN concentrations.

For Lower Campbell Reservoir, the regression was highly significant (p<0.001) (Table 10). Log_{10}PAR had a higher standardized coefficient than TN and temperature, meaning that log_{10}PAR had a slightly greater influence on PB than TN and almost twice that of temperature. There was a lower standard error for log_{10}PAR (0.014) than for TN (0.353), indicating that PAR was a more

consistent predictor of PB compared to TN. Although the standard error for temperature was lower than log_{10}PAR, the standardized coefficient for temperature (0.344) indicated it was approximately half as important as log_{10}PAR (0.599) in describing PB in Lower Campbell Reservoir. The interaction term between log_{10}PAR and water temperature was not significant so it was removed from the equation. Based on these criteria, log_{10}PAR was the identified as the most important predictor of PB, closely followed by TN and distantly by temperature. The overall regression correlation coefficient (r^2) was 0.56, showing that the regression model explained 56% of the variance in PB: the other 44% was unexplained by the model.

Table 10. Regression equation parameters from the analysis linking habitat attributes to PB in Lower Campbell Reservoir.

Effect	Coefficient	Standard Error	Standardized Coefficient	p-value
Constant	-0.236	0.058	0	<0.001
TN	1.63	0.353	0.577	<0.001
Log_{10} of PAR	0.057	0.014	0.599	0.046
Temperature	0.007	0.003	0.344	<0.001

Using parameter values in Table 10, the back-transformed regression equation was as follows:

Equation 4

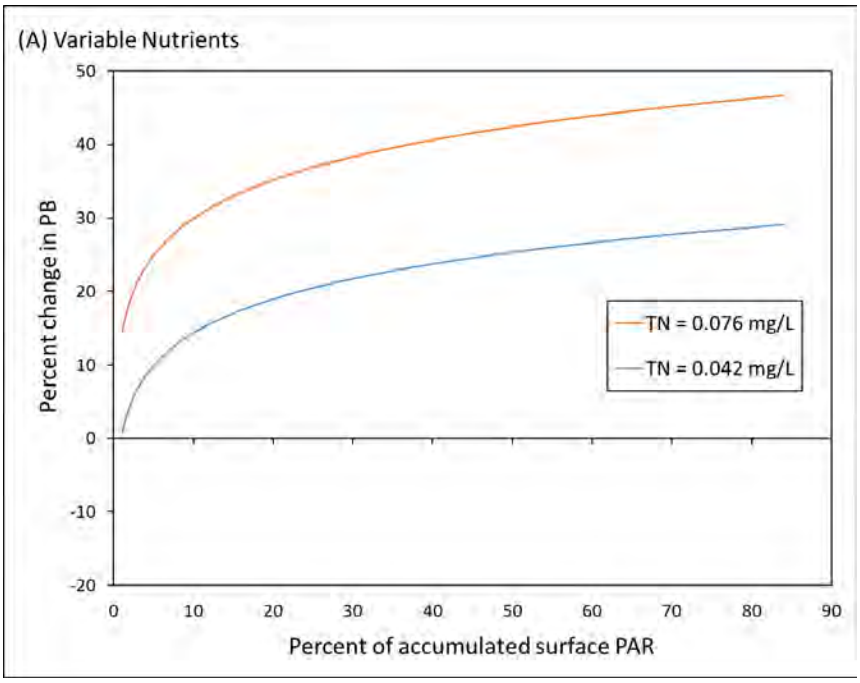
$$\boldsymbol{PB = (10^{-0.236}) * (10^{TN*1.63}) * \left(PAR^{0.057}\right) * (10^{temp*0.007}) - 1}$$

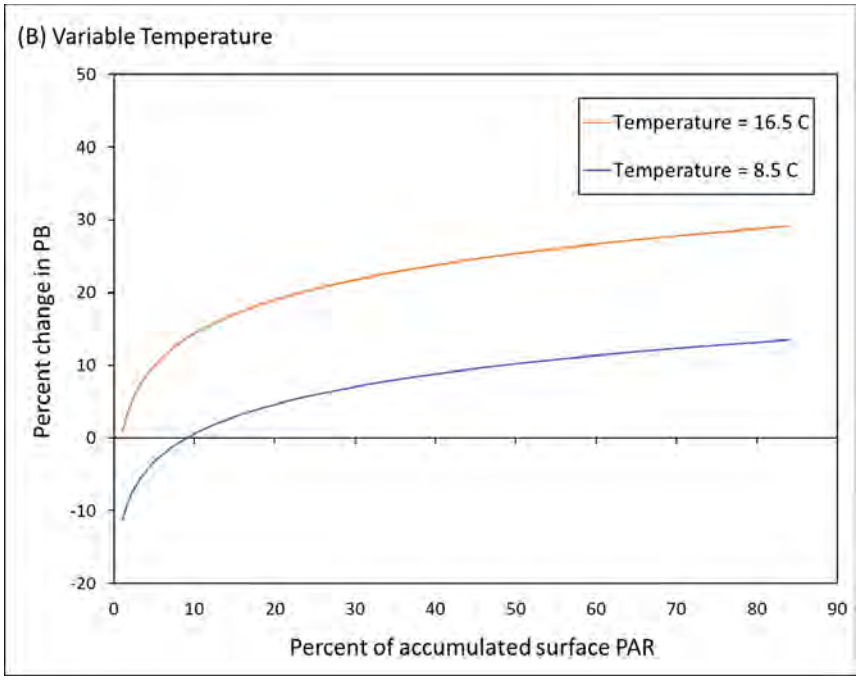
where: PB is peak biomass in units of μg chl-*a*·cm^{-2}, TN is total nitrogen concentration in units of mg·L^{-1}, and *PAR* is accumulated photosynthetically active radiation during the period of substrata incubation in units of mol·m^{-2}, and $temp$ is temperature in °C.

Sensitivity of PB to change in PAR, TN, and water temperature was explored by running Equation 4 over a range of values of the independent variables. Figure 16A shows the logarithmic response by PB to change in PAR when temperature is held constant, wherein a small change in PAR at low PAR results in a large change in PB and a large change in PAR at high PAR results in a small change in PB. This sensitivity of PB to PAR increases when TN concentration is increased from 0.042 mg·L^{-1} (summer value) to 0.076 mg·L^{-1} (fall value). Figure 16B shows the same logarithmic sensitivity of PB to change in PAR when TN concentration is held constant (typical summer value of 0.042 mg·L^{-1}) and there is an upwards shift in PB with a change in water temperature from 8.5°C to 16.5°C. The upwards shift in PB with greater TN concentration (surrogate for bio-available nutrients) is approximately parallel over the range of change in percent PAR, as is the upwards shift in PB with higher temperature over the range of percent PAR. These parallel lines show no

interaction of PAR and TN when temperature is held constant, and no interaction of PAR and temperature when TN is held constant.

Figure 16. Sensitivity of PB in Lower Campbell Reservoir to change in (A) TN and (B) water temperature over a full range of PAR. The simulations were calculated using Equation 4.





3.4.2. Upper Campbell Reservoir

The three habitat variables used in the regression model for Lower Campbell Reservoir (nutrient concentration, water temperature, and PAR) were also used to explain variation in PB in Upper Campbell Reservoir. Ammonium (NH_4-N) and all forms of phosphorus (SRP, TDP and TP) were not detectable in summer and fall 2016 in Upper Campbell Reservoir. Nitrate (NO_3-N) and TN were also not detectable in summer 2016 but 18 out of 24 samples had detectable NO_3-N and TN in fall 2016. Using Equation 4, we ran two models for PB with PAR, water temperature, and either TN or NO_3-N with an interaction term between PAR and water temperature. The results were identical for the two N species. Therefore, to be consistent with the Lower Campbell Reservoir, we present model results using TN.

The regression model for PB in Upper Campbell Reservoir explained most variation in the data (r^2 = 0.89) and was highly significant ($p < 0.0001$) as were all the terms included in the model ($p \leq 0.001$) (Table 11). TN had a relatively high standard error (0.342) and low standardized coefficient (0.568) compared to the other variables in the model so it was deemed to be less important in explaining variation in PB in Upper Campbell Reservoir. The combination of PAR and temperature explained much of the variation in PB, particularly the interaction between the two (Table 11). The interaction term is the coefficient for the product of PAR and water temperature and it explained 19% of variation in the data. The negative standardized coefficient for the interaction term was 1.14 × more important than the $\log_{10}$PAR and 4.85 × more important than temperature. The cumulative effect on PB of these two variables was negative.

Table 11. Regression equation parameters from the analysis linking habitat attributes to PB in the Upper Campbell Reservoir.

Effect	Coefficient	Standard Error	Standardized Coefficient	*p*-value
Constant	-0.477	0.055	0	< 0.0001
TN	2.925	0.342	0.568	< 0.0001
Log_{10} of PAR	0.299	0.028	3.799	< 0.0001
Temperature	0.014	0.004	0.893	0.001
Log_{10} of PAR: Temperature	-0.014	0.002	-4.328	< 0.0001

Using parameter values in Table 11, the regression equation was as follows:

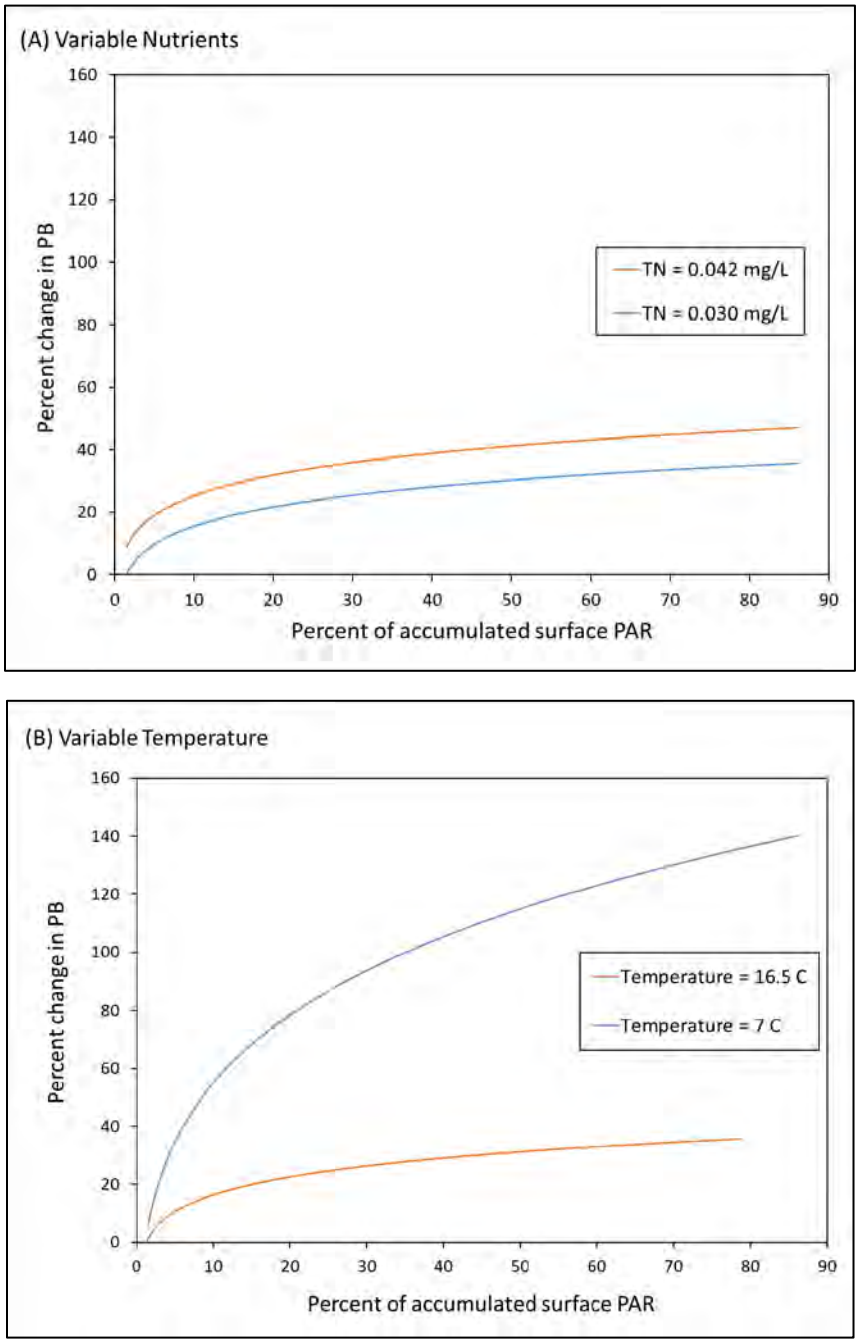
Equation 5

$$PB = (10^{-0.477} \times 10^{2.925 \times TN} \times PAR^{0.299} \times 10^{0.014 \times Temperature} \times PAR^{-0.014} \times 10^{-0.014 \times Temperature}) - 1$$

where: PB is peak biomass in units of μg chl-*a*·cm^{-2}, TN is total nitrogen concentration in units of mg·L^{-1}, PAR is accumulated photosynthetically active radiation during the period of substrata incubation in units of mol·m^{-2} and temperature is measured in °C.

