Biofilm, Invertebrate and Fish Communities Associated With Vegetation Strata in the Drawdown Zone of the Arrow Lakes Reservoir. Final Report

March 2002

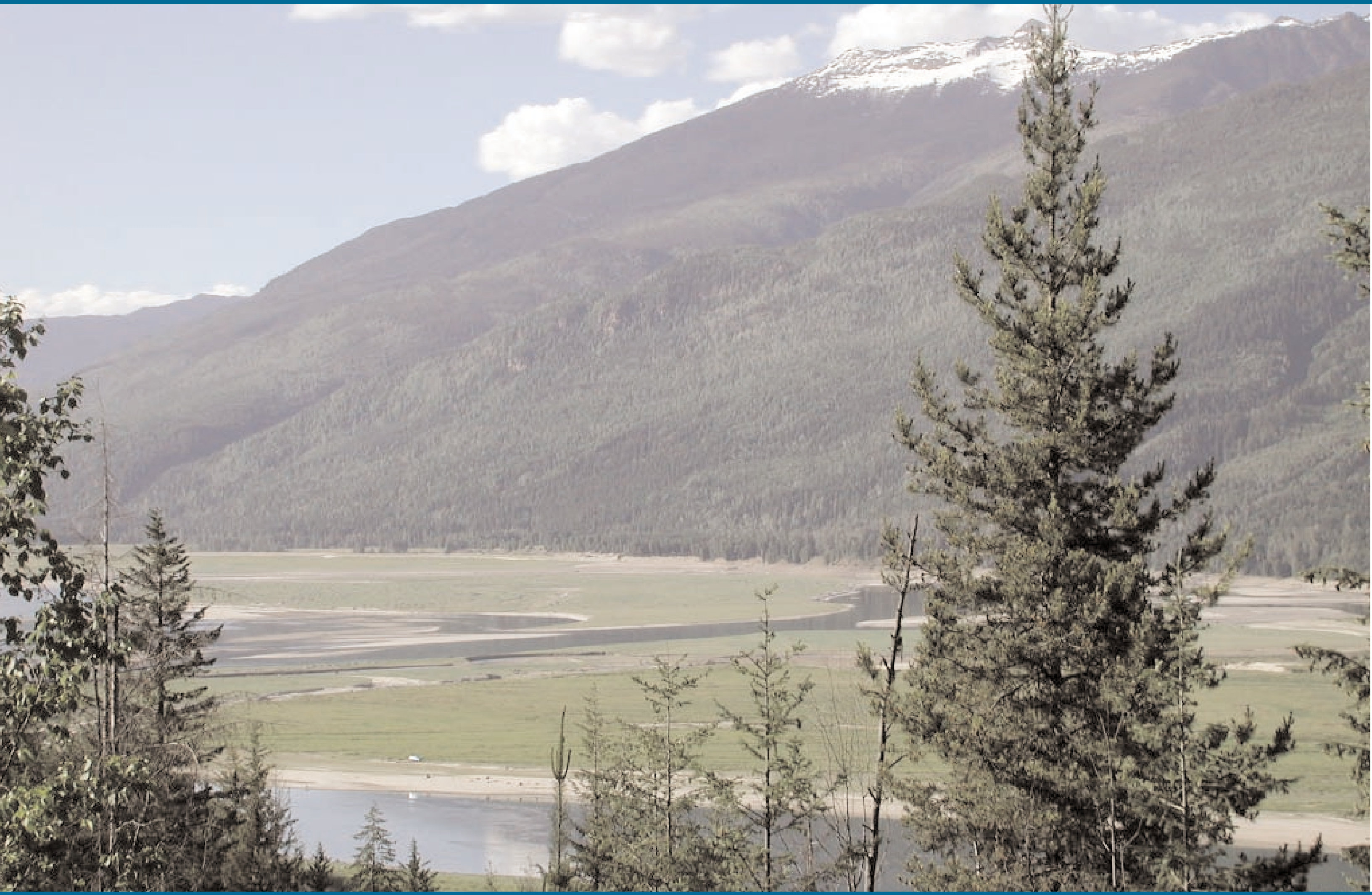

Photo courtesy of Wendy Beauchamp

Prepared by: C.J. Perrin, Limnotek Research and Development Inc., Golder Associates (RL&L Ltd.) and J.G. Stockner, Eco-Logic Ltd.

Prepared for: BC Hydro Strategic Environmental Initiatives Program
Evaluation of the Ancillary Benefits of Upper Arrow Reservoir Drawdown Zone Revegetation Project

BC hydro

BIOFILM, INVERTEBRATE AND FISH COMMUNITIES ASSOCIATED WITH VEGETATION STRATA IN THE DRAWDOWN ZONE OF THE ARROW LAKES RESERVOIR

Final Report

Submitted to
BC Hydro
Strategic Environmental Initiatives Program
Burnaby, B.C.

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SUMMARY

An experiment was implemented in 1999 to examine the effect of submersed vegetation on the abundance and composition of periphyton, benthic invertebrates, and fish in the drawdown zone of Revelstoke Reach in the Arrow Lakes Reservoir. In this reach, vegetation communities are stratified by elevation with barren soils at lowest elevations and native mixed grasses at highest elevations. In some barren areas, fall rye is planted early in the spring each year to control dust before inundation in late spring. Survival of plant species while under water each summer is determined by time under water and characteristics of each species to tolerate submersed conditions. This report describes results of the experiment and it provides an interpretation of the findings.

Periphyton on all plants was comprised mainly of diatoms and filamentous green algae. Densities on leaves were <18,000 cells/cm^2 and most were <6000 cells/cm^2. In comparison to other oligotrophic systems, these densities were extremely low. Lab methods used to remove confounding effects of extensive silt and sand in the samples were found to yield underestimates of actual cell densities.

A total of 66 benthic invertebrate taxa including naidid, enchytrid, and lumbriculid worms, nematodes, ostracods, tubificids, water mites, gastropods, aquatic insects, beetles, terrestrial insects, zooplankton, and freshwater shrimp were found in aboveground and belowground plant samples. Most abundant were the oligochaete worms, nematodes and ostracods. Benthos densities reached 43,727 animals$\cdot$m^{-2} in aboveground samples and almost 64,000 animals$\cdot$m^{-2} in belowground samples. These densities were very high compared to those in other oligotrophic systems.

Vegetation establishment increased the areal biomass of benthic invertebrates by two to four times over that found in barren soils. The submersed vegetation greatly increased the areal extent of substrata for colonization by benthos, allowing a diverse and abundant fauna to flourish. While the simple presence of plants increased benthic invertebrate biomass, invertebrates favoured dead and decaying plant matter (fall rye) over submersed living plants (lenticulate sedge and reed canary grass). The plant-benthos link was mediated by the epiphytic biofilm in which benthic diatoms were a major component. Direct feeding on dead and decaying plant matter was a major process contributing to the association between benthos and fall rye.

It was here that further links to the aquatic ecosystem appeared truncated. Sucker species that are mainly detritivous feeders may have responded to increased benthos in association with dead and decaying fall rye but we could find no link between the plant – benthos association and sport fish that are mainly visual predators. All sportfish were eating mainly terrestrial invertebrates that landed on the water surface. There was no evidence of these fish eating taxa found in association with the plant substrata. One reason for this outcome was that benthos were generally not available to visual feeding habits of those species. In this respect, the establishment of vegetation in the drawdown zone of Revelstoke Reach greatly increased the capacity of the reach to host a diverse and abundant benthic community but it did not directly lead to an equal change in abundance of sportfish.

Notwithstanding this finding, a small fishery is now present in the reach where it was not present before vegetation establishment. Cover is available in shallow habitat for fish to use as they mainly feed on surface organisms. An abundance of terrestrial invertebrates may use the vegetation in the spring and become inundated with rising water. These invertebrates may not be directly associated with plant substrata after flooding (and thus not found in our samples) but may provide an abundance of food for sportfish in the water column and on the water surface when the water surface elevation is rising. Detection of this process was not included in our experimental design but may be an important factor explaining the presence of surface-feeding sportfish and the presence of a fishery based mainly on fly gear.

Fish may move in and out of vegetation cover, potentially confounding our ability to distinguish effects of location on fish presence, absence, and abundance. If this project is pursued further, the focus must clearly be placed on improving ways to quantitatively resolve this link between the strong association of benthos and plants with higher trophic levels. Recommended techniques include radio tracking fish and following stable isotopes between trophic levels.

This study provided functional responses and descriptive data that can be directed used in simulation modeling. This modeling will help in showing spatial and temporal dynamics of vegetation establishment and the associated benthic community and it can be used to examine time course change in carbon flux in Revelstoke Reach. Output from this modeling will be a valuable tool to explore the benefits of similar planting treatments in other large reservoirs managed by BC Hydro and other power utilities.

ACKNOWLEDGMENTS

This project was completed with Strategic Environmental Initiatives Program (SEIP) funding from BC Hydro. Mr. Ed Hill and Dr. Wayne Duval were the contract authorities. Several people at Golder Associates (RL&L Ltd) contributed to the fish sampling, analysis, and reporting. They included Larry Hildebrand, Dan Sneep, Mike Hildebrand, Bob Chapman, and Dr. Gordon Walder. We appreciate discussion with Dr. Will Carr and Ann Moody who completed a companion study to this one describing physical and chemical aspects of soils, vegetation biomass and vegetation nutrient content. We also appreciate discussion with Josh Korman on issues related to the experimental design and system modeling. Chemical lab work was completed at the Pacific Environment Science Centre under a contract agreement with Limnotek. Danusia Dolecki completed benthic invertebrate enumerations and biomass determinations. Special thanks goes to Brian Gadbois (BC Hydro, Revelstoke) who worked with us to complete the sample outplanting; complete the retrieval of vegetation, periphyton and benthos samples; and manage the distribution and retrieval of creel cards. Mr. Francis Maltby assisted with sample collections in the field. Kiyo Masuda organized field logistics during the outplanting activities, assisted with the actual outplanting, contributed to the fish sampling, and he compiled most data for this report. Kath Bowie of BC Hydro, Power Supply Operations, provided data on water surface elevations and flows in the Columbia River. Wendy Beauchamp completed all GIS applications and mapping shown as Figure 1.

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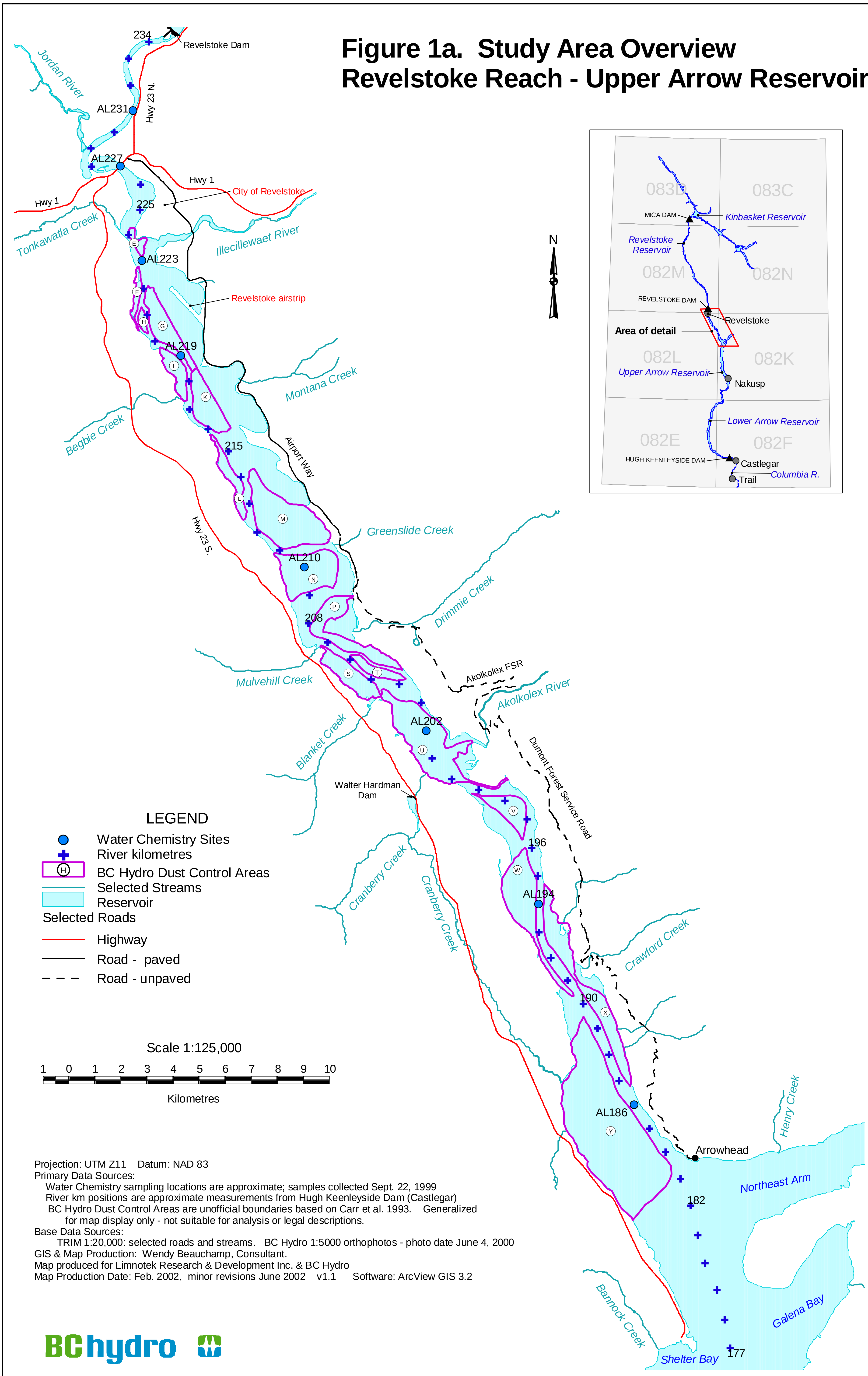
1.0 INTRODUCTION

Annual seeding with fall rye (*Secale cereale*) has proved to be an effective technique in controlling dust in the Revelstoke Reach of the Upper Arrow Lakes Reservoir at drawdown (Carr et al. 1993). The fall rye grows rapidly after planting in early April and it stabilizes sediment and silt substrata that are exposed after snow melt, thereby reducing dust concentrations during wind events in spring and early summer. In some areas of the drawdown zone, organic matter produced from the fall rye enhances establishment of native grasses including perennial species such as reed canary grass (*Phalaris arundinacea*), marsh reed grass (*Calamagrostis canadensis*), and sedges (mainly Lenticulate sedge (*Carex lenticularis*) Columbia sedge (*Carex aperta*) and Sitka sedge (*Carex sitchensis*). After almost 10 years of annual seeding, native vegetation has become established in areas of the drawdown zone close to Revelstoke, but seeding with fall rye is still required in selected downstream areas for effective dust control (B. Gadbois, BC Hydro, Revelstoke).

Interactions between planting of fall rye, natural invasion of native vegetation, and the annual flooding – dewatering cycle has produced the following elevation gradient defined by composition of vegetation communities:

1. Bare sediment and silt, not supporting vegetation, not seeded with fall rye and can be a source of dust before inundation. This stratum is at elevations less than 434.3 m. In Figure 1, it is present in area Y, lower elevations of area X, area W, lower elevations of area V, islands making up area U2, U3, and U5 which includes most of the flats in the downstream half of Revelstoke Reach.
2. Bare sediment and silt, not supporting vegetation but may be seeded and fertilized annually to prevent dust production during drawdown in April and May. This zone is present in areas T1, S, P, N, and M that are mainly in the upstream half of the Revelstoke Reach as shown in Figure 1.
3. A transition zone between elevations of 434.3 m and 435.8 m containing a mixture of established vegetation and barren patches. Barren sites may be seeded and fertilized each year for dust control. This stratum is present as a narrow band between high elevations where native grasses are established and low elevations that are barren of vegetation. It is present in areas X, V, S, P, M, I, and K (Figure 1).
4. Areas where native vegetation has become established and annual seeding for dust control is not required. These areas are at elevations of 435.5 – 440 m. They are typical throughout areas E, F, and G and along a top elevation band throughout the reach (Figure 1).

Figure 1a. Study Area Overview
Revelstoke Reach - Upper Arrow Reservoir



Projection: UTM Z11 Datum: NAD 83
Primary Data Sources:
Water Chemistry sampling locations are approximate; samples collected Sept. 22, 1999
River km positions are approximate measurements from Hugh Keenleyside Dam (Castlegar)
BC Hydro Dust Control Areas are unofficial boundaries based on Carr et al. 1993. Generalized for map display only - not suitable for analysis or legal descriptions.
Base Data Sources:
TRIM 1:20,000: selected roads and streams. BC Hydro 1:5000 orthophotos - photo date June 4, 2000
GIS & Map Production: Wendy Beauchamp, Consultant.
Map produced for Limnotek Research & Development Inc. & BC Hydro
Map Production Date: Feb. 2002, minor revisions June 2002 v1.1 Software: ArcView GIS 3.2

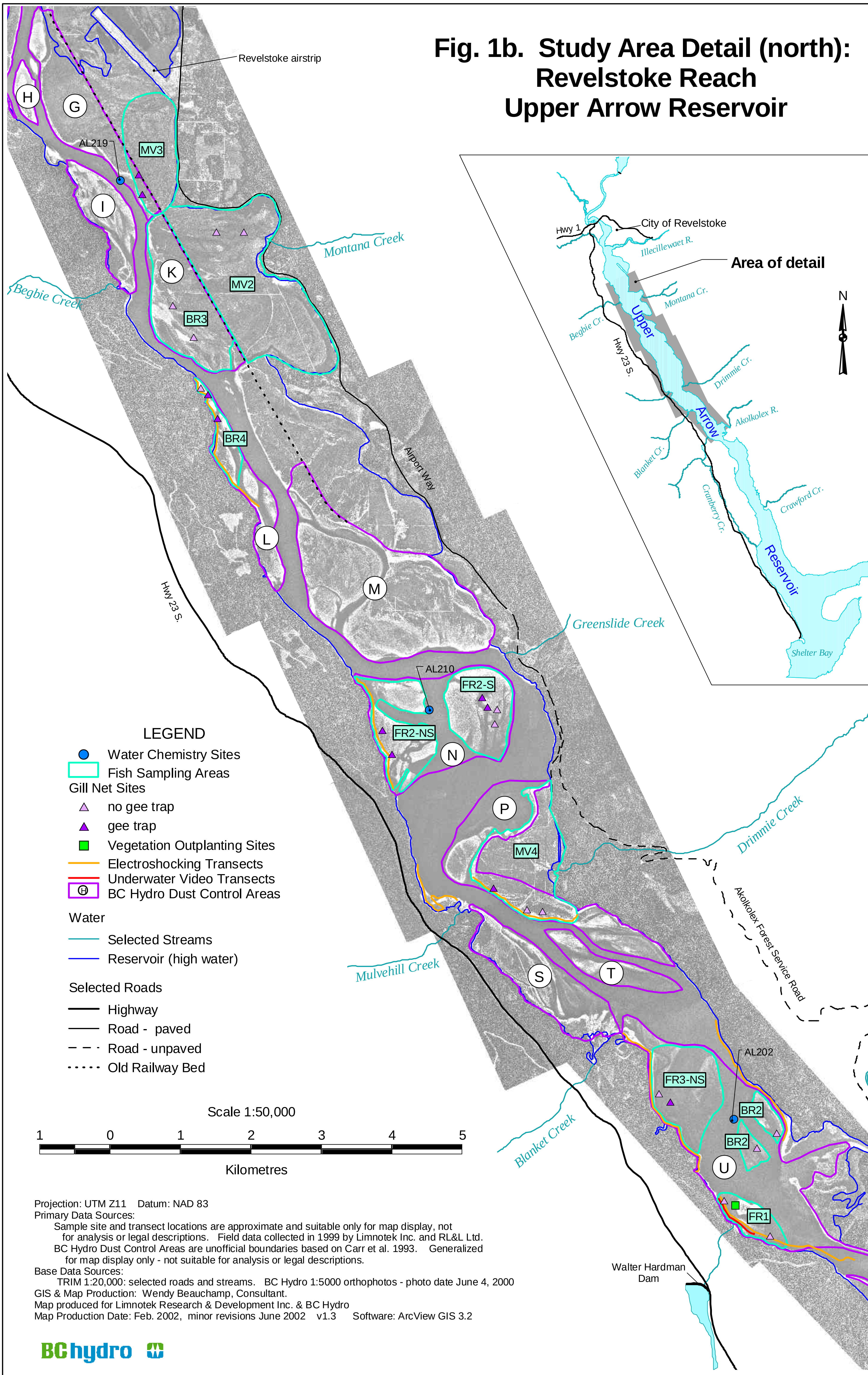
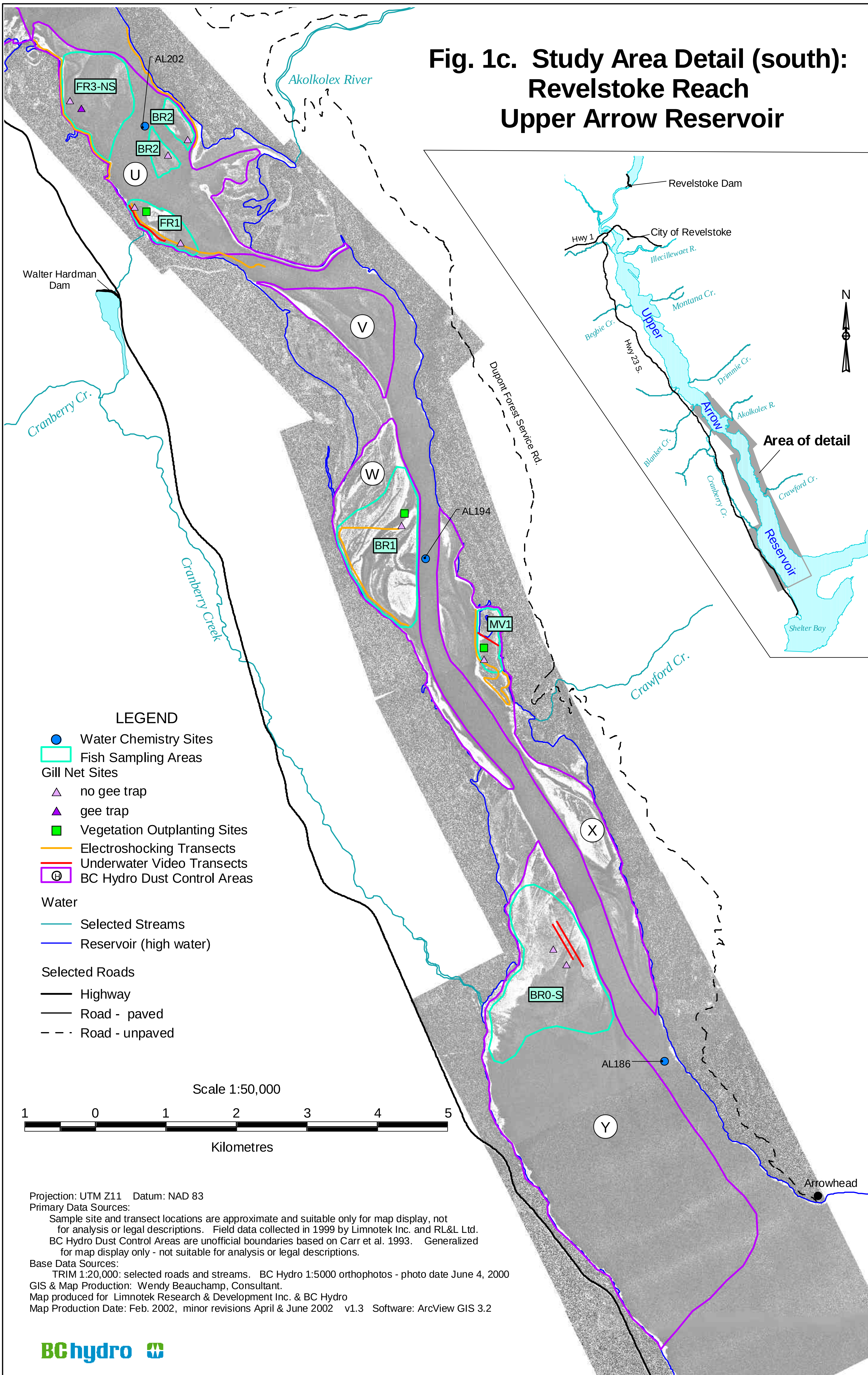


Fig. 1b. Study Area Detail (north): Revelstoke Reach Upper Arrow Reservoir

Fig. 1c. Study Area Detail (south): Revelstoke Reach Upper Arrow Reservoir



Observations in recent years by local residents suggest that the annual seeding and establishment of vegetation may provide a benefit to rainbow trout and other fish species of the Upper Arrow Reservoir (B.Gadbois, BC Hydro, pers. comm.). Fish have been observed to follow rising water in the drawdown zone each year, possibly feeding on benthos or surface invertebrates. An active rainbow trout fly fishery developed after annual seeding started where no fishery was present before. An abundance of stranded fish in numerous depressions of the drawdown zone has attracted unprecedented numbers of eagles, ravens and other wildlife to the Revelstoke Reach in winter and early spring each year. Suckers and other species have been observed scavenging in the advancing shallow water where annual vegetation is established. These fish are not typically observed where vegetation has not been established.