Sensitivity of PB in Upper Campbell Reservoir to changes in PAR, TN and water temperature was explored by running Equation 5 with one variable at a fixed value and other variables at changing values (Figure 17). As in Lower Campbell Reservoir, small change in PAR at low PAR resulted in a large change in PB and a large change in PAR at high PAR resulted in a small change in PB. Again, PB increased regardless of PAR when TN concentration was increased from 0.030 (summer value) to 0.042 mg·L^{-1} (fall value). Parallel lines in Figure 17A showed no interaction between PAR and TN concentration on PB. In contrast, PB response to change in PAR was different at low temperature compared to higher temperature, resulting in diverging response by PB to PAR at the different temperatures (Figure 17B). This divergence showed the significant effect of the interaction between PAR and temperature on PB in Upper Campbell Reservoir. The greater response of PB to change in PAR at the lower temperature that was typical of the fall sampling period showed greater sensitivity of PB to PAR at the lower temperature in the fall. This finding means that during isothermal conditions in the fall there was large change in PB over relatively small change in water depth and PAR compared to the response in summer.

Figure 17. **Sensitivity of PB in Upper Campbell Reservoir to change in (A) TN and (B) water temperature over a full range of PAR. The simulations were calculated using Equation 4.**



3.5. The Performance Measure Called *L*

3.5.1. Defining Pre- and Post-WUP Periods

The performance measure, ***L***, was based on the application of Equations 1 and 4 for Lower Campbell Reservoir and application of Equations 1 and 5 for Upper Campbell Reservoir. ***L*** was the sum of products of areas of littoral strata and PB within each of those strata. ***L*** was contrasted between blocks of years before and after implementation of the water use plan (WUP, See Section 1). Although the WUP was ordered in 2012, BC Hydro began implementing hydrological conditions for the WUP in 2005. Given this start date, the pre-WUP time period was defined as 1998 to 2004. The post-WUP time period was 2006 to 2015 in Lower Campbell Reservoir and 2006 to 2016 in Upper Campbell Reservoir (Table 12).

Table 12. Pre- and post-WUP years for Lower and Upper Campbell Reservoirs.

Reservoir	Pre-WUP years[1]	Post-WUP years[1]
Lower Campbell Reservoir	1998 to 2004	2006 to 2015
Upper Campbell Reservoir	1998 to 2004	2006 to 2016

[1]Selected in consultation with BC Hydro.

3.5.2. Changes in Water Surface Elevation between Pre- and Post-WUP Periods

Before calculating ***L*,** the WUP effect on metrics of water surface elevation was tested to see if the WUP actually changed mean elevations and thus littoral area that is a function of elevation (Figure 10 and Figure 11). Those metrics were mean annual water surface elevation, mean annual minimum water surface elevation, and mean annual maximum water surface elevation. A *t*-test was used to determine if there was a statistically significant difference in the mean value of each metric between the two blocks of years (years before WUP and years after WUP), thereby testing for a year effect on water elevation and thereby littoral area. A year effect is essentially the same as a WUP effect given the assumption that effects of WUP exceeded non-WUP variance over time. .

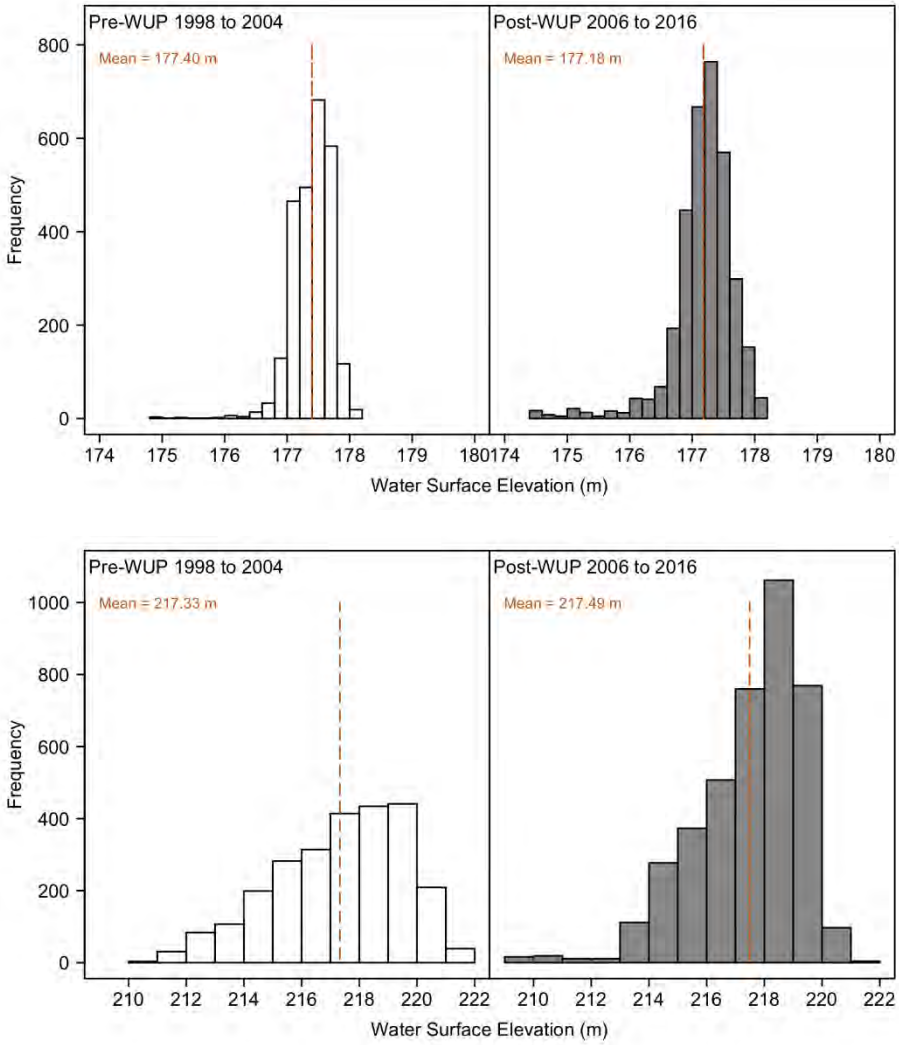
There was no statistical year effect on mean minimum water surface elevation (p=0.40 for Lower Campbell, p=0.76 for Upper Campbell) and mean maximum water surface elevation (p=0.72 for Lower Campbell, p=0.30 for Upper Campbell). There was a statistically significant 0.1% decline in mean annual water surface elevation in Lower Campbell Reservoir in the summer and fall (Table 13) due to WUP. There was also a statistically significant 0.2% decline in mean annual water surface elevation in Upper Campbell Reservoir in the summer and a statistically significant 0.2% increase in the fall (Table 13). .

Table 13. Mean ± SD water surface elevation (m) for Lower and Upper Campbell Reservoir during the summer (June 1 to September 25) and fall (September 26 to December 31) for pre- and post-WUP years.

Season	Reservoir	Pre-WUP	Post-WUP	*F*-statistic	Probability
Summer	Lower Campbell	177.33 ± 0.31	177.09 ± 0.30	278.6	<0.001
	Upper Campbell	218.63 ± 1.39	218.23 ± 1.29	596.8	<0.001
Fall	Lower Campbell	177.42 ± 0.33	177.26 ± 0.51	49.3	<0.001
	Upper Campbell	217.07 ± 1.91	217.61 ± 1.43	42.2	<0.001

The effect of annual ranges of water surface elevation on ***L*** were next examined. The pre- and post-WUP range of water surface elevations in Lower Campbell Reservoir was 174.5 m to 178.2 m and in Upper Campbell Reservoir it was 209.5 m to 221.6 m during both time periods. Within these ranges, the patterns of elevation frequencies differed between the two blocks of years (Figure 18). In Lower Campbell Reservoir, the frequency distribution was wider in post WUP years than in pre-WUP years, mainly due to more occurrences of relatively low elevations in post-WUP years than in pre-WUP years. In Upper Campbell Reservoir, the frequency distribution had a sharper peak close to the mean in post-WUP years compared to pre-WUP years, meaning there was greater prevalence of elevations close to the mean in the post-WUP years than in pre-WUP years.

Figure 18. Frequency distribution of mean daily water surface elevations during pre-WUP and post-WUP years in Lower Campbell Reservoir (top panel) and Upper Campbell Reservoir (lower panel).

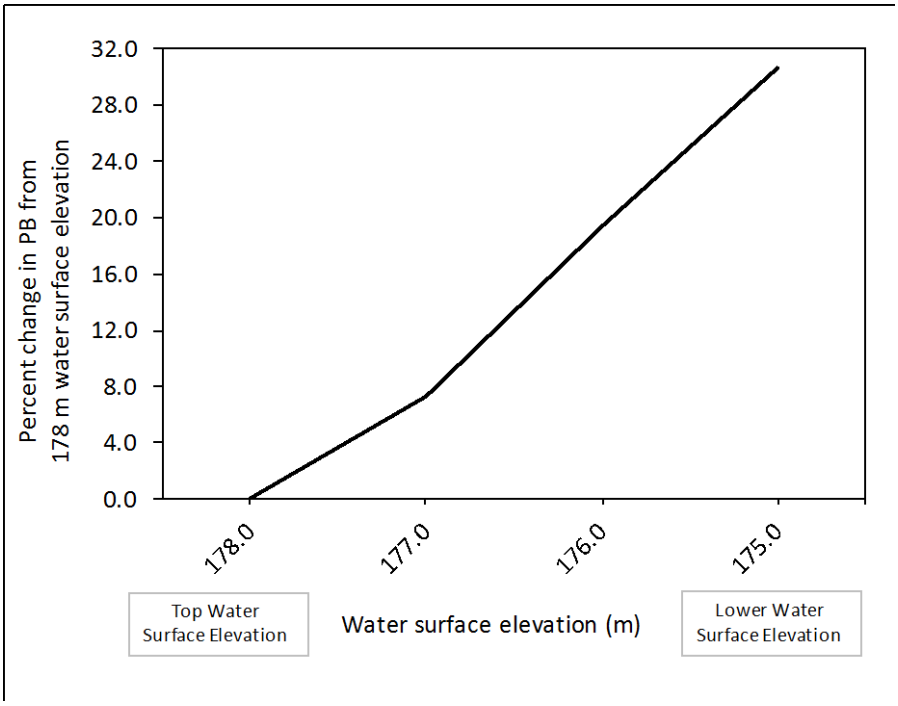


3.5.3.Sensitivity of *L* to Changes in Water Level

L was calculated for Lower Campbell Reservoir using Equations 1 and 4 to determine how changes from the maximum operating level[4] of 178.0 m might affect PB in the littoral zone. Temperature was held constant at 16.5 ºC and TN concentration was held constant at 0.041 mg/L, which were typical values for summer. PAR varied with water depth. The model assumed a 60-day incubation period to reach PB. With a 1.0 m drop in water surface elevation from 178.0 m to 177.0 m, PB increased by 7.3% (Figure 19) despite a decline in littoral area of 3.4% (Figure 10). If water surface elevation further declines to 175.0 m, PB is predicted to increase by 30.6% compared to PB at 178.0 m. This percent increase in PB with declining littoral area is due to overall shallower water depth within the littoral zone over the range of elevations of 178 – 175 m. Shallower depths results

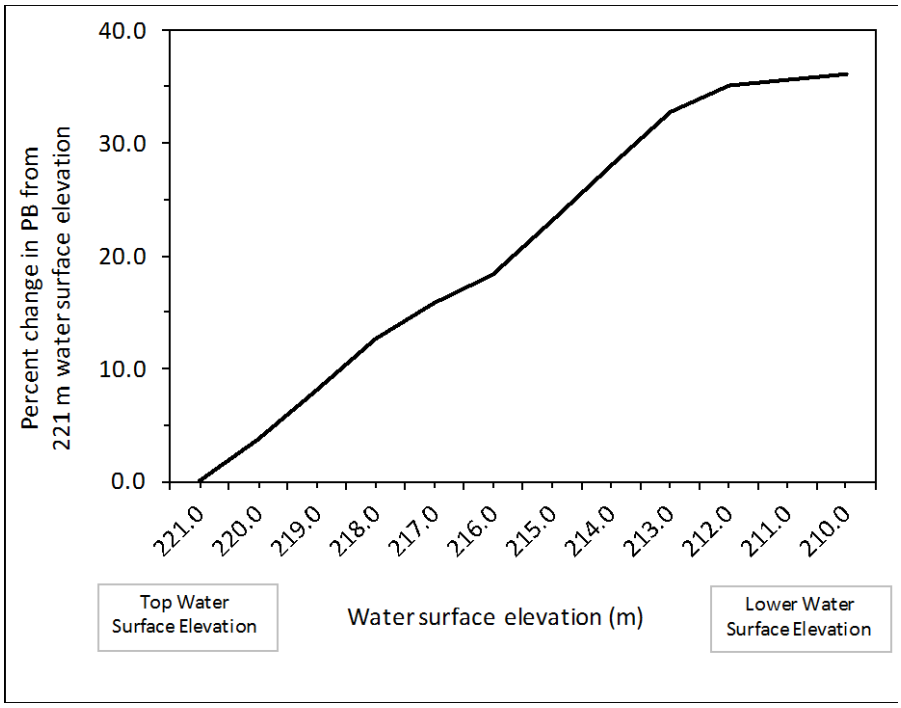
in greater PAR over the whole littoral area and that effect of PAR on PB is greater than the effect of the small change in littoral area on PB. The net result is an increase in PB with declining water surface elevation between 178 m and 175 m. This simulation shows that operating within the target water surface elevation summer range of 177.5 m down to 176.5 m, results in an increase in littoral PB of 13% to 25%, respectively, compared to operating at a full pool elevation of 178.0m.

Figure 19. Percent change in littoral PB in Lower Campbell Reservoir within the range of water surface elevations occurring during pre-WUP and post-WUP years.



The same simulation was run for Upper Campbell Reservoir using Equations 1 and 5. Temperature was held at 16.5°C and TN concentration was held at 0.030 mg/L, which were typical of summer. PAR varied with water depth. Again, the model assumed a 60-day incubation period to reach PB. With a 1.0 m drop in water surface elevation from 221.0 m to 220.0 m, PB increased by 3.8% (Figure 20) coinciding with <1% increase in littoral area (Figure 11). PB further increased by 36.1% when water surface elevation dropped from 221.0 m to 210.0 m. This increase in PB was again due to shallower water depths within the littoral area causing greater PAR over the whole littoral area. Given that PAR is an important driver of PB (Equation 5), the net result was an increase in PB with little change in area of the littoral zone as water surface elevation declines. This simulation shows that water surface elevation in Upper Campbell can decrease up to 11.0 m and littoral productivity is not expected to decline because of gains in littoral area at the bottom end of the littoral zone offsetting losses at the upper end. It also shows that operating Upper Campbell Reservoir within the summer range of 220.5 m down to 217.0 m, would increase PB by 1.8% to 15.8%, respectively, compared to operating the reservoir at 221.0 m.

Figure 20. Percent change in littoral PB in Upper Campbell Reservoir within the range of water surface elevations occurring during pre-WUP and post-WUP years.



3.5.4.Effect of WUP Operations on Periphyton Biomass

Mean daily water surface elevation for the pre-WUP period in Lower Campbell Reservoir was 174.88 m to 178.07 m, while mean daily elevation for the post-WUP period was 175.06 m to 178.17 m (Table 14). In Upper Campbell Reservoir, daily water surface elevation was 210.84 m to 221.63 m pre-WUP and 212.91 m to 221.24 m post-WUP (Table 14).

Table 14. Minimum, mean and maximum daily water surface elevation (m) for Lower and Upper Campbell Reservoir pre- and post-WUP.

Reservoir	Statistic	Pre-WUP	Post-WUP
Lower Campbell	Minimum	174.88	175.06
	Mean	177.37	177.17
	Maximum	178.07	178.17
Upper Campbell	Minimum	210.84	212.91
	Mean	217.94	217.96
	Maximum	221.63	221.24

To estimate PB as daily water surface elevation changed in Lower and Upper Campbell reservoirs pre- and post-WUP, a linear regression was calculated from the simulated PB data used for Figure 19 and Figure 20. The data used to construct this regression model were based on predictions of ***L***, which sums periphyton biomass present in individual substrata. The regression equation for Lower Campbell Reservoir using mean summer conditions was:

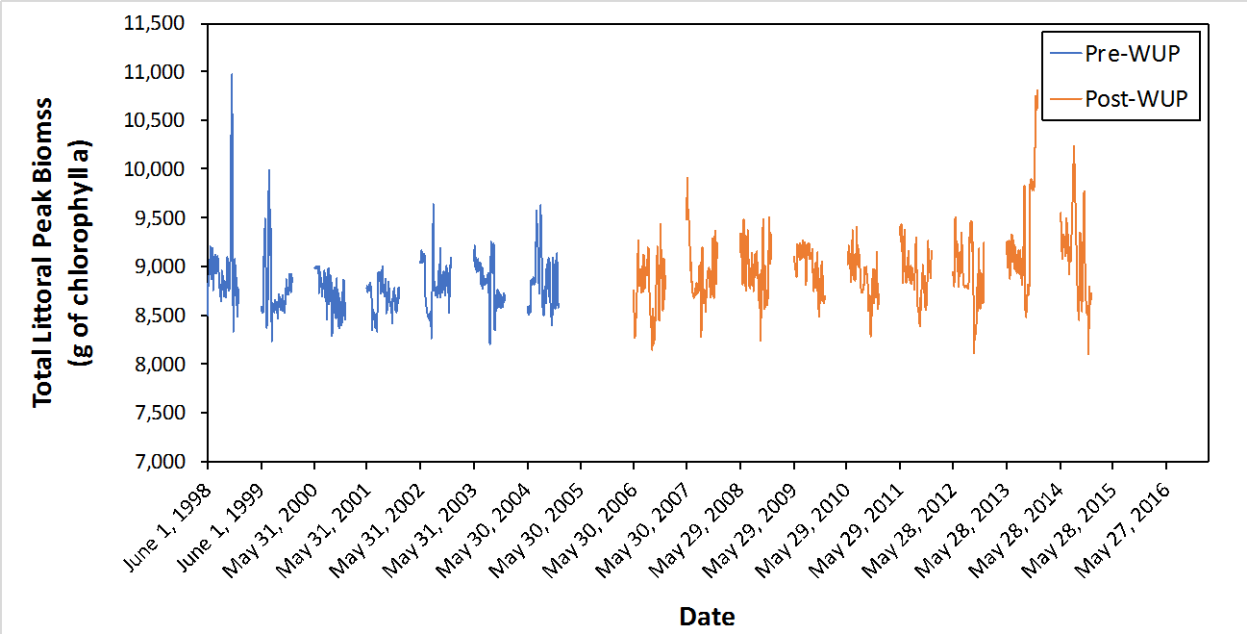
Equation 6

$$\boldsymbol{PB = 163155 - 870.20 * Water\ Elevation}$$

Where fit of the linear model to the data (r^2) was 0.99. This model shows that water elevation can replace PAR, temperature, and nutrient concentration as shown in Equation 4 to predict PB with essentially no unexplained variance (r^2 shows a 99% fit of the model to the data).

Figure 21 shows that the magnitude, range and seasonal patterns in PB , calculated on daily time steps, are similar between pre- and post-WUP periods. The variation observed in Figure 21 can be attributed to fluctuations in water surface elevation (Equation 6). As water surface elevation increases, there would be a gain in littoral area with newly wetted substrata at the upper end of the littoral zone and a loss of littoral area at the bottom of the littoral zone, corresponding to a vertical shift in the littoral zone associated with changes in the amount of PAR reaching individual strata.

Figure 21. Estimated PB in Lower Campbell Reservoir based on water surface elevation changes during pre- and post-WUP years as defined in Table 12.



The regression equation for Upper Campbell Reservoir using mean summer conditions was:

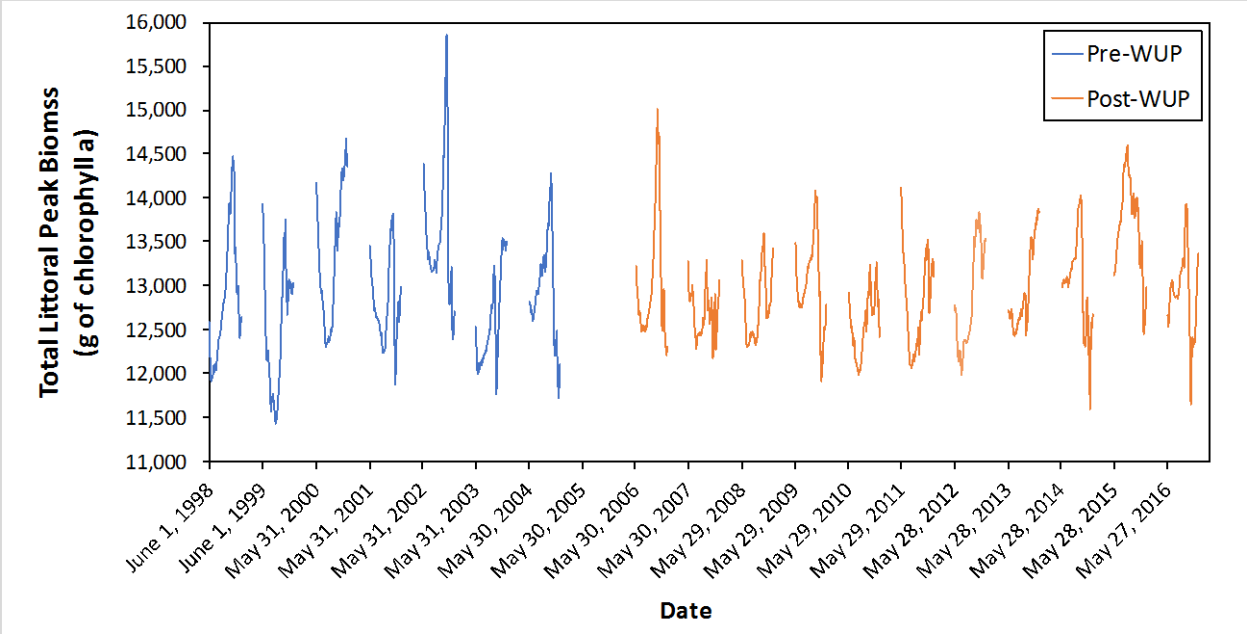
Equation 7

$$PB = 102402 - 410.46 * Water\ Elevation$$

Where fit of the linear model to the data (r^2) was 0.98. Again this model shows that water elevation can replace PAR, temperature, and nutrient concentration as shown in Equation 5 to predict PB with essentially no unexplained variance.

As with Lower Campbell Reservoir, Figure 21 shows that the magnitude, range and seasonal patterns in PB, calculated on daily time steps, are similar between pre- and post-WUP periods.

Figure 22. Estimated PB in Upper Campbell Reservoir based on water surface elevation changes during pre- and post-WUP years as defined in Table 12.



Using data from Figure 21 and Figure 22 a *t*-test was applied to test for year effects on PB in each reservoir. This approach was the same as was used to test for year effects on water surface elevation (Table 13), wherein a test of year effects is the same as a test of WUP effects. Results showed that, following implementation of the WUP, PB decreased by 0.01% in Upper Campbell Reservoir and increased by 2.0% in Lower Campbell Reservoir. The modelled change was statistically significant (p<0.001) in Lower Campbell Reservoir but not statistically significant (p=0.636) in Upper Campbell Reservoir (Table 15).

Table 15. PB mean ± SD in Lower and Upper Campbell Reservoir pre- and post-WUP years as defined in Table 12.