These observations indicate a potential benefit of vegetation establishment to the benthic food web in the drawdown zone of the Revelstoke Reach. Nutrient loading from fertilizer added at the time of planting fall rye or at the time of plant decomposition after inundation may increase trophic production, ultimately increasing availability of food for fish. The greatest effect of nutrient loading may be through the local benthic food web, but it may also affect pelagic systems downstream.

The purpose of this study was to examine the effect of vegetation composition and biomass among elevation strata on the abundance, composition and biomass of fish, benthic invertebrates, and periphyton in the Revelstoke Reach. The work focussed on quantifying benthic processes. The experimental design was structured for eventual use of certain endpoints in a simulation model to be used in exploring dynamics of fish use of the drawdown zone and to examine biomass and carbon flux associated with vegetation establishment in drawdown zones. A positive effect would indicate benefits of annual seeding and natural re-vegetation beyond the primary goal of dust control. Descriptions of the soils and vegetation communities in the same experimental design as was used in this project are provided in a companion report prepared by Moody and Carr (2000). The present report provides results and discussion of study of fish, benthic invertebrates, and periphyton associated with vegetation strata in 1999.

2.0 EXPERIMENTAL DESIGN

2.1 Periphyton and Benthic Invertebrates

An important feature of the Revelstoke Reach is that vegetation communities are stratified by elevation. The communities are largely determined by the length of time they are under water during the growing season each year. Diverse communities of native vegetation have invaded the highest elevations above 435 m. These zones are flooded for less than 150 days each year and when water reaches full pool, water depths are relatively shallow (<5 m). At the other extreme, barren sites where vegetation has not become established are at elevations less than 434 m with most close to 431 m. These zones are flooded for more than 150 days each year and water depths are mostly >8m at full pool.

This natural stratification introduced confounding between two factors, one being vegetation type and the other being elevation. Consequently, effects of vegetation type and elevation on endpoint measurements that are associated with plant substrata (e.g. invertebrate abundance or biomass) could not be separated using conventional in situ sampling techniques. Any difference in measurements of the endpoints found in grab samples collected from substrata at different elevations could only be attributed to combinations of vegetation type (the substrata of interest) and elevation. Since the objective of the study was to examine specific effects of vegetation type, alternate techniques were required.

To get around this problem, sampling of outplanted substrata containing several vegetation types at several elevation strata was laid out. In this design, replicated samples of selected plant species were dug up, placed in containers that allowed plant growth to continue when replanted back into the ground, and moved to selected elevation strata for removal and sampling at points in time after inundation. This process of digging up intact plants and root masses and replanting at alternate locations was called "outplanting". At time of sampling, the containers were easily pulled from substrata using a line and winch operated from a boat, eliminating the need for conventional grab equipment. This approach allowed measurements of endpoints to be collected from all selected vegetation types recovered from all elevation strata. This layout eliminated confounding between vegetation type and elevation.

Four vegetation types were selected for study:

- Barren soil where no vegetation was growing. It was collected from existing barren sites at lowest elevations;
- Fall rye planted in 1999. It was collected from sites where a fall rye monoculture was growing;
- Reed canary grass. It was collected from sites where mixed perennial native grasses were thriving; and
- Lenticulate sedge (*Carex lenticularis*). It was collected from sites where sedge and perennial native grasses were thriving.

Fall rye was selected because of interest in potential benefits it may provide beyond its primary purpose of providing dust control after planting each year. Reed canary grass and lenticulate sedge were selected because they were two of the most abundant and common plant species at mixed vegetation sites. These two species were considered most representative of the mixed plant communities (A. Moody, AIM Consultants. Pers. comm.).

Three elevation and vegetation combinations were selected to cover the range throughout the Revelstoke Reach:

- Lowest elevation (430.9 m) characterized by barren sediment or soil, hereafter called the barren site;
- Low elevation where fall rye was planted in 1999 (431.2 m), hereafter called the fall rye site; and
- A high elevation stratum supporting mixed native vegetation (435.6 m), hereafter called the mixed vegetation site.

Actual elevations of these strata were determined in two steps. The strata were first identified from existing air photo coverage reported by Carr et al. (1993). Actual elevations were the water surface elevations of the Arrow Lakes Reservoir at the time the water elevation passed the vegetation zone during reservoir filling in 1999.

Two dates were selected to cover the anticipated period of biofilm accrual and invertebrate colonization on plant material:

- T=1 was within 10 days after inundation to examine the initial community associated with the flooded foliage and root masses; and
- T=2 was approximately 80 days after inundation to examine what was expected to be a fully developed community associated with the flooded foliage and root masses remaining at that time.

Samples were also collected immediately before inundation to capture terrestrial invertebrates on the aboveground foliage and in the belowground root and soil matrix. These samples were not further examined in this project because they were unrelated to processes after flooding.

By random selection of the plants, the experiment contained two factors (vegetation type and elevation) that could be independently analyzed within one or each of the two time blocks. Alternatively, time could be another factor to support a 3-factor design. Each of these layouts was a randomized complete block design that could be analyzed using multi-factor analysis of variance. Three replicates were arbitrarily assigned. Endpoints that could be examined in the analysis were:

- Direct measures or indices of invertebrate abundance, composition and diversity associated with aboveground plant foliage and belowground soils, sediment, and plant roots;
- Invertebrate biomass associated with aboveground plant foliage and belowground soils, sediment, and plant roots;
- Periphyton abundance, composition and diversity on plant leaf matter;
- Plant nutrient content (reported by Moody and Carr 2000); and
- Plant biomass (reported by Moody and Carr 2000).

To determine rates of colonization, one sample of each vegetation type that was outplanted in separate containers was collected weekly for an 8 week period after T=1. The high elevation mixed vegetation site was used for all collections. All endpoints were the same as those measured in the main experiment, including invertebrate abundance, nutrient content of vegetation, etc. The most important data in these measurements was change in biomass of benthic invertebrates.

2.2 Fish

Because fish can move around the reach, a separate design was required to examine associations of fish and vegetation type. Examination of fish associated with small outplanted plants was not an option. No quantitative fish survey had been completed in the reach before this project, leaving little evidence of distribution, species composition, and abundance at any location. Because these preliminary data were lacking, a simple design of examining spatial variation in fish endpoints across replicated areas of the reach containing the three vegetation strata was selected. The location strata were consistent with those used in the outplanting experiment and they included barren sites, barren areas planted with fall rye in 1999, and areas where native vegetation was present.

Potential confounding of measurements of fish abundance and species composition among location strata was movement of fish between locations. Fish that move in to new shallow habitat with the rising water surface elevations in spring may be there for several reasons. Rainbow trout may move to spawning streams with rising water, which means that their capture may have nothing to do with direct utilization of the newly-flooded habitat. Fish may eat terrestrial insects that are entrained with rising water but then leave for other habitat after that food supply is depleted. Still others may move in to stay in newly-flooded habitat for the duration of the summer growing season using food associated with the plant biofilm and soils.

To minimize risk of confounding, fish sampling occurred in September, which is relatively late in the growing season when fish movement was expected to be less than earlier in the growing season. Fish found at a given location in the late summer were more likely to be directly using the habitat as opposed to simply moving through. For this reason, data collected later in the summer was interpreted with greater confidence than would have been the case with spring data.

3.0 STUDY SITE

Arrow Lakes Reservoir is located between the Monashee and Selkirk Mountain ranges. Construction of Hugh L. Keenleyside Dam in 1968 resulted in the expansion of two lakes (Upper Arrow and Lower Arrow) that were originally separated by a reach of free-flowing Columbia River. These two lakes and large sections of the adjoining Columbia River were flooded to create one long waterbody. The upper and lower sections of Arrow Reservoir are still referred to locally as Upper Arrow Lake and Lower Arrow Lake, respectively. Revelstoke Dam forms the upper boundary of Arrow Lakes Reservoir and, at full pool, the reservoir extends to within 10 km of that dam.

The study was completed in the drawdown zone of Upper Arrow Reservoir that included 2,850 ha over a lineal distance of 40 km between Revelstoke and Shelter Bay (Figure 1). In this study, that area is called the Revelstoke Reach. In this reach, water surface elevations typically range between 440 m and 420 m over an annual cycle of drawdown in winter and refilling in spring and summer. In some years, the water surface elevation may not reach 440 m, resulting in continuous exposure of some dust-producing areas of the drawdown zone in summer months. In 1999, snowpack was about 120% of normal. Water surface elevations rose from 429.51 m at the start of field activities in the first week of June, reached a maximum elevation of 440.09 m on July 29 and declined to 438.55 m on August 25 when field activities were completed (Figure 2).

Nutrient concentrations in Revelstoke Reach are typical of oligotrophic waters as defined by Wetzel (1983) and characterized in British Columbia by Stockner and MacIsaac (1996) and Perrin and Blyth (1998). They are also similar to those reported for the main basins of Arrow Lakes Reservoir by Pieters et al. (1998). Results from analysis of water samples collected along Revelstoke Reach on September 22 during this study (Appendix A) showed that soluble reactive phosphorus concentrations were <1 $\mu g \cdot L^{-1}$, total phosphorus concentrations were 4-5 $\mu g \cdot L^{-1}$, NH^{+}_{4} -N concentrations were <5 $\mu g \cdot L^{-1}$ and NO^{-}_{3}-N concentrations were 138 – 152 $\mu g \cdot L^{-1}$. The water has moderate conductivity and dissolved solids (120 µS/cm and 56 $mg \cdot L^{-1}$ respectively), moderate acid neutralizing capacity (alkalinity of 51 $mg \cdot L^{-1}$) and it is slightly alkaline (pH of 7.8).