Reservoir	Pre-WUP	Post-WUP	*F*-statistic	Probability
Lower Campbell	8,809.06 ± 282.52	8984.60 ± 361.42	239.5	<0.001
Upper Campbell	12,948.37 ± 745.32	12,938.28 ± 570.76	0.224	0.636

3.6. Benthic Invertebrate Composition

Benthic invertebrates in the littoral zone of Lower Campbell Reservoir included the mayfly, caddisfly, and true fly orders of aquatic insects, oligochaetes, and an assemblage of mites, nematode worms, ribbon worms, Hydra, ostracods, gammarid amphipods, molluscs (gastropods and bivalves), crayfish and damselflies (Figure 23). Densities were similar between the basket (23,645 ± 13,144 invertebrates·m^{-2}) and Ponar (25,732 ± 15,782 invertebrates·m^{-2}) samplers although fewer taxa were captured in the Ponar grabs (mean richness = 12.5) compared with the baskets (mean richness = 17.5). Regardless of sampling method, the benthic invertebrate community mostly comprised chironomids (>17,000 individuals·m^{-2}) and oligochaetes (>1800 individuals·m^{-2}). Mean biomass was greater in the basket samples (1,296 mg·m^{-2}) compared to the Ponar grab samples (883 mg·m^{-2}) mainly due to the presence of one large signal crayfish (*Pacifastacus leniusculus)* caught in a single basket sampler. The lone crayfish comprised 97% of biomass in that sample and skewed the results presented in Figure 23. However, the chironomids still represented a high proportion (15%) of the total biomass compared to the other invertebrate groups (≤1%) excluding the other category which included the crayfish and accounted for 81% of the mean biomass in basket samples. In the Ponar samples, chironomids, mayflies, and oligochaetes accounted for 54%, 12% and 9% of the total littoral biomass respectively. Overall, the results show that regardless of sampler type, the littoral zone had relatively higher abundance of chironomids and oligochaetes, and lower abundance of mayflies, caddisflies, non-chironomid true flies, and other aquatic invertebrates.

Similarities and differences were found in Upper Campbell Reservoir (Figure 24). The benthic invertebrate assemblage again included aquatic insects, oligochaetes, and a group of "other" taxa including incidental ostracods, Hydra, and nematodes. However, invertebrate densities in the baskets (19,652 ± 25,869 invertebrates·m^{-2}) were highly variable compared to those in the Ponar grab samples (8,704 ± 4,178 invertebrates·m^{-2}). The assemblage mostly comprised chironomids but density of the "other" taxa was greater than oligochaete density. Invertebrate biomass was similar and variable between the two types of sampler. Chironomids were the single largest group contributing to overall biomass and the Ponar grab sampler captured more oligochaete biomass than did the basket samplers.

Figure 23. Density (top panel) and areal biomass (lower panel) of benthic invertebrates in Lower Campbell Reservoir.

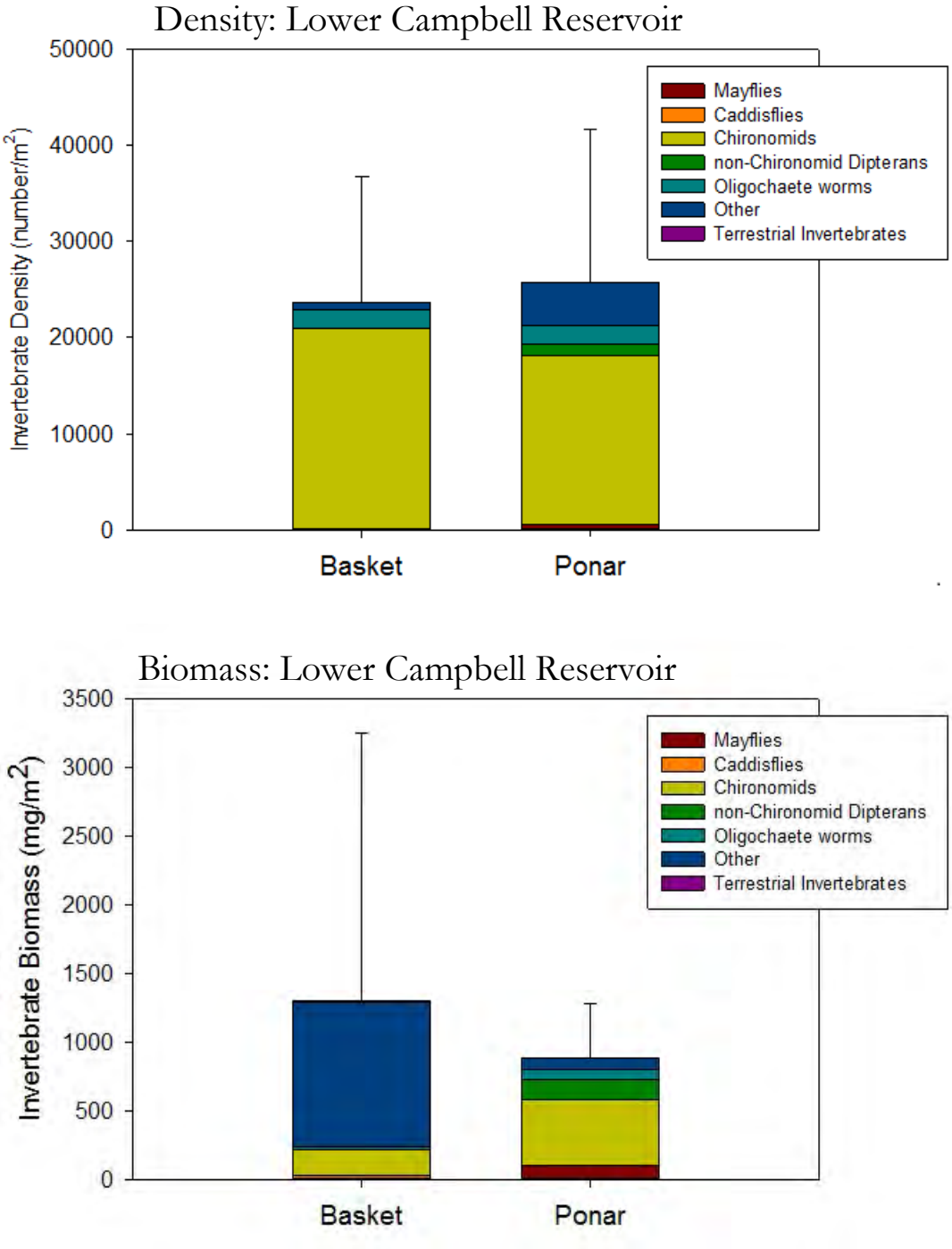
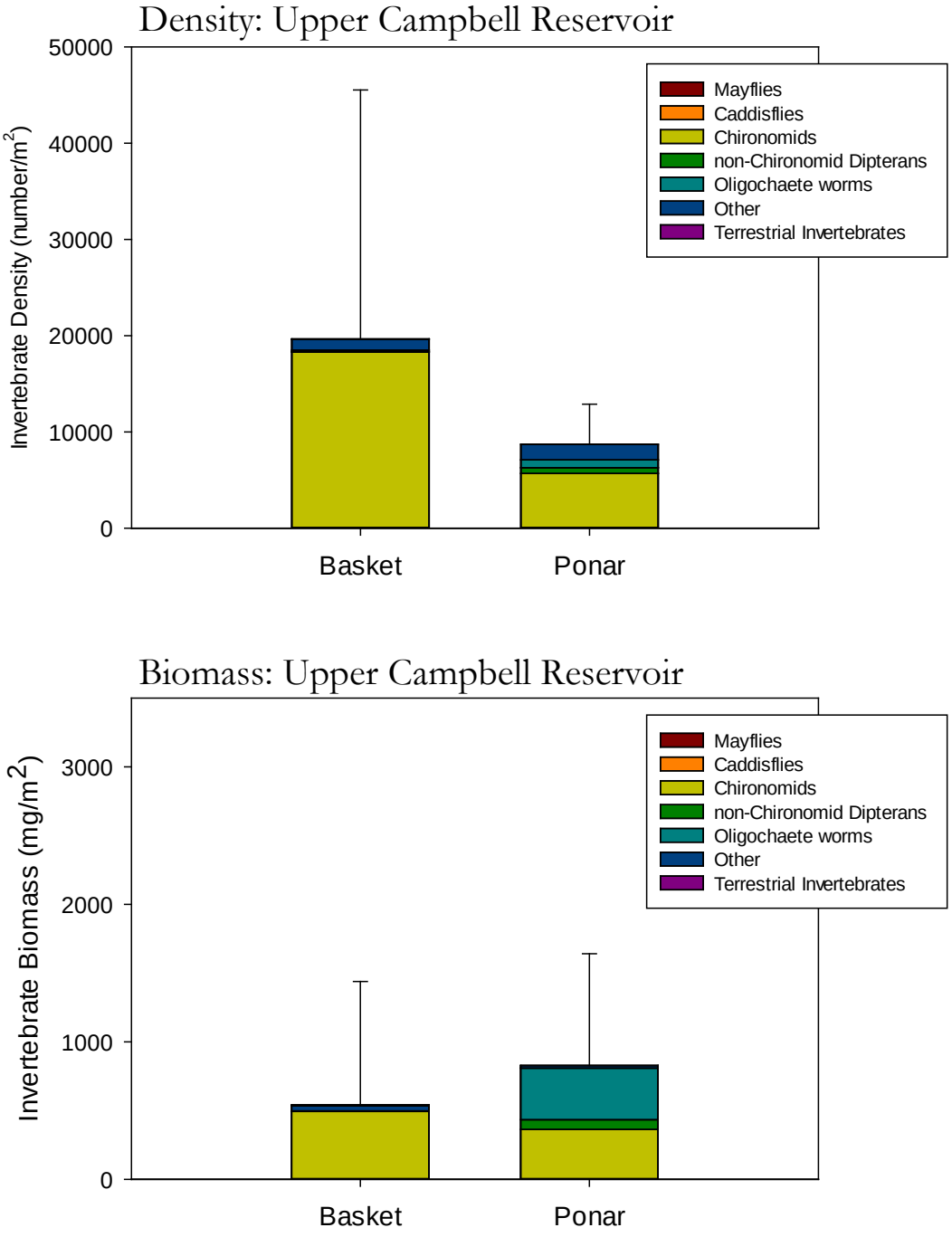


Figure 24. Density (top panel) and areal biomass (lower panel) of benthic invertebrates in Upper Campbell Reservoir.



3.7. Fish Stomach Contents

Stomachs from fish collected in gill nets on October 5, 2015 from Lower Campbell Reservoir contained an assortment of prey from aquatic and terrestrial habitats (Table 16). The cottids ingested aquatic taxa that mainly included mayflies and chironomids that are common in littoral habitat, as well as individuals from terrestrial and zooplankton taxa. Coastrange Sculpin (*Cottus aleuticus*) exclusively had terrestrial taxa in its stomach but only one fish was collected of this species, which is not representative of food preferences. In contrast, other cottids including Prickly Sculpin (*C. asper*) had an assortment of aquatic taxa in their stomachs including benthic insects and zooplankton. Based on quantifying prey abundance, Rainbow Trout ingested zooplankton almost exclusively while Cutthroat Trout ingested a wider range of prey including other fish, zooplankton, and terrestrial taxa, with a minor component of benthic insects and other aquatic taxa.

Table 16. Contents of fish stomachs, by fish species, captured during gill net sampling on Lower Campbell Reservoir on October 5, 2015.

Metric		Average metric value by fish species				
		Cottus aleuticus	*Cottus asper*	*Cottus* sp.	*Oncorhynchus clarki* (Cutthroat trout)	*Oncorhynchus mykiss* (Rainbow trout)
Number of fish sampled		1	8	3	23	61
Mean fork length (mm)		170	102	146	297	243
Mean weight (g)		85	12	46	334	201
Average number of fishes per stomach		0	1	0.7	0.7	0
Average number of invertebrates per stomach		1	4.8	0.7	29.8	2678
Percent of total number of invertebrates among all samples	Mayflies	0.00%	9.30%	50.00%	1.50%	0.00%
	Stoneflies	0.00%	0.00%	0.00%	0.00%	0.00%
	Caddisflies	0.00%	7.00%	0.00%	0.10%	0.00%
	Chironomids	0.00%	23.30%	0.00%	0.70%	0.00%
	Other aquatic invertebrates[1]	0.00%	2.30%	0.00%	6.90%	0.00%
	Terrestrial[2]	100.00%	2.30%	0.00%	37.10%	0.10%
	Zooplankton[3]	0.00%	55.80%	50.00%	53.70%	99.90%

[1]Mites, Coleoptera (beetles), non-chironomid dipterans, amphipods, and Hemipterans.

[2]Araneae (spiders), Coleoptera (winged beetles), Collembola (springtails), Diptera adults, Hemiptera adults (true bugs), Hymenoptera (bees, wasps, sawflies and ants), Odonata adults (damselflies and dragonflies), Psocodea (bark lice), and Blattodea (waterbugs).

[3]Cladocerans (Daphnia sp., Bosmina/Eubosmina sp., Leptodora kindtii, Chydoridae sp., Simocephalus sp., Polyphemus sp., and Sida sp.), copepods (Cyclops sp., and Diaptomus sp.), and Ostracods

Stomachs from Cutthroat trout and Rainbow Trout captured using gill nets in Upper Campbell Reservoir in 2016 included mainly zooplankton with a minor component of aquatic benthic invertebrates (mainly chironomids) and terrestrial invertebrates (Table 17). Only the Cutthroat Trout ingested fish prey, with an average of one prey fish per stomach. The main difference in fish stomach contents between reservoirs was among the Cutthroat Trout that ingested proportionately more zooplankton and fewer terrestrial invertebrates in Upper Campbell Reservoir than in Lower Campbell Reservoir[7]. It is important to note that the data in Table 16 and Table 17 are based on abundances of individual prey items found in stomachs rather than biomass, which could not be determined because prey were subject to various degrees of digestion. The biomass of one prey fish and thus the energy from that prey fish could greatly exceed biomass and energy from large numbers of benthic invertebrates.

[7] This result contrasts with the stomach contents analysis conducted for JHTMON-5, in which no zooplankton was identified in the stomach contents of a separate group of seven Cutthroat Trout, based on visual estimates of the relative proportion of major prey groups (by biomass) in the field (Hocking *et al.* 2017). This difference highlights the variability in Cutthroat Trout diet among individuals. In addition, it is possible that the small size of zooplankters meant that individuals were not detected during the field inspections conducted for JHTMON-5, yet they were detected during the more precise laboratory analysis that was undertaken for this study to measure prey abundance.

Table 17. Contents of fish stomachs, by fish species, captured during gill net sampling on Upper Campbell Reservoir on August 29–31, 2016.

Metric		Cutthroat Trout	Rainbow Trout
Number of fish sampled		26	29
Mean fork length (mm)		306	217
Mean weight (g)		359	152
Average number of fishes per stomach		1	0
Average number of invertebrates per stomach		120	940
Percent of total number of invertebrates among all samples	Mayflies	0%	0%
	Stoneflies	0%	0%
	Caddisflies	0%	0%
	Chironomids	2.00%	0.20%
	Other aquatic invertebrates[1]	0.40%	0%
	Terrestrial[2]	0.90%	3.50%
	Zooplankton[3]	96.60%	96.40%

[1] The "Other" category includes mites, non-chironomid dipterans, and amphipods.

[2] Terrestrial invertebrates included Araneae (spiders), Coleoptera (winged beetles), Collembola (springtails), Diptera adults, Hemiptera adults (true bugs), Hymenoptera (bees, wasps, sawflies and ants), and Psocodea (bark lice).

[3] Zooplankton included cladocerans (Daphnia sp., Bosmina/Eubosmina sp., Leptodora kindtii, Polyphemus sp., and Sida sp.), and Ostracods.

3.8. Stable Isotope Modelling

3.8.1. Summary of Stable Isotope Signatures by Taxa

Nitrogen and carbon stable isotope signatures of all fish, invertebrates and primary nutrient sources were fairly distinct from one another, which is evidence for species separation by energy source and trophic position within the Lower Campbell Reservoir and Upper Campbell Reservoir food webs (Figure 25). Cutthroat Trout had high $\delta^{15}N$ levels consistent with their top position within lake food webs. Rainbow Trout had lower $\delta^{15}N$ and $\delta^{13}C$ values than Cutthroat Trout, indicating increased pelagic zooplankton contribution to diet. Smaller littoral prey fish generally had a wide range of $\delta^{15}N$ and $\delta^{13}C$, overlapping that of large Cutthroat and Rainbow Trout, as well as terrestrial invertebrates. Prey fish generally had a lower $\delta^{15}N$ signatures than large Cutthroat Trout but slightly higher $\delta^{15}N$ and $\delta^{13}C$ signatures than Rainbow Trout, suggesting that higher proportions of their diets are made up of littoral, benthic, and terrestrial invertebrates (with the exception of Stickleback; see Perrin *et al.* 2016), compared to the more zooplankton-dominated diet of large-bodied Rainbow Trout. Littoral invertebrates had the widest variation in stable isotope signatures of the four invertebrate groups, overlapping both zooplankton and benthic and terrestrial invertebrates in signatures of both $\delta^{15}N$

and $\delta^{13}C$, and overlapping $\delta^{13}C$ values with all three fish groups in Lower Campbell Reservoir. In contrast, benthic invertebrates overlapped other invertebrate groups (except zooplankton $\delta^{13}C$ signatures), while littoral invertebrates had $\delta^{15}N$ values that were lower than any other invertebrates, but very close $\delta^{15}N$ values of littoral periphyton in Upper Campbell Reservoir. Again, both littoral and benthic invertebrates had ranges in $\delta^{13}C$ that overlapped that of all three fish groups. On average, terrestrial invertebrates had higher $\delta^{15}N$ and $\delta^{13}C$ values than all other invertebrates, indicative of their terrestrial habitat. Zooplankton had the lowest $\delta^{15}N$ signatures in Lower Campbell Reservoir (and second lowest in Upper Campbell Reservoir), consistent with their lower food web position, and had the lowest $\delta^{13}C$ signatures, close to that of attached algae and SPOM, consistent with their pelagic habitat.

Among primary nutrient sources, attached algae had the lowest $\delta^{13}C$ signatures, similar to that of zooplankton, while littoral periphyton scraped off rocks had the highest $\delta^{13}C$ of all consumers and diet sources in the Lower and Upper Campbell food webs. This result shows that the attached algae scraped from the mooring line ropes derived most of its carbon from autochthonous production. In contrast, littoral periphyton scraped off of rocks likely consisted of a high proportion of heterotrophic organisms, such as protozoa, bacteria and fungi, as well as terrestrial detrital material.

3.8.2.Primary Nutrient Source Contributions to Reservoir Consumers

Of the four primary nutrient sources examined in the Lower and Upper Campbell reservoirs, leaf litter (i.e., carbon derived from terrestrial plants) contributed the most to upper-level consumer diets (Table 18, Table 19). Littoral periphyton had the next highest contribution to large Cutthroat Trout diets in both systems, whereas phytoplankton had the next highest contribution to the diets of Rainbow Trout.

Consistent with their benthic association and feeding habits (e.g., chironomids from Figure 23), the majority of the diet of benthic invertebrates was dominated by littoral periphyton and SPOM (approximately 40% and 26%, respectively) in Lower Campbell Reservoir, whereas all four basal nutrient sources contributed similarly to benthic invertebrates in Upper Campbell Reservoir (Figure 26). Basal nutrient sources to littoral invertebrates differed between the two reservoirs with diets dominated by attached algae and SPOM in Lower Campbell Reservoir (approximately 30% each) and diets more dominated by leaf litter and littoral periphyton in Upper Campbell Reservoir (approximately 30% each) (Figure 26).

The diets of littoral prey fish were largely dominated by terrestrial invertebrates in both reservoirs (approximately 55-60%), followed by zooplankton and littoral invertebrates in Lower Campbell Reservoir (19% and 21%, respectively), and benthic invertebrates (21%) in Upper Campbell Reservoir (Figure 27). Given the high proportion of terrestrial invertebrates in prey fish diets, the most prevalent primary nutrient source in prey fish diets was leaf litter (60% in Lower Campbell and 70% in Upper Campbell). In contrast, attached algae, littoral periphyton, phytoplankton, and SPOM each contributed to less than 10% of littoral prey fish diets. The exception to this was phytoplankton

in Lower Campbell which indirectly contributed to 20% of prey fish diets, likely due to the higher number of stickleback (zooplankton consumers) within this group of fish.

Cutthroat Trout diets were dominated by fish (55%) and Rainbow Trout diets were largely composed of zooplankton (40%) and terrestrial invertebrates (42%) (Figure 28). These diet estimates based on stable isotope analyses differ from stomach content results presented in Section 3.7, although the two sets of estimates cannot be compared directly because stomach contents data are based on prey abundance rather than biomass, which is more indicative of energy sources. In comparison, in the JHTMON-5 report, stomach contents and stable isotope measures of Cutthroat Trout and Rainbow Trout diet are more similar, which can be explained by the presentation of stomach contents data based on biomass. Among the basal nutrient sources, leaf litter contributed the most to large trout diets, including an average estimated 58% to Cutthroat Trout and 46% to Rainbow Trout diets. Phytoplankton contributed the second highest proportion of basal nutrient sources to both large Cutthroat Trout and Rainbow Trout diets. In contrast, attached algae, littoral periphyton, and SPOM each contributed to less than 10% of basal nutrient sources in large trout diets on average.

Figure 25. Carbon – nitrogen stable isotope bi-plots (mean ± SD) of basal nutrient sources, invertebrates, and fish from Lower Campbell Reservoir in 2015 and Upper Campbell Reservoir in 2016.

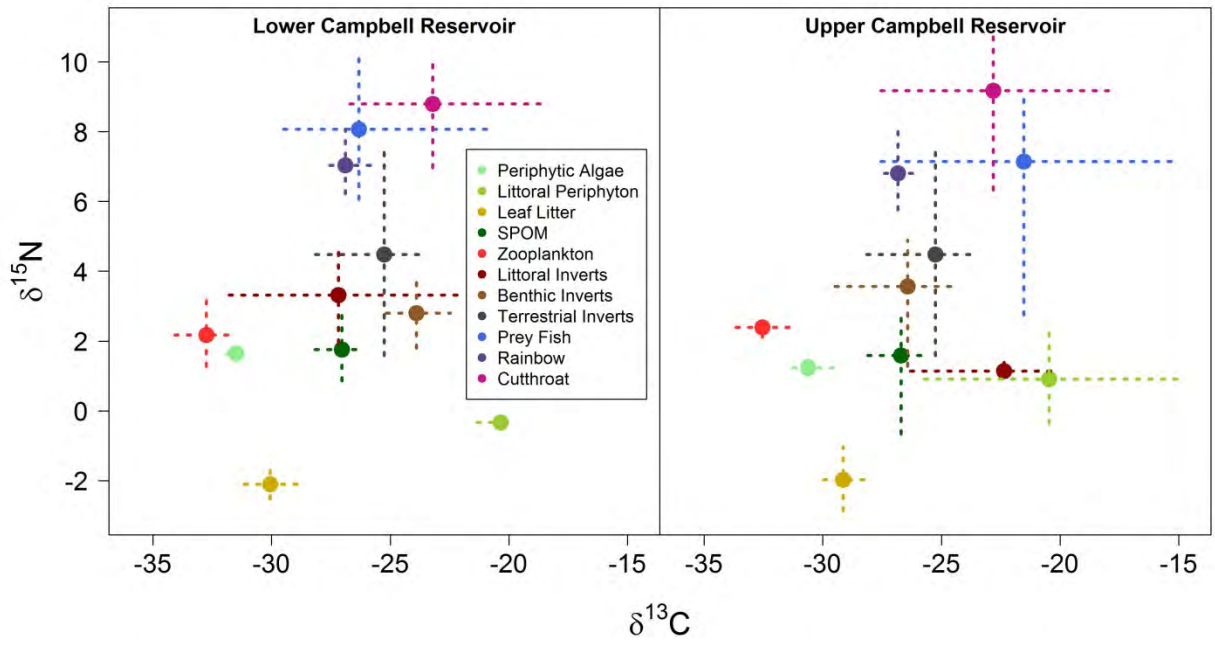


Figure 26. Estimated proportions of basal nutrient diet sources to littoral and benthic invertebrates in Lower Campbell Reservoir in 2015 and Upper Campbell Reservoir in 2016. Estimates are calculated as means with 5% and 95% percentile ranges of posterior probability distributions from carbon – nitrogen

Bayesian mixing models based on isotopic signatures from littoral and benthic invertebrates and their potential diet sources.