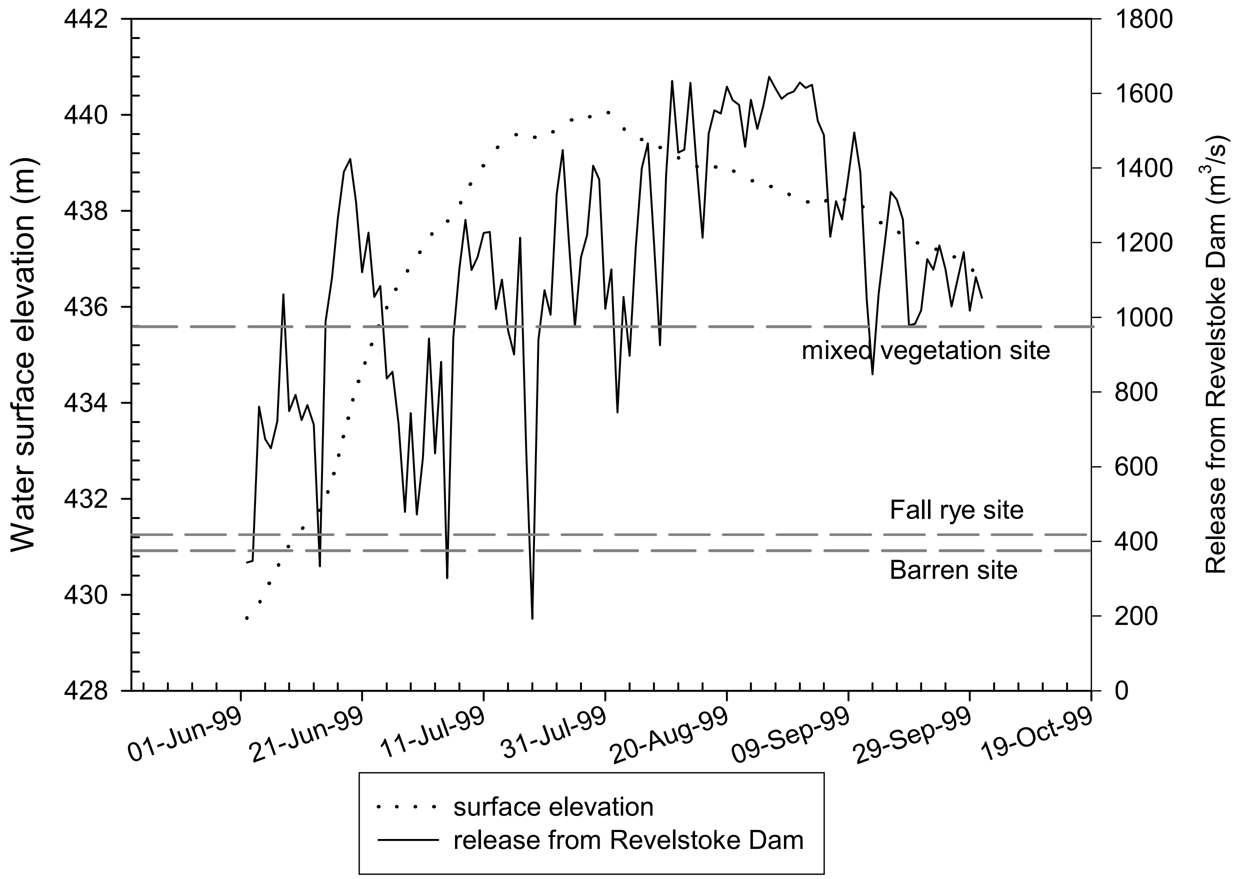


Figure 2 Release from Revelstoke Dam and water surface elevation in Revelstoke Reach of Arrow Lakes Reservoir, 1999. The intersection of the dashed lines (indicating elevation of study strata) with the dotted line (indicating water surface elevation) corresponds with the approximate time of inundation (read from the x-axis).

The hourly mean water temperature determined with an Onset logger placed at each sampling site for the duration of the study was 9.7°C (7.4-12.1°C) at the barren site, 9.6°C (6.9-12.4°C) at the fall rye site, and 10.6°C (8.0-12.5°C) at the mixed vegetation site. The higher average temperature at the mixed vegetation site was due to flooding approximately 10 days after the lower elevation sites (Figure 2). It was not exposed to slightly cooler water in the period of June 8 through June 23 that did occur at the barren and fall rye sites.

Mean Secchi depth transparency, determined from measurements on each day of sampling at the mixed vegetation site was 3.1 m. Secchi disk transparency is the mean depth at which a weighted white disk, 20 cm in diameter, disappears from view when being lowered and the depth at which it reappears upon raising after it has been lowered beyond visibility. Secchi depth corresponds approximately to 10% of surface irradiance and is mainly a function of light scattering properties associated with particulates in the water column. This characteristic means that when plankton or other particulate density increases in the water column, Secchi depths decline and when particle density goes down, Secchi depths increase. The measurement is comparable across space and time, making it a universal measure to compare spectral properties of surface waters.

The compensation depth separates the zone of net photosynthesis from the zone of net respiration. It can be measured as the intercept of a regression of irradiance measured as photosynthetically active radiation (PAR) against water depth or it can be estimated as twice the Secchi depth transparency, which is approximately 1% of surface irradiance. Based on Secchi depth measurements, the compensation depth in Revelstoke Reach was approximately 6 m during the study period. Given the top water surface elevation of 440 m, net photosynthesis was likely active on substrata at the mixed vegetation site (situated at 435.6 m) throughout the study. But, net photosynthesis would have shifted to net respiration on or about June 29 at the lower elevation barren and fall rye sites (situated close to 431 m). After June 29, water depths exceeded 6 m at those locations.

The status of vegetation development in all areas of the reach in 1999 is listed in Table 1. Descriptions in the table were based on personal communications with Dr. Will Carr (Carr Environmental) and B. Gadbois (BC Hydro, Revelstoke).

Table 1. Description and treatment status of reach areas in 1999 over the south to north gradient.

Reach Area (labels are from Carr et al. 1993)	**Location**	**River km measured from Hugh Keenleyside Dam**	**Status in 1999**
Y	Large, low gradient flat at the outlet of Cranberry Cr.; 427 – 428.5 m.	185-188	• No vegetation; • No seeding in 1999; • Dust production area in April and early May; and • Inundation occurred on May 18.
X1 and X2	7.4 km band along the east side upstream of Cranberry Cr.	188-195	• Native grassland at upper elevations (40% of area) grading to barren dust producing zones at lower elevations (50% of area); and • No seeding in 1999
W1 and W2	5.4 km along the west shore across from X1	190-196	• 90% bare and no vegetation; • 10% native grassland at the northwest end; • Dust source in 1999; and • No seeding in 1999.
V	2 km band on the west side and exposed island downstream of Akolkolex River	196.5-199.2	• Higher elevation is a continuation of the native grasslands in area W1 (50% of area); • No vegetation in 50% of area; • Dust production in April and May; and • No seeding in 1999.

Reach Area (labels are from Carr et al. 1993)	Location	River km measured from Hugh Keenleyside Dam	Status in 1999
U1 to U4	East and west banks and islands 2.5 km downstream and 3.4 km upstream of the inflow of the Akolkolex River	199-205	• U1 on the west bank is barren of vegetation and was 100% planted with fall rye in 1999; • Islands called U2 and U5 are bare dust sources without vegetation and not planted in 1999; and • U3 is a narrow steep band along the river. It is barren of vegetation and it was not planted in 1999. The north end of U3 is typically planted but not in 1999.
T1 and T2	Low elevation islands at the upstream end of U1	203.5-206	• Barren and no vegetation on T1; • T1 was seeded in 1999; and • No vegetation on T2 and not seeded in 1999.
S	Narrow band on the west bank between Mulvehill Creek and Blanket Creek	205-207	• Dust production source; • Seeded in 1999 mainly to create stubble to enhance growth of native grasses; and • Higher elevations have established native grasses.
P	Flats at outflow and to the south of Drimmie Creek	205-208	• Upper elevation has native grasses with some willow invading (60% of area); • Lower elevations are barren; and • Lower elevations planted in 1999.
N	Islands and large flat extending from the west shore at the widening of the river upstream of the outflow of Drimmie Creek	208.5-211	• Bare flats that are dust production areas; and • Seeded in 1999
M	Southwest tip of extensive naturally re-vegetated flats across the river from area N	210.5-214	• Upper elevations all vegetated with native grasses grading to lower elevations that are mostly barren of vegetation; and • Seeded in 1999.
L	Islands and margin of the river downstream of the Begbie Creek Rec. site	213-216	• Some grass invasion at the top of the margin but dust production occurs on adjacent islands; and • Not planted in 1999.
K	Tip of extensive flats upstream of area M on the east side of the river	216-218	• Mainly transition strata of mixed vegetated and non-vegetated patches; and • Patches that are bare were seeded in 1999.
Ia and Ib	West shoreline and islands upstream of the Begbie Rec. Site	217-219.5	• Mainly transition strata having native grasses and minor bare patches.
E,F, G	At outflow of Illecillewaet River and flats adjacent to the Revelstoke airport	218.5-224	• Established with native grasses; and • No seeding required.

4.0 METHODS

4.1 Outplanting and Retrieval of Samples

Each outplanted sample consisted of a block of substratum material 30 cm x 30 cm x 15 cm (length, width, depth) containing soil or sediment and associated plant material (barren soil and sediment, fall rye, lenticulate sedge, or reed canary grass). Barren samples were collected from area W1 (river km 188, Figure 1). Fall rye samples were collected from area U4 (river km 201, Figure 1). Lenticulate sedge and reed canary grass samples were collected from area X1 (river km 193, Figure 1).

Each sample was dug from substrata with a flat shovel and placed in a woven plastic sack having dimensions of 71 cm x 102 cm. The sack material consisted of 1-2 mm wide strips of nylon that was woven to allow water and gas exchange but prevent sample loss upon retrieval. The bottom seam was sown with cotton-synthetic thread that did not decompose under water. The top edge of the sack was reinforced and custom fabricated with grommets through which a drawstring closure was installed for use during sample retrieval. A total of 72 samples for T=1 and T=2 sample collections in the main experiment were prepared for outplanting (3 replicates x 4 plant types x 3 vegetation strata x collections on 2 dates (T=1 and T=2)).

A total of 32 samples for the time series sampling between T=1 and T=2 (1 replicate x 4 plant types x 1 vegetation strata x 8 collection dates) were prepared for outplanting at the same time that samples were prepared for the main experiment.

After samples were placed in the sacks they were transported by boat to each of the outplanting locations. These locations were a barren site at river km 195 (elevation of 430.9 m), a fall rye site at river km 201 (elevation of 431.2 m) and a mixed vegetation site at river km 193 (elevation of 435.6). The actual locations, shown in Figure 1, were selected mainly according to logistical criteria and the need for a large expanse of the selected vegetation type without patches of other strata being present. The barren site was characterized by the absence of vegetation over an area of several hectares. Similarly the fall rye site was characterized by a monoculture of fall rye planted on barren soil over several hectares. The mixed vegetation site was characterized by a diversity of native grasses and sedges covering several hectares. The sites were within a few kilometers of each other to limit time required for travel and sampling on each sampling date. At each of these locations, holes having the same dimensions as the samples were dug for random placement of the samples back into the soil. Samples in their sacks were planted back into those holes. Excess sack material was accordion folded to lie flush with the ground surface and held in place with packed soil. Quarter inch poly rope was passed through the sack grommets and attached to an anchoring stake and then to a labeled float. The anchoring stake was required to prevent float line movement from gradually cinching the mouth of the sack closed after inundation. One float was attached to one replicate each of barren soil, fall rye, reed canary grass and lenticulate sedge sample. This outplanting process was completed on June 5 through June 7 at the barren, fall rye, and mixed vegetation locations. Water inundation occurred on June 8, June 10, and June 23 at the fall rye, barren, and mixed vegetation sites respectively.

The time course sampling proceeded over approximately 10 weeks with final samples collected on September 9 (Table 2). Because dates of inundation differed among locations, samples for a given time under water were sampled on different dates. T=1 samples were collected 6 – 10 days after inundation. T=2 samples were collected 77 – 78 days after inundation. Sample collections in the time series between T=1 and T=2 occurred weekly (Table 2).

Table 2. Duration of subaqueous exposure of plants and sampling dates at all locations.

Experiment	Location	Time*	Date of inundation	Sampling date	Days under water
main	Barren	T=1	10-Jun-99	18-Jun-99	8
main	Fall rye	T=1	8-Jun-99	18-Jun-99	10
main	Mixed vegetation	T=1	23-Jun-99	29-Jun-99	6
main	Barren	T=2	10-Jun-99	26-Aug-99	77
main	Fall rye	T=2	8-Jun-99	25-Aug-99	78
main	Mixed vegetation	T=2	23-Jun-99	9-Sep-99	78
Time series	Mixed vegetation	T1+1	23-Jun-99	8-Jul-99	15
Time series	Mixed vegetation	T1+2	23-Jun-99	14-Jul-99	21
Time series	Mixed vegetation	T1+3	23-Jun-99	20-Jul-99	27
Time series	Mixed vegetation	T1+4	23-Jun-99	28-Jul-99	35
Time series	Mixed vegetation	T1+5	23-Jun-99	5-Aug-99	43
Time series	Mixed vegetation	T1+6	23-Jun-99	10-Aug-99	48
Time series	Mixed vegetation	T1+8	23-Jun-99	24-Aug-99	62
Time series	Mixed vegetation	T1+9	23-Jun-99	2-Sep-99	71

*in the time series experiment, sampling at T1+7 was skipped and a T1+9 date was added to complete the collection of all outplanted samples.