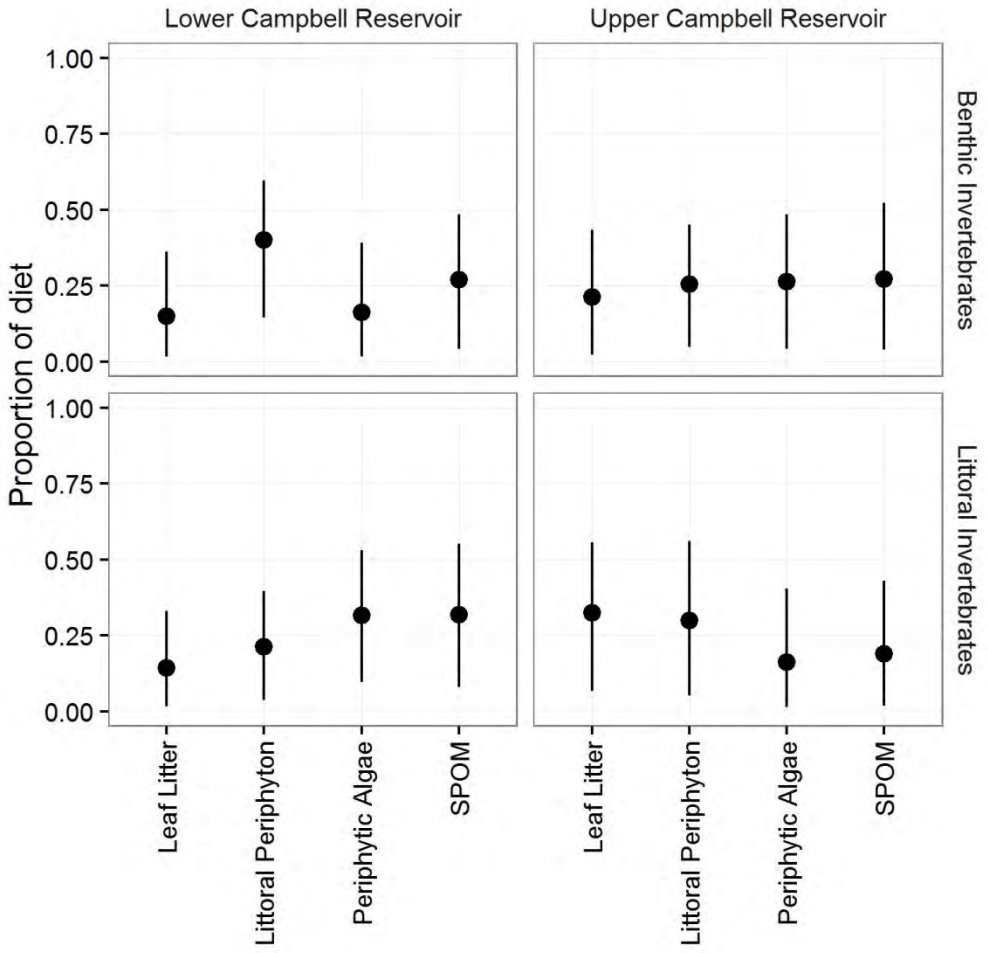


Figure 27. **Estimated proportional contributions of invertebrate food sources to diets of littoral prey fish (juvenile trout and Sculpin spp., and Threespine Stickleback) in Lower Campbell Reservoir in 2015 and Upper Campbell Reservoir in 2016. Estimates are calculated as means with 5% and 95% percentile ranges of posterior probability distributions from carbon – nitrogen Bayesian mixing models, based on isotopic signatures from prey fish and their potential diet sources.**

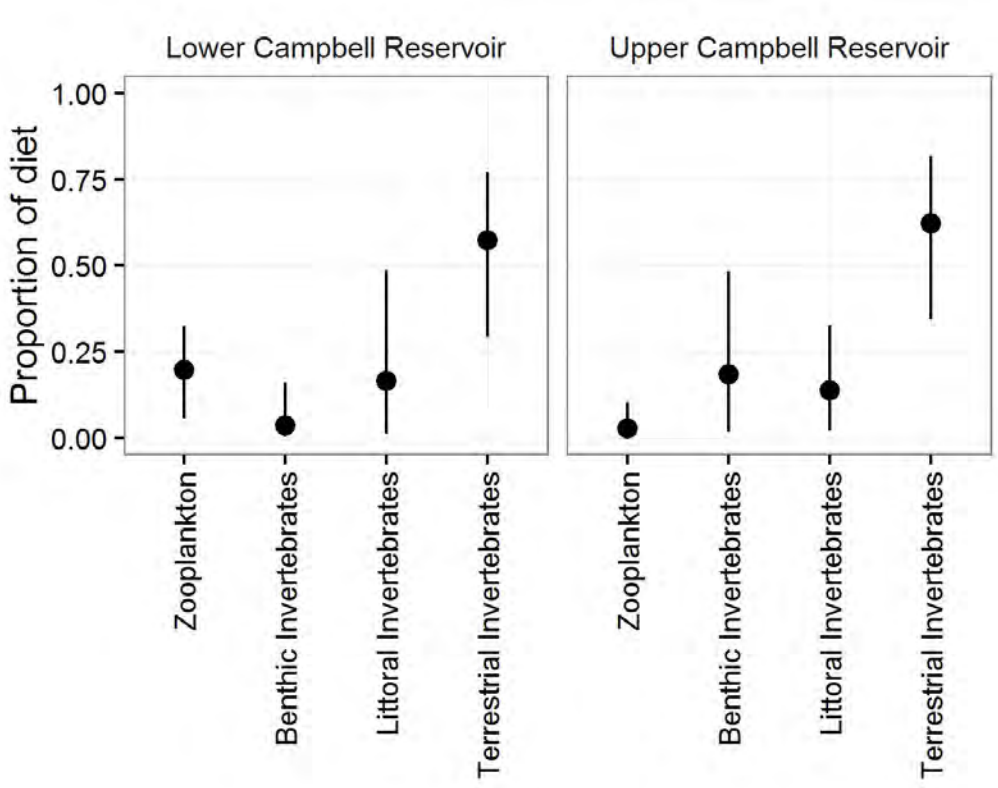


Figure 28. **Estimated proportional contributions of invertebrate and fish food sources to diets of Cutthroat Trout and Rainbow Trout in Lower Campbell Reservoir in 2015 and Upper Campbell Reservoir in 2016. Estimates are means with 5% and 95% percentile ranges of posterior probability distributions from carbon – nitrogen Bayesian mixing models, based on isotopic signatures from these consumers and their potential diet sources.**

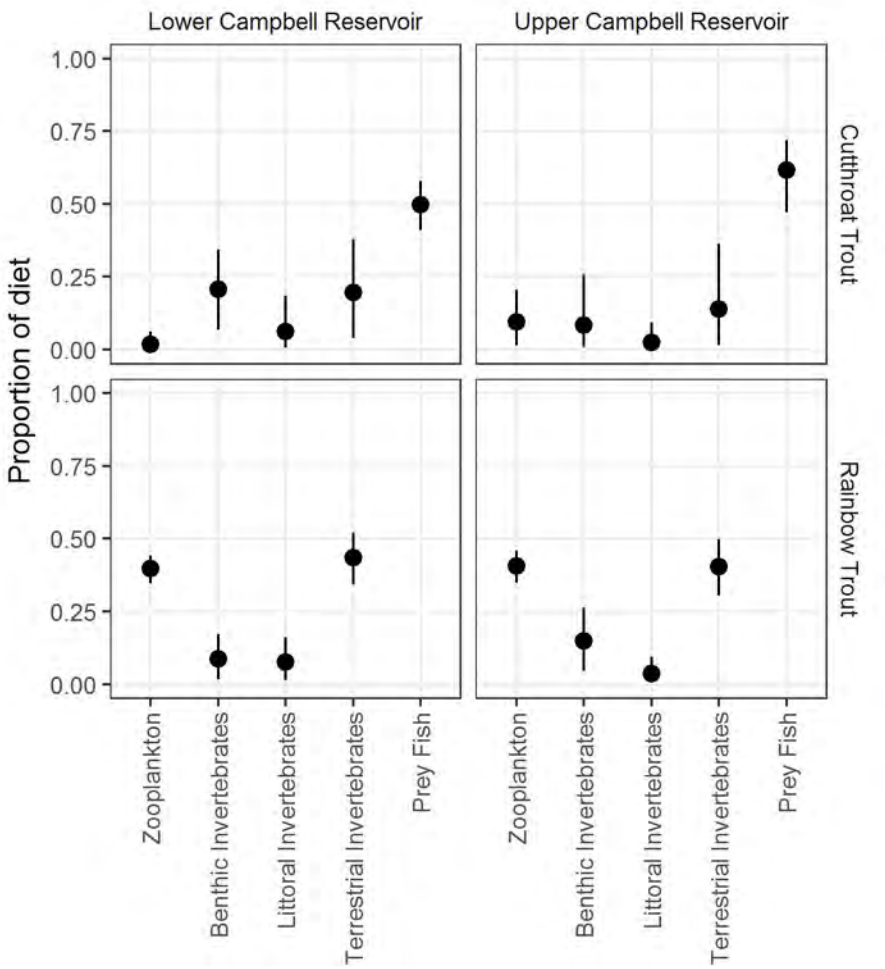


Table 18. Proportional contributions of basal nutrient sources to Cutthroat Trout and Rainbow Trout in Lower Campbell Reservoir in 2015 and Upper Campbell Reservoir in 2016.

Waterbody	Consumer	Source	Total primary nutrient sources in diet
Lower Campbell Reservoir	Cutthroat Trout	Attached Algae	0.095
		Leaf Litter	0.542
		Littoral Periphyton	0.128
		SPOM	0.116
		Phytoplankton	0.119
	Rainbow Trout	Attached Algae	0.041
		Leaf Litter	0.461
		Littoral Periphyton	0.052
		SPOM	0.049
		Phytoplankton	0.396
Upper Campbell Reservoir	Cutthroat Trout	Attached Algae	0.083
		Leaf Litter	0.614
		Littoral Periphyton	0.095
		SPOM	0.087
		Phytoplankton	0.122
	Rainbow Trout	Attached Algae	0.047
		Leaf Litter	0.449
		Littoral Periphyton	0.050
		SPOM	0.049
		Phytoplankton	0.405

Table 19. Mean proportional contribution of intermediate consumers (zooplankton, littoral, benthic,and terrestrial invertebrates, littoral prey fish), and basal nutrient sources to Cutthroat Trout and Rainbow Trout diets in Lower Campbell Reservoir in 2015 and Upper Campbell Reservoir in 2016.

Waterbody	Consumer	Mean Estimated Diet Contributions						
		Intermediate Consumer		Primary Nutrient Source[1]				
				Attached Algae	Leaf Litter	Littoral Periphyton	SPOM	Phyto-plankton
Lower Campbell Reservoir	Cutthroat Trout	Zooplankton	0.022	0.000	0.000	0.000	0.000	0.022
		Benthic Invertebrates	0.207	0.037	0.034	0.081	0.055	0.000
		Littoral Invertebrates	0.073	0.023	0.011	0.016	0.023	0.000
		Terrestrial Invertebrates	0.201	0.000	0.201	0.000	0.000	0.000
		Prey Fish	0.496	0.035	0.296	0.031	0.038	0.097
		Total	**1.000**	**0.095**	**0.542**	**0.128**	**0.116**	**0.119**
	Rainbow Trout	Zooplankton	0.396	0.000	0.000	0.000	0.000	0.396
		Benthic Invertebrates	0.089	0.016	0.015	0.035	0.024	0.000
		Littoral Invertebrates	0.081	0.025	0.012	0.017	0.026	0.000
		Terrestrial Invertebrates	0.434	0.000	0.434	0.000	0.000	0.000
		Total	**1.000**	**0.041**	**0.461**	**0.052**	**0.049**	**0.396**
Upper Campbell Reservoir	Cutthroat Trout	Zooplankton	0.099	0.000	0.000	0.000	0.000	0.099
		Benthic Invertebrates	0.102	0.027	0.022	0.026	0.028	0.000
		Littoral Invertebrates	0.033	0.006	0.011	0.010	0.007	0.000
		Terrestrial Invertebrates	0.157	0.000	0.157	0.000	0.000	0.000
		Prey Fish	0.608	0.050	0.424	0.059	0.052	0.022
		Total	**1.000**	**0.083**	**0.614**	**0.095**	**0.087**	**0.122**
	Rainbow Trout	Zooplankton	0.405	0.000	0.000	0.000	0.000	0.405
		Benthic Invertebrates	0.151	0.040	0.032	0.038	0.041	0.000
		Littoral Invertebrates	0.041	0.008	0.013	0.012	0.008	0.000
		Terrestrial Invertebrates	0.403	0.000	0.403	0.000	0.000	0.000
		Total	**1.000**	**0.047**	**0.449**	**0.050**	**0.049**	**0.405**

[1] Zooplankton and terrestrial invertebrate diets assumed to be entirely composed of phytoplankton and leaf litter respectively.