Each sack was retrieved by pulling on the attached line using a hand winch and davit on board a workboat. Tension on the line initially closed the sack around the enclosed soil and plant material. The sack was then pulled free of the bottom and raised to the water surface. An aluminum mesh tray suspended from the davit was lowered under the sack. The tray and sack was winched above the water surface to allow the sample to dewater. The tray and sample was then lowered into the boat. The sample was sectioned into 2 approximately equal parts (surface area of 15 cm x 30 cm) with a serrated blade knife. One section was placed in a poly bag, while the other was left in the sack. Both parts were placed into a labeled bucket for transport to a field laboratory.

4.2 Laboratory

At the field laboratory, the subsample contained in the sack was washed to remove all soil, leaving clean aboveground and belowground plant biomass. This biomass was packed on ice in plastic bags and shipped to the soils laboratory for measurement of plant biomass and nutrient content (see Moody and Carr (2000) for details).

From the other subsample, a few older (not new growth) leaves from plant material were clipped, placed in a 150 mL glass jar and preserved in Lugol's iodine-potassium iodide solution for later determination of algal cell counts and biovolume. The remainder of the aboveground plant material was cut from the roots, placed in a sealed plastic bag and preserved in 10% formalin (3.7% formaldehyde). The sample bag was placed in a heavy polyethylene bag and sealed. Belowground material (roots and soil) was teased apart to ensure penetration of preservative and sealed in a bucket in 10% formalin.

The aboveground and belowground material was separately analyzed for benthic invertebrate composition, abundance, and biomass. Total contents of each sample were washed through a 1 mm and 250 µm sieve and all animals were retained, identified and enumerated. Enumerations were separated into microbenthos (<1 mm) and macrobenthos (>1 mm). All macrobenthos was manually picked from the 1 mm sieve. Microbenthos was enumerated from any one of 16 to 128 subsamples produced from splitting the sample retained on the 250 µm sieve. All splitting was completed using a Folsom plankton splitter. The washing process was used for both the aboveground leaf material and for the belowground soils and roots. The residue from each sample was re-sorted until acceptable accuracy of picking (>95%) was achieved. Invertebrates were enumerated and identified using a GSZ Zeiss stereomicroscope under magnification of 10 –100 times. Additional examination of crucial organism body parts was done using an Olympus inverted microscope under magnifications of up to 400 times. All animals were identified to the lowest reliable taxon (mainly genus). Edmundson (1959), Merritt and Cummins (1996), and Pennak (1978) were used as taxonomic references. Aquatic and terrestrial taxa along with incidental fish were included in the taxa that were enumerated.

After enumeration, organisms were dried to a constant weight for 72 h at 60°C and weighed on a Mettler H18 micro scale. Macro weights, (organisms not passing through the 1mm sieve) were measured to ±0.1mg - 2mg. Micro weights, (organisms smaller than 1 mm) were calculated from a weight of a split fraction, multiplied by a split factor from subsampling. Total weight of organisms per sample was expressed as the sum of micro and macro weights.

This method yielded error greater than the accuracy of a single weight measurement (±0.1mg - 2mg), especially for the split part of the samples having low numbers of organisms. To increase the accuracy of a measurement, whenever possible, larger portions of samples were analyzed. For leaf samples at T=1 and early in the time series when numbers of organisms could be small, the entire sample was analyzed. In this case, the accuracy of the scale was the source of error (±0.2mg).

Analysis of biofilm samples was difficult because a mass of fine particulate inorganic clay and silt particles with a small amount of sand was present on leaf surfaces. Several laboratory techniques were tried in attempts to 'clear' the fines from the periphyton so that microscopy could proceed. Unfortunately most techniques were ineffective, and produced inconsistent results. The method chosen for processing all samples was as follows.

The Lugol's preserved samples of vegetation clippings were vigorously shaken within the sample jars for exactly 2 minutes. They were settled for 1 minute to allow heavier sand and silt to settle, and then the supernatant liquid was carefully decanted into a large graduated beaker and diluted with distilled water to either a 500 or 1000 mL volume. After gently stirring for 1 minute, a 25 mL aliquot was withdrawn and placed in a 25 mL Utermohl settling chamber and allowed to settle overnight.

Counts were completed under a Carl Zeiss inverted phase-contrast plankton microscope. Counts were done at 250X magnification (16X objective, field diameter = 1mm.) and large micro-periphyton (20-200µm), e.g. diatoms, filamentous green, blue-greens, were enumerated from random transects. Samples contained many empty (dead) diatom frustules that were distinguished from the 'living' cells by the absence of a chloroplast. The final settled samples, despite settlement and dilution, still contained a large amount of clay and silt, which made counting a slow process. If bacteria or flagellates were observed, a random transect (ranging from 10 to 15mm) was counted at 1562X magnification (100X objective). This high magnification permitted quantitative enumeration of minute (<2µ) autotrophic picoplankton cells (0.2-2.0µm) [Class Cyanophyceae], and also of small auto-, mixo- and heterotrophic nano-flagellates (2.0-20.0 µm) [Classes Chrysophyceae and Cryptophyceae]. Between 250-300 cells were consistently enumerated in each sample, following recommendations by Lund et al. (1958). The compendium of Canter-Lund & Lund (1995) was used as the taxonomic reference.

Several biofilm samples were examined before and after shaking to determine how much periphyton remained on the plant surface after shaking. Results showed that over 75% of the biofilm was removed by shaking, indicating that present counts were underestimates of actual amounts. In addition, some blades of the 3 vegetation types were examined under low power (10X) to view the modes of attachment (stalks, discs, mucilage, etc.) and places of attachment relative to the geometry of the plants blades and stems.

4.3 Fish

Fish sampling was conducted from 17 to 26 September 1999. The study area extended from just upstream of Beaton Flats (Km 187, measured from Hugh L. Keenleyside Dam) to Km 220 at the Revelstoke airstrip (Figure 1). Within this area, samples were collected from

13 randomly selected sites within three different vegetation and reservoir bed elevation strata. Five low elevation barren sites, characterized by an absence of vegetation, were sampled. One of these sites had abundant submerged stumps. Four sites were sampled in a high elevation mixed vegetation stratum, where native grasses and sedges were established. Reed canary grass and other perennial native grasses characterized vegetation cover within these sites. Four sites were sampled where fall rye was planted in 1999. One of the fall rye sites had abundant submerged stumps. General descriptions of these sites and their locations are given in Table 3.

Table 3. Locations and descriptions of fish sampling sites the Revelstoke Reach of Arrow Reservoir, 17 to 26 September 1999.

Site*	Stratum	Stumps present/absent	River km**	Bank***	Description
BR0-S	Barren	Present	187-189	LUB	large barren site with submerged stumps near mouth of Cranberry Creek; depth 4-6 m; nil velocity
BR1	Barren	Absent	193.4-195.3	LUB	barren site; approximately 1.5 km downstream of Tree Island; depth 4-6 m; nil velocity
BR2	Barren	Absent	201.4-202.5	RUB, MID	two small barren sites separated by a shallow channel; across and slightly upstream of Walter Hardman generating station; depth 5-8 m; nil velocity
BR3	Barren	Absent	216-218.4	RUB	large barren site near mouths of Montana and Scott creeks; next to two mixed vegetation sites; depth 2-4 m; low velocity along edge of site near mid-channel
BR4	Barren	Absent	214.3-216	LUB	narrow barren site 1.5 km downstream of Begbie Creek; depth 3-6 m, medium velocity along outer edge of site
FR1	Fall rye	Absent	200.3-201.3	LUB	narrow fall rye site at outlet of Walter Hardman generating station; depth 3-7 m; nil velocity
FR2-NS	Fall rye	Absent	209-211	LUB	fall rye site without submerged stumps; across from Greenslide Creek; depth 4-6 m, low velocity along outer edge of site
FR2-S	Fall rye	Present	209-210.5	MID	fall rye site with submerged stumps; near mouth of Greenslide Creek; depth 5-8 m, low velocity

Site*	Stratum	Stumps present/absent	River km**	Bank***	Description
FR3-NS	Fall rye	Absent	202-203.5	LUB	fall rye site without submerged stumps; about 1 km downstream of Blanket Creek; depth 5-9 m; nil velocity
MV1	Mixed vegetation	Absent	192.2-193.2	RUB	small mixed vegetation site at mouth of Tank Creek; depth 1.5-3.5 m; nil velocity
MV2	Mixed vegetation	Absent	215.1-218.3	RUB	large mixed vegetation site at mouths of Montana and Scott creeks; depth 1-2 m; nil velocity; emergent vegetation in many places
MV3	Mixed vegetation	Absent	218.3-220.1	RUB	mixed vegetation site at the Revelstoke airstrip; depth 2-5 m, some velocity along outer edge of site
MV4	Mixed vegetation	Absent	206-208.5	RUB	large mixed vegetation site across from Mulvehill Creek; depth 1.5-3 m; nil velocity

*Sites are labelled on the map shown in Figure 1
**River km is measured from the Hugh Keenleyside dam
***LUB refers to the left bank viewed facing upstream; RUB refers to the right bank viewed facing upstream; MID refers to a mid-channel location.

Gill nets, boat electroshocking, and Gee minnow traps were used to collect fish from each of the three vegetation strata. Remote underwater video observation was also performed in each of the three vegetation strata. All sampling took place at night, with the exception of four gill net sets. The position of each sampling location was determined using a Garmin 12 handheld GPS unit. Geographic co-ordinates describing the paths travelled while conducting boat electroshocking and underwater video surveys are provided in Appendix C of the CD accompanying this report. The geographic co-ordinates for all gill net sampling locations are provided in Appendix D included on the CD accompanying this report.

Gill nets were the primary sampling method used to sample each habitat type (i.e., barren, mixed vegetation, and fall rye). In total, 28 gill nets were set at 13 different sites, including 10 in barren sites, 10 in fall rye sites, and 8 in mixed vegetation sites. The nets consisted of six panels, each 15.2 m long by 2.0 m deep, arranged from smallest to largest mesh size. Mesh sizes used were 25.4 mm, 38.1 mm, 50.8 mm, 63.5 mm, 76.2 mm, and 88.9 mm, stretched-measure mesh. The nets were constructed of monofilament material with float line along the top of the nets and lead line along the bottom of the nets. Gill nets were set and retrieved from the front or side of the boat and secured at each end with an anchor attached to the lead line and a float attached to the float line. The amount of rope used to attach the anchors and floats, and the use of sinking and floating nets, allowed nets to be set at either the surface or bottom of the water column. All nets were set horizontally and in areas of low current velocity.

With the exception of four sets, gill nets were set at night. The average duration of sets was 4.25 hours. Information recorded for each gill net set included set and pull times, water temperatures, location in water column, orientation to flow, depth, and fish catch summaries. Captured fish were placed into a tub of fresh water until they were processed. Fish that were alive when the nets were pulled were released, with the exception of some rainbow trout that were sacrificed to collect ageing structures and stomachs.

Gee minnow traps (baited with dog treats) were used as a complementary sample method, in conjunction with some of the gill net sets. In total, 100 Gee minnow traps were set during the study. Ten traps were attached to one anchor of each of 10 gill net sets. The traps were checked when the gill nets were pulled.

Boat electroshocking was completed using a Smith-Root Inc. high output electroshocker operated out of a jet drive riverboat. Previous studies conducted in the Columbia River have shown that, due to high water clarity, boat electroshocking during daylight hours is inefficient at catching certain sportfish species such as rainbow trout. In the present study, boat electroshocking was conducted at night.

Eight boat electroshocking sites were sampled. Three were in the barren habitat type, three were in fall rye habitat sites, and two were in mixed vegetation habitat sites. In total, 16.9 km of nearshore habitat was sampled by boat electroshocking, for a total sampling time of 16,560 seconds (4 hours and 36 minutes of actual time the shocker was on). Information recorded at each boat electroshocking site included length and width sampled, sampling time, electroshocker settings, substrate types, instream cover types and availability, vegetation, observations on habitat and fish distribution, and fish catch summaries. During boat electroshocking, fish were captured in dip nets and placed in a livewell on the boat. However, some fish were observed and identified, but not captured. Both captured and observed fish were included in the calculation of catch-per-unit-effort (CPUE) values.

A remote underwater video (RUV) system was employed to observe fish using habitat at one barren site, one fall rye site, and one mixed vegetation site. The objective was to obtain a visual record of fish use of plant habitat, with an emphasis on rainbow trout, in the three different habitat types. The RUV unit consisted of an 8 mm (high resolution, low-lux) Sony camcorder mounted inside an underwater housing and attached by a bracket to a 45 kg lead bomb. The entire unit was raised and lowered by means of a cable attached to a sounding reel. A light bar mounted above the camera housing enabled use of the RUV at night. A video display console was used to continuously monitor the image. A video cassette recorder (VCR) was attached to the unit to record fish presence and surrounding habitat characteristics for subsequent analysis. A gasoline-powered generator provided power to the system. The RUV unit was lowered to the bottom of the water column and the boat was directed over the habitat type being observed. A handheld Garmin 12 GPS unit was used to determine the positions of the beginning and end of transects where underwater video was recorded. Using this system, the location and depth of observed fish and the associated habitat features were simultaneously recorded.

The length and weight of each captured fish was measured along with records of capture method, date, and site location. Data records also included presence or absence of tags, sex and maturity (if determined), indication of survival of fish during shocking and handling, indication of whether the whole fish or only the stomach was preserved, retention of ageing structures, and comments on abnormalities or other observations. Fork lengths were measured to the nearest millimetre and weights were recorded to the nearest gram. The minimum weight that could be measured by the balance used in this study was 5 g. Weights for some of the smallest fish were therefore recorded as less than 5 g, and these weights were treated as being equal to 5 g when computing mean weights for groups of fish.

Ageing structures and stomachs were collected from rainbow trout and bull trout. Rainbow trout of sufficient size were sacrificed and scales and otoliths were collected. Stomachs were taken from sacrificed rainbow trout, placed in labelled jars, and preserved in 10% formalin for later analysis of contents. Ageing structures and stomachs were also taken from any bull trout that succumbed to the sampling procedures. Ageing of fish was performed using techniques described by Mackay et al. (1990).

In the laboratory, all animals in the size fraction >250 μm that were in the stomach samples were identified to the lowest reliable taxon (mainly genus) and enumerated. For animals that were partly digested, head counts were used as the basis for the enumeration.

4.4 Fishery

An informal creel survey was completed to examine the extent of the fishery for rainbow trout in Revelstoke Reach. A questionnaire was laid out on a creel card requesting information on angling effort and catch. Data included: date, time, boat type, number of rods fishing, duration and time of angling, launch location, angling location, and catch. Because anglers were hesitant to indicate exactly where they were fishing, they were asked if they were active in any one or more of three reaches: downstream of the Akolkolex River, between the Akolkolex River and Mulvehill Creek, and between the Highway 1 bridge and Mulvehill Creek (Figure 1).

The cards were distributed to the local fish and game and fly fishing clubs with a request for anglers to fill out a card each time they were fishing. When a fish was killed, anglers were asked to return stomachs in sample bottles that were supplied to them. The contents of 12 randomly selected stomachs were identified and enumerated in the lab to determine the composition of food organisms selected by the angled fish.

Anglers were asked to return the stomach samples and completed cards to Mr. Brian Gadbois (BC Hydro) who was well known by most members of the clubs.

4.5 Data Analysis

A wide range of benthos metrics was measured, providing a robust set of data for many analytical approaches. The main objective was ultimately to examine elevation and plant effects on one or more of those metrics. We also wanted to focus on one metric that could later be used as an endpoint in a simulation model to explore time course change in the structure and function of littoral communities in Revelstoke Reach, including biomass and carbon storage and flux.

To reach these goals we structured the benthos analysis into two parts. The first was a description of the benthos community using data collected from substrata at T=2 or after 78 days under water. Most extensive development of the invertebrate community was expected at that time compared to that found in samples collected earlier. We used this subset of data to describe what was present and to show the diversity of taxa that were found in association with plants. Counts by taxa were stratified by elevation and plant species and presented for aboveground samples and belowground samples. Most taxa were combined into major groups for a simple description of community composition. The second analysis dealt with examining the elevation and plant species effects on a benthic invertebrate endpoint. We selected an endpoint having greatest relevance to ecosystem function. There was a choice of several count (numbers/sample) or biomass (mg/sample) measurements including:

- abundance of each invertebrate taxon,
- abundance of groups of taxa,
- total abundance of all taxa,
- macrobenthos (animals >1mm in size),
- microbenthos (all animals <1mm in size),
- richness of invertebrate taxa, and
- total invertebrate biomass

Each metric was measured on aboveground and belowground material. While the inclusion of all or many endpoints was of academic interest, this approach was not practical because the interaction of resulting statistics would be too complex for later input in a simulation model. The purpose of the analyses was to simplify complexity making it easy to understand, not make it more difficult for later use. We wanted one endpoint that reflected whole community response to effects of elevation and plant species. We did not ignore other metrics but used them to help interpret elevation and plant species effects on the one to which statistical analyses were applied.

Total invertebrate biomass (dry weight per sample) was selected as the single endpoint of interest. Biomass is an integrated measure of abundance and animal size across all taxa. It provided evidence of whole community change to treatment, which was of immediate interest for interpretation of the experiment and for later use in simulation modeling. There was less interest in taxa-specific change to treatments because individual or small groups of invertebrate taxa reveal less insight into community function that does biomass, which integrates count and size criteria. Biomass is also something that fish actually see as visual predators, making it useful for interpreting fish use of the study area. Biomass can also be compared to other sources of food to examine relative importance of benthos for fish. Biomass is an index of carbon content in benthos. In this respect, processes that modify benthos biomass can also be interpreted with respect to dynamic change in carbon content in an area of the Revelstoke Reach and it can be compared to the same units derived for plants in the study area. Measures of biomass and carbon content are important because later modeling will investigate whether plant establishment and its associated aquatic community provides a carbon sink or is simply temporary storage ultimately leading to loss of carbon to the atmosphere.

Total invertebrate biomass was the sum of biomass determined on aboveground and belowground plant material.

Elevation and plant species effects on benthic invertebrate biomass were examined in four sequential steps. Time effects were first examined to determine if T=1 and T=2 samples may be combined to increase sample size for an ultimate 2-way (elevation and plant species as the main factors) analysis of variance (ANOVA). If a time effect was detected in any one combination of site and plant species, only T=2 data were selected for that final analysis because it would indicate independence of data collected at points in time. Overall absence of a time effect would indicate that T=1 and T=2 data may be combined to increase precision of the final ANOVA. If a time effect was detected, it was further explored using regression techniques to quantitatively describe time course change in plant biomass and the associated accrual of benthic invertebrate biomass using the time series data collected at the high elevation mixed vegetation site. Finally, an ANOVA was run to support interpretation of elevation and plant species effects on benthic invertebrate biomass. In all analyses, aboveground and belowground invertebrate biomass was combined into a single measure of biomass and expressed as biomass/sample (mg/sample) or biomass per m^2 ($mg \cdot m^{-2}$). The rationale for this approach was to examine whole plant effects on availability of benthos by plant or by area. Conversion to areal units was based on ground surface area, not surface area of plant tissue.

All data were $\log_{10}(x+1)$ transformed prior to ANOVA and regression analysis to standardize the data and minimize variation caused by different scales of measurement. All procedures were run in Systat v8 (SPSS 1998) and a significant probability level was set at p=0.05.

5.0 RESULTS

5.1 Periphyton

Analysis of periphyton focused on the accrual of biomass during time series measurements between T=1 and T=2 at the mixed vegetation site. The number of total living diatom cells with intact chloroplasts ranged from <100 cells/cm^2 to >16,000 cells/cm^2 (Figure 3). Reed Canary grass was the most heavily colonized plant; supporting an average of 5,000 - 6,000 cells/cm^2 after exponential growth was apparent in August. Cell density peaked at >16,000 cells/cm^2 in early September. Lenticulate sedge blades supported the second highest density of periphyton diatoms, averaging 2,000 - 3,000 cells/cm^2. Mean densities were highly variable and without a clear seasonal trend. Lowest diatom density was found on fall rye, averaging <200 cells/cm^2, and without a seasonal trend.

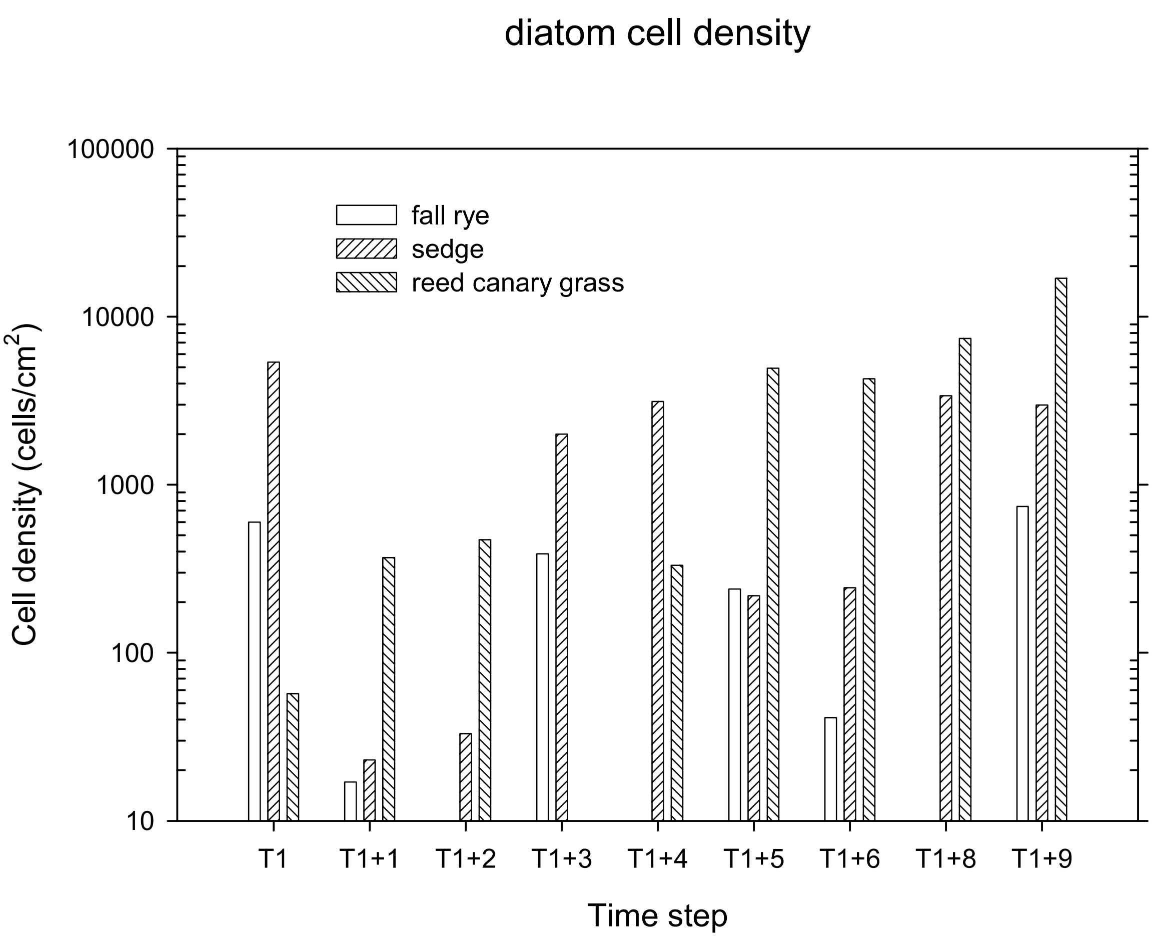


Figure 3. Mean counts of all diatom cells on each of the plant types at the mixed vegetation strata during the time series sampling.

The abundance of filamentous green algae was much less than diatoms (Figure 4). Filamentous greens comprised 10% - 15% of the total periphyton cell density in most samples. The filament densities were greatest on reed canary grass, much less abundant on lenticulate sedge and they were rarely seen on fall rye. Seasonal patterns were very similar to those noted for diatoms, with reed canary grass supporting the most diverse and abundant assemblages that peaked (>1,400 filaments/cm^2) in late-August. The average densities of filamentous greens on lenticulate sedge blades were <200 filaments /cm^2, and fall rye only briefly supported about 30 filaments/cm^2 in mid-July, but on most sampling dates none could be detected.