4. DISCUSSION

4.1. The *L* Performance Measure

Solving equations 1 and 4 provided answers to management questions 1 and 2 (Section 1) for Lower Campbell Reservoir and similarly solving equations 1 and 5 answered the same questions for Upper Campbell Reservoir. Equation 1 showed that *L* (the performance measure defined as PB on substrata in the littoral zone and substituted for ELZ in the project terms of reference) can be calculated as the sum of products of littoral area and PB within that area. Equation 1 was sensitive to variation in periphyton biomass, modified by different habitat attributes in Equation 4 for Lower Campbell Reservoir and Equation 5 for Upper Campbell Reservoir, within depth strata of the littoral zone. Synthesis of the results showed that a decline of water surface elevation within ranges normally encountered in both reservoirs can actually increase algal biomass within the littoral zone.

This finding reflects the bathymetry of the reservoirs and is mainly due to increased PAR reaching periphyton over shallower depths than occur near the maximum water surface elevations. This sensitivity of PB to water surface elevation is because PAR is the most important driver of PB when other habitat attributes are held constant. These findings show that *L* is effective in showing change in periphyton accrual due to changes in reservoir water surface elevation and thus answers management question 1. The periphyton community was mainly composed of diatoms and chlorophytes, which are typical along coastal lake shorelines. Habitat attributes that determine growth of periphyton were effectively measured and among them, PAR was found to be the strongest predictor in determining *L* with temperature and nutrient concentrations being less important. This finding of the relative importance of the habitat attributes answers part of management question 2.

Care is needed when interpreting Figure 20 and Figure 21 that show the relative change in L with change in water surface elevation for each reservoir. Calculation of areas of littoral strata was based on the DEM, and error associated with this was assumed to be minor. A larger source of error is the uncertainty associated with Equation 4 and Equation 5 that predicted PB as a function of habitat attributes. Analysis of Equation 4 showed that 56% of the variance in PB in Lower Campbell Reservoir could be determined by PAR, TN concentration, and temperature with PAR being most important based on value of the standardized regression coefficients. Equation 5 showed that 89% of the variance in PB in Upper Campbell Reservoir could be determined by PAR, TN concentration, and temperature. These findings mean that 44% of the variance in PB in Lower Campbell Reservoir and 11% of variance in PB in Upper Campbell Reservoir could not be explained by the three predictor variables and was due to unmeasured variables and error. By suspending the samplers in the water column without contact with the reservoir bottom, invertebrate grazers would be expected to be excluded. None were found on the Styrofoam balls at the time of sampling, which supports this view, although grazing by very small substrata-associated zooplankton may have occurred. Care was taken in sampling and handling the Styrofoam balls but this attention does not rule out error associated with sample processing. Other factors potentially affecting measurement of PB and the habitat attributes are unknown. A conclusion from these findings is that actual amount of change in PB over a range of water surface elevations may be somewhat different than the models predict with differences potentially being less for Upper Campbell Reservoir where fit of the model to the data was better than for Lower Campbell Reservoir.

Relatively small effects of water temperature and TN concentration on PB was a statistical outcome that does not mean that these attributes were not important in determining growth of periphyton. Indeed, these variables are known to be very important (Goldman and Carpenter 1974, Bothwell 1988, Bothwell 1989, Biggs 2000, Guildford and Hecky 2000). The statistical outcome indicates that the data range was not enough to show an effect. Water temperature over the depth of the littoral zone (upper 20m) in Lower Campbell was 8 – 22°C during the period of measurement in summer and fall and it was 7 – 17°C in Upper Campbell (Figure 7). Presence of a larger temperature effect

might be expected at lower temperatures potentially occurring in winter. Concentrations of the various forms of N and P were some of the lowest recorded for lakes in general and reflect the ultra-oligotrophic status of Lower and Upper Campbell Reservoirs, which is typical of lakes and reservoirs on northern Vancouver Island (Suttle and Harrison 1988, Stockner and MacIsaac 1996, Perrin and Harris 2006) including John Hart Reservoir that is immediately downstream of Lower Campbell (Perrin *et al.* 2012). The lack of detection of any fraction of phosphorus indicates that bio-available phosphorus concentration was in a range that can limit the growth and biomass of periphyton, consistent with the results of Bothwell (1989). The lack of NO_3-N was unusual but not surprising. Given that NO_3-N is a mobile anion in forest soils, this finding indicated very tight nitrogen cycling and reuse within the forested watershed of Lower Campbell Reservoir and Upper Campbell Reservoir, in addition to uptake by primary producers in the reservoirs. Lack of detectable NH_4-N was not surprising because it is a reduced form of inorganic N that readily changes to NO_3-N in oxidized waters like the Campbell Reservoirs. Lack of NO_3-N means that NH_4-N is not likely to be detected either, as was the case. TN was used as a surrogate for the pool of bio-available N and P. TN was mostly organic N, given the lack of NH_4-N and NO_3-N. Organic N can be labile but these compounds must first be mineralized by microbial decomposition. Hence, TN is not a direct measure of N available to algae: it is only an indicator of potentially available N, and will include N within living phytoplankton cells. These very low concentrations of N and P indicate that free N or P ions will be quickly sequestered by phytoplankton and periphyton, limiting the concentrations detected in water samples using wet chemistry techniques. In this respect, the variation in PB may have reflected small changes in the bio-availability of inorganic N and P but TN was not a strong predictor because it was not a direct measure of bio-availability of any form of growth-limiting nutrient. Thus, nutrients are expected to exert a strong control on algal growth in Lower Campbell Reservoir, although the issues discussed above meant that the study was unable to fully quantify the contribution of this factor.

Depth-specific PAR was a strong predictor of PB in Lower Campbell Reservoir (Table 10) and Upper Campbell Reservoir (Table 11). At greatest depths of the littoral zones, PB was found in trace amounts, but it increased logarithmically with PAR and thus with declining water depth. Greatest change in PB occurred with small change in PAR at low PAR and smaller changes occurred at larger changes in PAR at high PAR. The biomass accrual followed a classic logarithmic pattern in summer showing that logarithmic growth kinetics were most important in explaining biomass accrual throughout the incubation periods. During fall in Upper Campbell Reservoir, a break in slope of the accrual curves was found after 40 days of incubation, but only at depths in the littoral zone >10 m where PAR was near the lowest and thus most limiting of algal growth.

Lack of a plateau in the curves showed that a true PB was not achieved, even after the two-month incubation period in Lower Campbell Reservoir and during summer after a 90-day incubation in Upper Campbell Reservoir. A true PB was found in the fall in Upper Campbell Reservoir at water depths >10 m where the model (Equation 5) showed PB would be low due to low accumulated

PAR during the incubation. The long periods of time without detecting PB is consistent with the extremely low N and P concentrations that would have strongly curtailed the algal growth rates. The curves show that incubation periods longer than three months are needed to achieve detection of true PB.

This finding answers another part of management question 2: "To what extent does colonization rate, growth rate, and survival rate impact the utility and reliability of ELZ" (which is called *L* in this report; see Section 1.4.2). The answer is that the combination of colonization, growth, and survival are integrated in the accrual curves that ultimately show PB within a standardized measurement period. Given that PB, defined as the largest amount of biomass accrued on a substratum over a standard time period, was a function of logarithmic accrual that is consistent with patterns of algal growth (Bothwell 1989), a conclusion is that *L* is sensitive to the algal colonization, growth, and survival kinetics.

Equations 1 and 2 were set up to answer the third management question that states, "Following implementation of the Campbell River WUP, does littoral productivity increase as predicted by the ELZ performance measure?" In effect, equations 1 and 2 provide a framework to test whether the WUP affects the ELZ performance measure or, more correctly, the *L* term in Equation 1. The first part of this analysis was to test for WUP effects on metrics of water surface elevation that were determinants of littoral habitat area. In Lower Campbell Reservoir, the 0.1% increase in mean annual water surface elevation in Lower Campbell Reservoir in summer and fall was estimated to contribute to a 2% increase in PB due to the WUP. In Upper Campbell Reservoir, the 0.2% increase in water surface elevation in summer and a similar decrease in fall did not produce a statistically significant change in PB due to WUP, which indicates that that the WUP did not change *L* in Upper Campbell Reservoir

An important question is whether the predicted 2% increase in algal PB in Lower Campbell Reservoir in summer due to the WUP is ecologically important. It is well within the range of variability of algal biomass encountered on any date (Figure 12 and Figure 13). As such, the change due to WUP would not be detectable using even the most controlled conditions that were applied in this study (accrual on Styrofoam balls that excluded grazing effects). In this respect, we conclude that while the change in PB due to WUP was theoretically possible based on model simulations, it was too small to have ecological importance. This is reinforced by the results of the stable isotope analysis (Section 4.3), which show that littoral productivity makes a minor contribution to fish production in the reservoirs. This conclusion answers the third management question: implementation of the WUP was predicted to cause a 0.1% decrease in periphyton biomass accrual in Upper Campbell Reservoir and a 2% increase in Lower Campbell Reservoir. These predicted changes are within the range of model error and are not deemed to be ecologically significant.

Simulations of change in *L* over typical ranges of water surface elevations in each reservoir in summer when biological production is expected to be most active showed that algal biomass is

lower at the maximum operational water surface elevation compared to lower elevations. This reflects the bathymetry of the reservoirs, which controls the amount of PAR that reaches elevations within the littoral zone. The amount of accumulated PAR is very sensitive to bathymetric variability within the littoral zone, as shown by the result that PB was predicted to increase with a decline in water level below the maximum operational elevation, despite an associated decrease in total littoral area. PAR is a major driver of algal accrual in the littoral zone and thus changes at the substrata – water interface have significant effects.

4.2. Fish Stomach Contents

Fish stomach contents were used as a first step to examine links between algal production in the littoral zone and fish use of that habitat, thus addressing the fourth management question, "How does littoral productivity translate into fish production in Campbell Reservoirs?" The stomach content data showed that the most common prey for Cutthroat Trout and Rainbow Trout in Upper Campbell and Lower Campbell reservoirs were zooplankton and terrestrial taxa, with benthic insects that are common in littoral habitats making almost no contribution to diets. Fish were also a common diet item for Cutthroat Trout but not Rainbow Trout. Other aquatic invertebrate taxa including Coleoptera (beetles), non-chironomid dipterans, amphipods, and hemipterans represented a small proportion of stomach contents. Cottids ingested a wider assortment of prey, potentially from wide ranging habitats. The stomach contents of Cutthroat Trout and Rainbow Trout in Upper Campbell Reservoir were largely composed of zooplankton (based on abundance). These findings show a disconnect between biological production of fish food assemblages in littoral habitat where benthic insects are prevalent, and food actually ingested by fish of management interest (Cutthroat Trout and Rainbow Trout). This evidence implies that the littoral-derived algal production is not important in supporting resident fish species and that food production from riparian areas and pelagic habitat is more important.

4.3. Stable Isotope Modelling

Stable isotope analysis provided a second line of evidence to evaluate trout diets. The stomach contents analysis provided detailed information about the taxonomic composition of trout diets. However, for quantifying energy fluxes, we place greatest weight on the results of the stable isotope analysis. This is because the technique provides an integrated signature of fish diet over the growing season (Perga and Gerdeaux 2005), whereas stomach contents analysis provides a "snapshot" of diet composition at one time. Further, the stomach contents analysis yielded results based on abundance rather than biomass. These data are helpful to understand the detailed composition of trout diets but they are not necessarily directly correlated with energy flow to fish due to differences in prey size.

Stable isotope data showed similar results to stomach content analyses in that littoral-derived algal production was not very important relative to other basal nutrient sources. Terrestrial primary production contributed to 54% and 61% of Cutthroat Trout diets and to 46% and 45% of Rainbow Trout diets in Lower Campbell and Upper Campbell reservoirs, respectively, illustrating the

importance of allochthonous nutrient sources in the ultra-oligotrophic reservoirs. Riparian leaf litter (i.e., terrestrial vegetation) was consumed directly by benthic and littoral invertebrates and is the basal carbon source for terrestrial invertebrates, which themselves made up much of the diets of littoral prey fish (e.g., juvenile trout, sculpin, and sticklebacks), and larger Cutthroat and Rainbow Trout. High contributions of allochthonous carbon inputs to lentic food webs have been shown elsewhere for small unproductive lakes (Carpenter *et al.* 2005, Cole *et al.* 2006, Cole *et al.* 2011) and humic lakes (Jansson *et al.* 2000); however, it is not well-recognized that this terrestrial pathway can make a major contribution to fish productivity in large clear reservoirs.