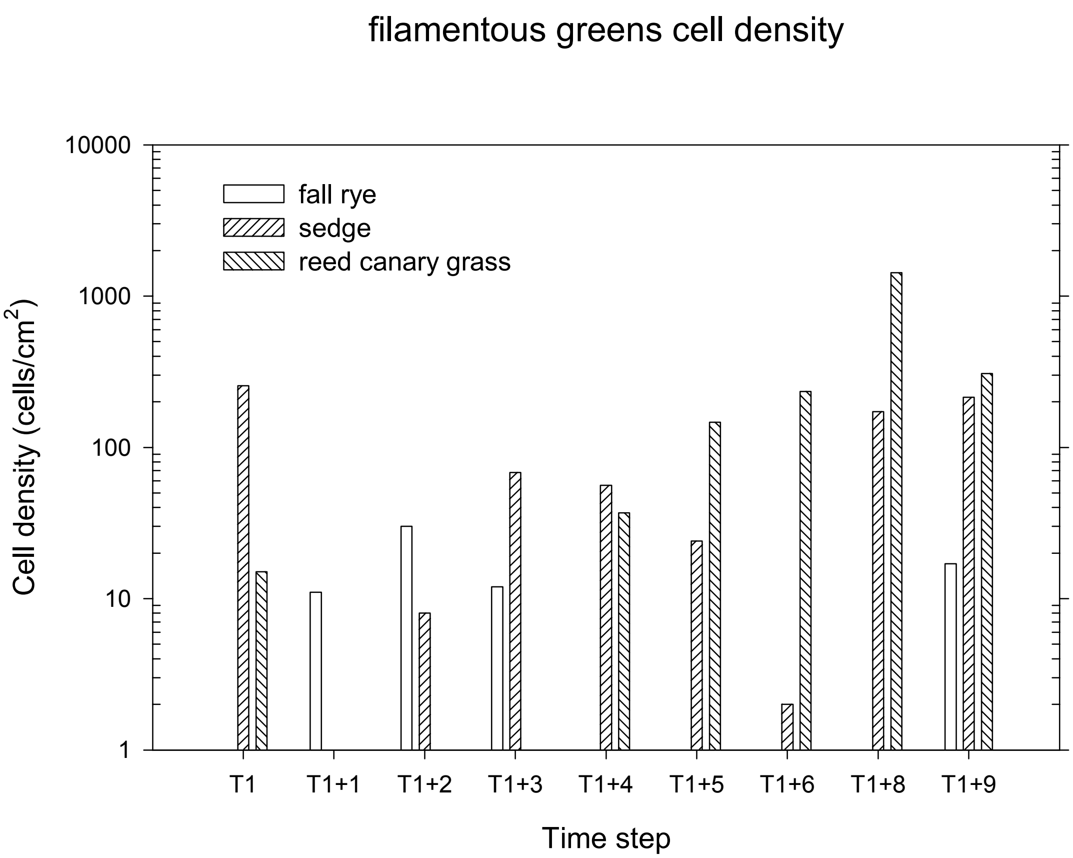


Figure 4. Mean counts of filamentous green algal cells on each of the plant types at the mixed vegetation strata during the time series sampling.

The assemblages of both diatoms and filamentous green algae were sparse. Most abundant diatom taxa were *Tabellaria flocculosa, T. fenestrata, Fragilaria construens, F. capucina, F. vaucheriae, Achnanthes minutissima, Navicula* spp. *and Cymbella* spp. Major species of filamentous green algae were *Mougeotia* sp., *Ulothrix* sp., *Rhizoclonium* sp. and *Zygnema* sp.

Because of the large amounts of clay and silt in most all samples, it was extremely difficult to examine samples at high power (1560X) for visible signs of microbial biofilm development. Nonetheless, examination of blades from samples of lenticulate sedge and reed canary grass at lower powers revealed little obvious settlement of bacteria, flagellates, ciliates or rotifers. But, a fall rye grass sample from 29 June contained extensive microbial development on most blades. The silt content was low enough for a high-power scan, which revealed several 'millions' of bacteria/cm^2, 75,500 micro-flagellates/cm^2 (5-10 μm), and 10-12000/larger protozoans/cm^2 (40-60μm), plus several stalked ciliates and a few rotifers. This sample was taken only 6 days after inundation, indicating rapid development of the microbial community on fall rye after inundation. A microbial community of this complexity was never observed on reed canary grass or lenticulate sedge samples.

5.2 Invertebrates

5.2.1 Community Description

A total of 66 benthic invertebrate taxa including naidid, enchytrid, and lumbriculid worms, nematodes, ostracods, tubificids, water mites, gastropods, aquatic insects, beetles, terrestrial insects, zooplankton, and freshwater shrimp were found in aboveground and belowground plant samples (Table 4). In one lenticulate sedge sample planted at the barren site, a juvenile burbot (*Lota lota*) having a length of 91.7 mm was captured. A total of 15 sculpins (*Cottus* sp.) were also in belowground samples of all plants and all elevations. They must have been at the sediment-water interface and were entrained in the sample upon retrieval. The most common and abundant taxa found on both the aboveground plant biomass and in the belowground soils were an assemblage of oligochaete worms (mainly Naididae, and Enchytraeidae), nematodes (Nematoda), chironomids (mainly Orthocladiinae) and ostracods (Ostracoda). Benthic zooplankton were common but less abundant than the benthic invertebrates, being associated both with the aboveground plant biomass and the substratum surface of belowground samples. Taxa included *Diaptomus* sp., *Cyclops* sp., *Alona* sp., *Chydorus* sp., *Bosmina* sp., *Ceriodaphnia* sp., *Daphnia* sp., and *Mysis* sp. Their presence indicated association of zooplankton in habitat close to the water – plant – soil interface.

Table 4. List of benthic taxa found in all aboveground and belowground plant and barren samples in Revelstoke Reach, 1999.

Order unless otherwise indicated[1]	Family or (Subfamily) or {tribe}	Genus	Stage	Taxa number
Benthic Invertebrates				
Diptera	Chironomidae			
	(Orthocladiinae)	*Brillia*	L	S1
		Bryophenocladius	L	S2
		Corynoneura	L	S3
		Cricotopus Sp1	L	S4
		Cricotopus Sp2	L	S5
		Cricotopus/Orthocladius	L	S6

Order unless otherwise indicated[1]	Family or (Subfamily) or {tribe}	Genus	Stage	Taxa number
		Orthocladius	L	S7
		Eukiefferiella	L	S8
		Thienemanniella	L	S9
		Psectrocladius	L	S10
		Heterotrissocladius	L	S11
		unrecogn. Ortho.	L	S12
	{Tanytarsini}	*Tanytarsus*	L	S13
		Rheotanytarsus	L	S14
		unrec. *Tanytarsini*	L	S15
		Stempelinella	L	S16
	{Chironomini}	*Chironomus*	L	S17
	{Chironomini}	*Paracladopelma*	L	S18
	{Chironomini}	*Phaenopsectra*	L	S19
	{Chironomini}	*Stictochironomus*	L	S20
	{Chironomini}	unrec 1st instar *Chironomini*	L	S21
	(Tanypodinae)	*Ablabesmyia*	L	S22
	(Tanypodinae)	*Thienemannimyia*	L	S23
	(Tanypodinae)	*Procladius*	L	S24
	(Prodiamesinae)	*Monodiamesa*	L	S25
	Chironomidae	unrec Chironomidae pupae	P	S26
	Chironomidae	unrec Chironomidae adult	AD	S27
	Muscidae		L	S28
	Ceratopogonidae	*Bezzia/Probezzia*	L	S29
	Empididae	*Chelifera*	L	S30
	Ephydridae	unrec. Ephydridae	L	S31
	Tipulidae	*Dicranota*	L	S32
	unrec Diptera sp1		L	S33
	unrec Diptera sp2		L	S34
	unrec Diptera	unrec Diptera pupae	PU	S35
Oligochaeta*	Naididae			S36
	Enchytraeidae			S37
	Lumbriculidae	*Lumbriculus*		S38
	unrec Oligochaeta	Earth Worm		S39
	Tubificidae	unrec Tubificidae		S40
	Tubificidae	Tubificidae eggs	eggs	S41
Nematoda***				S42
Ostracoda**				S43
Acari	Lebertiidae	*Lebertia*		S44
		unrec. *Acari*		S45

Order unless otherwise indicated[1]	Family or (Subfamily) or {tribe}	Genus	Stage	Taxa number
Oribatei	Eremaeidae	*Hydrozetes*		S46
Arachnoidea*		"spider"		S47
"Hydracarina"	Lebertiidae	*Lebertia*		S48
	Oxidae	*Gnaphiscus*		S49
Gastropoda*	Planorbidae	*Gyraulus*		S50
	Lymnaeidae	*Lymnaea*		S51
	Ancylidae	*Ferrissia*		S52
Ephemeroptera	Baetidae	*Baetis*	L	S53
	Ephemerellidae	*Ephemerella*	L	S54
Plecoptera	Capniidae	*Capnia*	L	S55
	Taeniopterygidae/ Chloroperlidae	*Taenionema/Sweltsa*	L	S56
Hymenoptera	Formicidae		AD	S57
	Trichogrammatidae		AD	S58
	Unrec. Hymenoptera l.		L	S59
Thysanoptera	Phloeothripidae		AD	S60
Hemiptera	Corixidae		NYMPH	S61
Homoptera	Aphidae		AD	S62
Collembola				S63
Hydroida	Hydridae	*Hydra*		S64
Mysidacea	Mysis (parts)			S65
	Gemmula			S66
	unrec. terr larvae			S67
Turbellaria*	Planariidae	*Polycelis*		S68
		Total benthic invertebrates		**S69**
Fish				
		Lota Lota		S70
		Cottus sp.		S72
		fish embryos		S75
Benthic Zooplankton				
Calanoida		*Diaptomus*		S76
Cyclopoida		*Cyclops*		S77
Harpacticoida		Harpacticoid		S78
Anomopoda (Cladocera)	Chydoridae	*Alona*		S79
		Chydorus		S80
	Bosminidae	*Bosmina*		S81
	Daphniidae	*Ceriodaphnia*		S82
		Daphnia		S83
		Eurycercus eggs		S84

Order unless otherwise indicated[1]	Family or (Subfamily) or {tribe}	Genus	Stage	Taxa number
		Ephippium eggs		S85
		Total benthic zooplankton		**S86**
Other Group subtotals				
Total chironomids (s1-s27)				S87
Total Diptera other than chironomids (s28-s35)				S88
Total Tubificidae (s40-s41)				S89
Total water mites (s44-s49)				S90
Total gastropods (s50-s52)				S91
Total mayflies (s53-s54)				S92
Total stoneflies (s55-s56)				S93
Total wasps (s57-s59)				S94
Other terrestrial invertebrates (s60-s62)				S95
Total Mysis (s65-s66)				S96
Richness				S97

1. other classifications are Class*, Subclass**, or Phylum***

Benthos densities reached 1,968 animals/sample or 43,727 animals$\cdot$m^{-2} in aboveground samples (Table 5). At all elevation strata, greatest benthos densities occurred on lenticulate sedge and lower densities occurred on reed canary grass and fall rye. At the high elevation mixed vegetation stratum, benthos densities on aboveground lenticulate sedge were 2.2 times greater than on reed canary grass and 2.6 times greater than on fall rye. These differences in densities between plant species were even greater at the lower elevations. Densities on all plants increased with rising elevation and increasing plant complexity (barren to mixed vegetation). Lenticulate sedge hosted 347 animals/sample (7,711 animals$\cdot$m^{-2}) at the low elevation barren site but benthos density was 1.8 times greater in the presence of a monoculture of fall rye and more than 5 times greater at the highest elevation having extensive mixed vegetation. The same vertical trend was found for zooplankton associated with the aboveground plant foliage.