Pelagic primary production was particularly important for Rainbow Trout: phytoplankton contributed approximately 40% to Rainbow Trout diets and 12% to Cutthroat Trout diets, largely through zooplankton as an indirect nutrient pathway. This finding confirms results of fish stomach analysis that demonstrated a large contribution of zooplankton to Rainbow Trout diets.

Littoral and benthic invertebrates had relatively variable diets made up of all four basal nutrient sources (e.g., littoral periphyton, SPOM, attached algae, and leaf litter). However, Cutthroat Trout eat fish, terrestrial invertebrates, benthic and littoral invertebrates, and zooplankton, in that order. Rainbow Trout eat terrestrial invertebrates, zooplankton, and benthic and littoral invertebrates, in that order. In turn, littoral prey fish (e.g., juvenile trout) eat terrestrial invertebrates, benthic and littoral invertebrates, and then zooplankton (with the exception of stickleback, which eat zooplankton, terrestrial invertebrates, and littoral invertebrates, in that order). Therefore, when these diet contributions are summed across trophic levels, the contribution of attached algae to Cutthroat Trout and Rainbow Trout in Lower Campbell Reservoir is estimated to be only 10% and 5% respectively. As expected, these results were similar to those observed in Upper Campbell Reservoir (with attached algae contributing 8% and 5% to Cutthroat and Rainbow Trout diets, respectively), where pelagic contributions are higher than in Lower Campbell Reservoir (Hocking *et al.* 2016) and any decline in littoral productivity through declines in periphytic algae would have correspondingly less impact on fish production.

The current data thus suggest that, while algal accrual can be used to make predictions regarding the functioning of ELZ as described above, the littoral food webs of the Lower and Upper Campbell reservoirs are more complex than assumed under the ELZ model. Desiccation and disturbance of littoral plant communities is recognized as the major mechanism by which drawdown operations can reduce productivity in reservoirs generally (e.g., Furey *et al.* 2004, Turner *et al.* 2005). Therefore, the low importance of autotrophic littoral periphyton productivity to the food webs of Lower and Upper Campbell reservoirs indicates that use of the ELZ model to inform water level management would likely overestimate the impacts to reservoir productivity of drawdown. However, the importance of terrestrial (allochthonous) carbon subsidies to the reservoir food-webs means that other effect pathways that are in addition to impacts on periphyton accrual need to be considered to fully understand the ecological effects of water level management operations. There is uncertainty regarding the sources, fluxes and processing of allochthonous carbon inputs to the study reservoirs, which confounds our understanding of how water level management affects fish production from

the reservoirs. Thus, while the results of the stable isotope analysis show that littoral production is of low importance for fish productivity in Lower and Upper Campbell reservoirs, they do not indicate that the effects of drawdown operation on fish productivity are negligible. This is consistent with the results of JHTMON-5 (Hocking *et al.* 2017), which showed that the contribution of littoral food sources to Cutthroat Trout was lowest in Upper Campbell Reservoir, followed by Lower Campbell Reservoir, and then John Hart Reservoir. This trend correlates with the magnitude of the annual water level range in each reservoir, suggesting a measureable drawdown effect on fish production, i.e., the contribution of littoral food sources is lowest in the reservoir with greatest water level fluctuations and vice versa. No relationship was found for Rainbow Trout (Hocking *et al.* 2017), which rely to a greater extent on pelagic sources of production such as zooplankton.

Another limitation of the ELZ model is that it only considers autotrophic periphyton production. However, periphyton in littoral areas may not solely comprise attached algae and instead is likely an assemblage of algae, protozoa, bacteria, fungi and detrital material. Our analysis supports the presence of a diverse range of taxa that include autotrophs, in addition to heterotrophs that process carbon from sources such as riparian leaf litter. Two sources of periphyton were analyzed (attached algae and littoral periphyton), which were found to have distinct isotope signatures. The periphyton present on stony hard substrates and macrophytes in the littoral zone of lakes is inhabited by an abundant and diverse algae and meiofauna assemblage (Schroeder *et al.* 2013), that can include dozens of living and dead algae and bacteria species. Depth-related factors such as light are important for structuring periphytic species assemblages (Schroeder *et al.* 2013), and the relative abundance of different algal taxa can explain up to 74% of periphyton $\delta^{13}C$ variability (Abe *et al.* 2013). The depleted $\delta^{13}C$ signature in the attached algae portion of periphyton in both Lower and Upper Campbell reservoirs (-31‰) was most similar to that of planktonic algae reported in the literature (average -32‰). The more enriched carbon signature of littoral periphyton scraped off of rocks of both reservoirs (-20‰) was more similar to that of lake benthic algae reported in the literature (average -26‰) (France 1995). The different signatures are likely due to several factors. Terrestrial allochthonous carbon sources contribute to littoral periphyton closer to shore and enrich the carbon signature. The presence of heterotrophs such as bacteria will enrich the carbon signature further. The algal portion of periphyton grown on the mooring line grew slowly under ultra-oligotrophic conditions with carbon derived from autochthonous production. More depleted $\delta^{13}C$ signatures are reported under slower growth rates in a variety of freshwater plants (MacLeod and Barton 1998). While the isotope signatures of the two periphyton sources were only based on a few samples in Lower Campbell Reservoir (n = 3 for each), the results from this reservoir were confirmed by those from Upper Campbell Reservoir in 2016 (n = 16 and four for littoral periphyton and attached algae, respectively).

In summary, the stable isotope techniques provided a powerful tool to quantify carbon fluxes within the reservoir food-webs and address management question 4: "How does littoral productivity translate into fish production in Campbell River reservoirs?" Of the basal nutrient sources, the contribution of attached algae (representative of autotrophic production by periphyton in the littoral

zone) to Cutthroat Trout and Rainbow Trout diets in Upper and Lower Campbell Reservoirs is estimated to be only 8–10% and 4–5% respectively. These low contributions show that the current ELZ approach is based on an incomplete conceptual model of the reservoir food webs that does not consider the primary driver of littoral fish production, which is terrestrial-derived carbon via sources such as leaf litter and terrestrial invertebrates. There remains uncertainty about how drawdown affects linkages between terrestrial (allochthonous) carbon sources and fish production.

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Personal Communications

Kaulback, Victor, Production Supervisor, BC Hydro, Burnaby, BC. E-mail correspondence with Leah Ballin, August 12, 2014.

PROJECT MAPS

JHTMON Campbell River Water Use Plan

Lower Campbell Reservoir Lake Sampling Locations

Legend

Sample Sites

- PAR Sensor
- Zooplankton Sampling
- Periphyton Sampling
- Benthic Invertebrate Sampling
- Littoral Invertebrate Sampling
- Terrestrial Invertebrate Sampling
- Fish Sampling

316000 318000 320000 322000 324000 326000 328000

5548000 5546000 5544000 5542000 5540000 5538000

LCR-LKMT05
LCR-LKGN06
LCR-LKTN02
LCR-LKGN01
LCR-LKIV02
LCR-PERWQ2
LCR-LKIV03
LCR-PERWQ3
LCR-LKMT06
LCR-LKZP03
Lower Campbell Reservoir
LCR-LKGN05
LCR-LKZP02
LCR-PERWQ1A
Campbell River
LCR-LKMT03
LCR-LKGN02
LCR-LKGN04
LCR-LKZP01
LCR-LKIV04
LCR-PERWQ4
LCR-PERWQ1
LCR-LKIV01
LCR-LKPAR
LCR-LKTN01
LCR-LKMT04
LCR-TIV02
LCR-BIV01
LCR-LKGN03
LCR-LKMT01
LCR-LKMT02
LCR-TIV01
Upper Campbell Reservoir

MAP SHOULD NOT BE USED FOR LEGAL OR NAVIGATIONAL PURPOSES

0 250 500 1,000 1,500 2,000 2,500 m

Scale: 1:45,000

NO.	DATE	REVISION	BY
1	21/06/2017	1230_MON4_LCR_SamplingLocs_2016Feb02	CGA
2			
3			
4			
5			

Date Saved: 21/06/2017
Coordinate System: NAD 1983 UTM Zone 10N

ECOFISH RESEARCH

Map 2

Path: M:\Projects-Active\1230_JHTMON\MXD\Fisheries\1230_MON4_LCR_SamplingLocs_2016Feb02.mxd

JHTMON Campbell River Water Use Plan

Upper Campbell Reservoir Lake Sampling Locations

Legend

Sample Sites

- Zooplankton Sampling
- Periphyton Sampling
- Littoral Invertebrate Sampling
- Fish Sampling
- Dam
- Quinsam Coal Mine

UCR-PERAIR
Strathcona Dam
UCR-LKGN01
UCR-PERWQ04
UCR-BIV04
UCR-PERWQ03
UCR-BIV03
UCR-LKGN02
UCR-PERWQ02
UCR-BIV02a
UCR-LKZP02
UCR-LKZP03
UCR-LKGN04
UCR-PERWQ01
UCR-BIV01a
UCR-LKZP01
UCR-LKGN08
UCR-LKMT10
UCR-LKTN10
UCR-LKMT09
UCR-LKTN09
UCR-LKGN07
Quinsam Diversion Dam Intake
Quinsam Coal Mine
Gooseneck Lake
Middle Quinsam Lake
Upper Quinsam Lake
Upper Campbell Lake
Camp Lake
Wokas Lake
Argonaut Mainline
Quinsam River
Cedar Creek Rd
Hwy 28
Western Mine Rd

MAP SHOULD NOT BE USED FOR LEGAL OR NAVIGATIONAL PURPOSES

0 0.5 1 2 3 4 km

Scale: 1:75,000

NO.	DATE	REVISION	BY
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2			
3			
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Date Saved: 22/06/2017
Coordinate System: NAD 1983 UTM Zone 10N

ECOFISH RESEARCH

Map 3

Path: M:\Projects-Active\1230_JHTMON\MXD\Fisheries\1230_MON4_UCR_SamplingLocs_2017Jun21.mxd

316000 318000 320000 322000 324000 326000 328000 330000

5548000 5546000 5544000 5542000 5540000 5538000

LCR-PERWQ2

LCR-PERWQ3

LCR-PERWQ1A

LCR-PERWQ4

LCR-PERWQ1

JHTMON CAMPBELL RIVER WATER USE PLAN

Lower Campbell Lake Bathymetry

Legend

- Sampling Stations

Inverse Distance Weighted Interpolation Elevation (m)

- < 157 m
- 157 - 159 m
- 159 - 163 m
- 163 - 167 m
- 167 - 170 m
- 170 - 173 m
- 173 - 176 m
- 176 - 177 m
- > 177 m

MAP SHOULD NOT BE USED FOR LEGAL OR NAVIGATIONAL PURPOSES

0 0.25 0.5 1 1.5 2 2.5 km

Scale: 1:50,000

NO.	DATE	REVISION	BY
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2			
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Date Saved: 15/03/2016
Coordinate System: NAD 1983 UTM Zone 10N

ECOFISH RESEARCH

Map 4

Path: M:\Projects-Active\1230_JHTMON\MXD\Bathymetry\1230_JHT_LowerCampbell_Bathymetry_2016Mar15.mxd

JHTMON CAMPBELL RIVER WATER USE PLAN

Upper Campbell Lake Bathymetry

UCR-PERWQ01
UCR-PERWQ02
UCR-PERWQ03
UCR-PERWQ04

Legend

- Sampling Stations

Topo to Raster Interpolation
Elevation (m)

- 155.1 - 157.1 m
- 157.1 - 162.1 m
- 162.1 - 167.1 m
- 167.1 - 172.1 m
- 172.1 - 177.1 m
- 177.1 - 182.1 m
- 182.1 - 187.1 m
- 187.1 - 192.1 m
- 192.1 - 197.1 m
- 197.1 - 202.1 m
- 202.1 - 207.1 m
- 207.1 - 212.1 m
- 212.1 - 217.1 m

MAP SHOULD NOT BE USED FOR LEGAL OR NAVIGATIONAL PURPOSES

0 0.25 0.5 1 1.5 2 2.5 km

Scale: 1:52,000

NO.	DATE	REVISION	BY
1	02/01/2017	1230_JHT_UpperCampbell_Bathymetry_2014Nov12	CGA
2			
3			
4			
5			

Date Saved: 02/01/2017
Coordinate System: NAD 1983 UTM Zone 10N

ECOFISH RESEARCH

Map 5

Path: M:\Projects-Active\1230_JHTMON\MXD\Bathymetry\1230_JHT_UpperCampbell_Bathymetry_2014Nov12.mxd