Benthos densities reached 2,169 animals/sample (almost 64,000 animals$\cdot$m^{-2}) in belowground samples (Table 6), approximately 10% greater than that found on the aboveground plant biomass. At the lower elevation barren and fall rye sites, greatest benthos densities occurred on lenticulate sedge and lower densities occurred on reed canary grass and fall rye, while at the highest elevation, greatest density of 2,169 animals/sample (48,000 animals$\cdot$m^{-2}) occurred on fall rye and slightly lower densities occurred on reed canary grass and lenticulate sedge. Lowest density of 56 animals/sample (1,244 animals$\cdot$m^{-2}) was found in barren soil at the barren low elevation site. But, in the presence of plants at the other sites, barren soil hosted greater invertebrate densities reaching 813 animals/sample (18,067 animals$\cdot$m^{-2}). Plant substrata generally hosted greater densities than were found in barren soil, particularly at the high elevation site where densities on plants were 2.1 to 2.7 times that found in barren soil. Densities increased two times (reaching 1,739 animals/sample on lenticulate sedge) to more than 14 times (reaching 813 animals/sample in barren soil) between lowest and highest elevation. This vertical trend was the same as that found on aboveground substrata.

The presence of plant biomass increased the capacity of a given area of reservoir bottom to support benthic invertebrates. Data from Tables 5 and 6 were combined and summarized in Figure 5 to show the plant effect (all species combined) across elevations on total invertebrate density. At the low elevation barren stratum, the presence of plants increased invertebrate density by more than 7 times (1,244 animals$\cdot$m^{-2} increased to 9,000 animals$\cdot$m^{-2}). At the low elevation fall rye site, the presence of plants increased benthos density by almost 2 times over than in barren soil (5,178 animals$\cdot$m^{-2} increased to 9,933 animals$\cdot$m^{-2}). At the high elevation mixed vegetation site, the presence of plants increased invertebrate density again by almost 2 times over that in barren soil (18,067 animals$\cdot$m^{-2} increased to 35,089 animals$\cdot$m^{-2}).

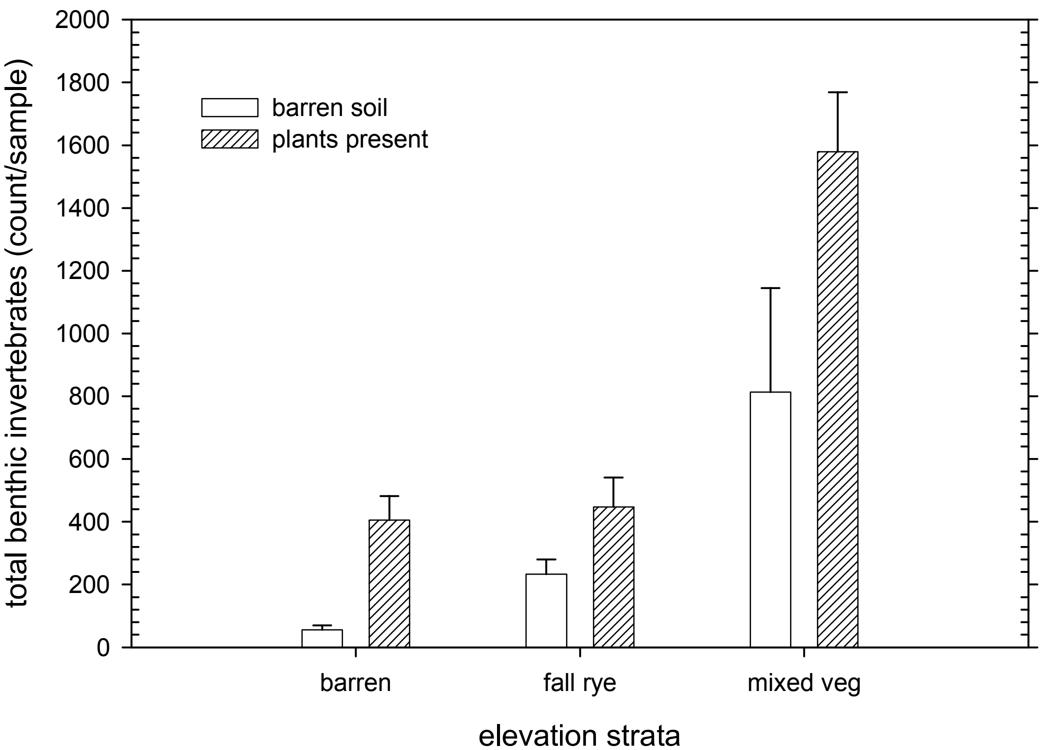


Figure 5. Mean benthic invertebrate density (±SE) found in barren soil and in association with plants at each elevation strata.

Average taxonomic richness (number of taxa) of the samples ranged from 4 to 20. More diverse communities occurred with the lenticulate sedge in aboveground samples (Table 5). In belowground samples there was no one plant species that supported more diverse invertebrate communities than the other plants across the plant – elevation combinations (Table 6). Richness in barren soil was 4 to 12 across elevations; it was 11 to 12 in fall rye samples, 9 to 14 in reed canary grass samples, and similarly it was 9 to 13 in lenticulate sedge samples.

Benthic zooplankton densities were between 16 animals/sample and 571 animals/sample in belowground material, indicating a substantial presence of zooplankton in samples at times of retrieval. Many of the zooplankton that were in belowground samples may actually have been associated with the aboveground plant foliage but settled to the soil/sediment surface when the sack was dewatered during retrieval. With this possibility, we cannot assume that zooplankton were stratified between the belowground and aboveground strata as inferred in Tables 5 and 6. Some of the zooplankton may also have been entrained in the top of the sample bag as it was retrieved through the water column. The top of the sack was closed upon retrieval, however, leaving an opening of only a few cm where the line passed through the grommets. Water would also have been displaced from the top opening during the vertical haul because the sack fabric would prevent water to pass. Under these conditions, entrainment during sample collection was likely negligible but it cannot be ignored as a possible factor confounding the zooplankton data.

Table 5. Mean count per sample of invertebrates on aboveground biomass collected from each plant species in each strata at T=2.

Order or other classification[1]	Family	Genus	Mean count of invertebrates per aboveground sample							
			Barren stratum		Fall rye stratum			Mixed vegetation stratum		
			reed canary grass	lenticulate sedge	fall rye	reed canary grass	lenticulate sedge	fall rye	reed canary grass	lenticulate sedge
Oligochaeta*	Naididae		2.3	122.0	11.0	13.3	256.3	333.0	483.3	1013.0
Oligochaeta*	Enchytraeidae		15.3	95.3	4.0	64.7	223.7	127.0	146.3	385.0
Oligochaeta*	Lumbriculidae	*Lumbriculus* sp.	0.7	8.0	1.0	0.7	3.3	4.3	6.3	15.7
Nematoda***			7.7	38.7	4.3	11.0	59.3	90.0	66.0	178.7
Ostracoda**			1.7	28.0	1.7	9.0	28.7	93.3	48.3	201.3
Hydroida	Hydridae	*Hydra* sp.	0.0	0.0	0.0	0.3	6.7	0.0	11.0	0.0
total chironomids			5.0	52.3	2.0	8.3	39.7	23.7	106.7	119.7
total other Diptera			0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.7
total Tubificidae			7.0	1.0	0.7	0.7	1.3	36.0	16.7	4.0
total water mites			0.7	0.0	0.0	0.7	4.0	0.0	0.3	1.3
total gastropods			3.0	1.3	0.3	0.3	0.3	37.7	6.0	46.3
total stoneflies			0.0	0.0	0.0	0.0	1.3	0.0	0.0	0.0
richness			11.3	14.7	7.7	8.7	13.3	13.3	17.3	20.0
Total benthic invertebrates			43.3	346.7	25.0	109.0	624.7	745.0	891.0	1967.7
Total zooplankton			1.0	8.7	2.3	1.7	15.3	6.0	32.7	133.3

1. or Class* or Subclass** or Phylum*** or other convenient taxonomic grouping

Table 6. Mean count per sample of invertebrates on belowground biomass collected from each plant species in each strata at T=2.

Order or other classification[1]	Family	Genus	Mean count of invertebrates per belowground sample											
			Barren Stratum				Fall rye stratum				Mixed vegetation stratum			
			barren	fall rye	reed canary grass	lenticulate sedge	barren	fall rye	reed canary grass	lenticulate sedge	barren	fall rye	reed canary grass	lenticulate sedge
Oligochaeta*	Naididae		2.7	8.0	42.7	42.7	10.7	11.3	0.0	65.0	240.0	796.3	426.7	362.7
Oligochaeta*	Enchytraeidae		21.3	24.0	32.0	32.0	85.3	10.7	32.0	75.7	64.0	64.0	32.0	64.0
Oligochaeta*	Lumbriculidae	*Lumbriculus*	0.0	57.0	25.0	27.7	5.3	70.7	22.3	12.0	4.3	95.7	61.3	38.0
Nematoda***			13.3	53.3	160.0	21.3	80.0	37.3	64.0	42.7	117.3	101.3	101.3	53.3
Ostracoda**			5.3	45.3	138.7	533.3	37.3	96.0	554.7	586.7	202.7	965.3	1024.0	1120.0
total chironomids			8.0	31.0	32.0	43.7	11.3	45.7	24.3	18.3	70.7	106.0	91.7	77.0
total other Diptera			0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	192.0	0.0
total Tubificidae			0.0	162.0	39.3	44.3	2.7	56.0	83.0	3.3	43.7	21.3	5.0	0.0
total water mites			0.0	5.3	0.0	0.0	0.0	0.0	0.3	10.7	42.7	0.0	0.0	0.0
total gastropods			0.0	0.0	21.7	12.3	0.0	0.0	0.3	1.0	10.7	19.3	29.7	24.3
total mayflies			0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	10.7	0.0	0.0	0.0
total Mysis			5.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	6.0	0.0	0.3	0.0
richness			4.0	11.0	9.0	9.3	6.3	12.0	9.0	11.3	12.3	11.7	14.0	12.7
Total benthic invertebrates			56.0	386.3	491.3	757.3	233.0	327.7	781.0	815.3	812.7	2169.3	1964.0	1739.3
Total zooplankton			16.0	37.3	149.3	170.7	16.0	53.3	128.0	154.7	570.7	48.0	474.7	544.0

1. or Class* or Subclass** or Phylum*** or other convenient taxonomic grouping

An important feature of the benthos community was that most animals were very small. Table 7 lists invertebrate densities by size class found among all combinations of plant species and site. Microbenthos having sizes <1 mm represented more than 80% of animal densities. In most cases microbenthos was more than 95% of those densities.

Table 7. Mean count of micro-benthos and macro-benthos on aboveground and belowground substrata between elevations.

Invertebrate group and associated substrata	Mean count of invertebrates per sample					
	microbenthos (<1 mm)			macrobenthos (>1 mm)		
	Barren Strata	fall rye strata	mixed vegetation strata	Barren strata	fall rye strata	mixed vegetation strata
aboveground benthos on sedge	332	614	1929	15	11	38
Belowground benthos on sedge	747	795	1717	11	21	22
aboveground benthos on reed canary grass	41	108	859	2	1	32
Belowground benthos on reed canary grass	480	757	1925	11	24	39
aboveground benthos on fall rye		23	725		2	20
Belowground benthos on fall rye	320	277	2112	66	50	57
Belowground benthos on barren soil	56	229	800	0	4	13

5.2.2 Invertebrate Biomass

Benthos biomass ranged from 2.4 mg/sample (0.053 $g \cdot m^{-2}$) in barren soil at the mixed vegetation site to 140 mg/sample (3.1 $g \cdot m^{-2}$) associated with fall rye at the mixed vegetation site (Figure 6). Biomass increased between T=1 (6-10 days after inundation) and T=2 (78 days after inundation) in many of the site and plant species combinations, but in some cases there was little or no change. These time effects on invertebrate biomass were examined in analyses of variance (ANOVA) run on $\log_{10}(x+1)$ transformed biomass data. Raw data were the combination of biomass on above ground and below ground biomass from the main experiment. Time series data between T=1 and T=2 were not included. A separate ANOVA was run on each combination of site and plant species (12 ANOVA's). Results in Table 8 showed that benthos biomass significantly increased between T=1 and T=2 on all plant species except reed canary grass at the high elevation mixed vegetation site. At the low elevation sites, the time effect was less apparent, being significant only with fall rye at the fall rye site and with lenticulate sedge at the barren site. These results suggest that time course development of the benthos community in association with submersed plants advanced over a longer time at the higher elevation sites hosting complex vegetation cover compared to more simple low elevation sites. Results may also suggest that community development is more restricted at the low elevation sites, reaching site-specific maximum biomass in a period of <2 weeks after inundation.

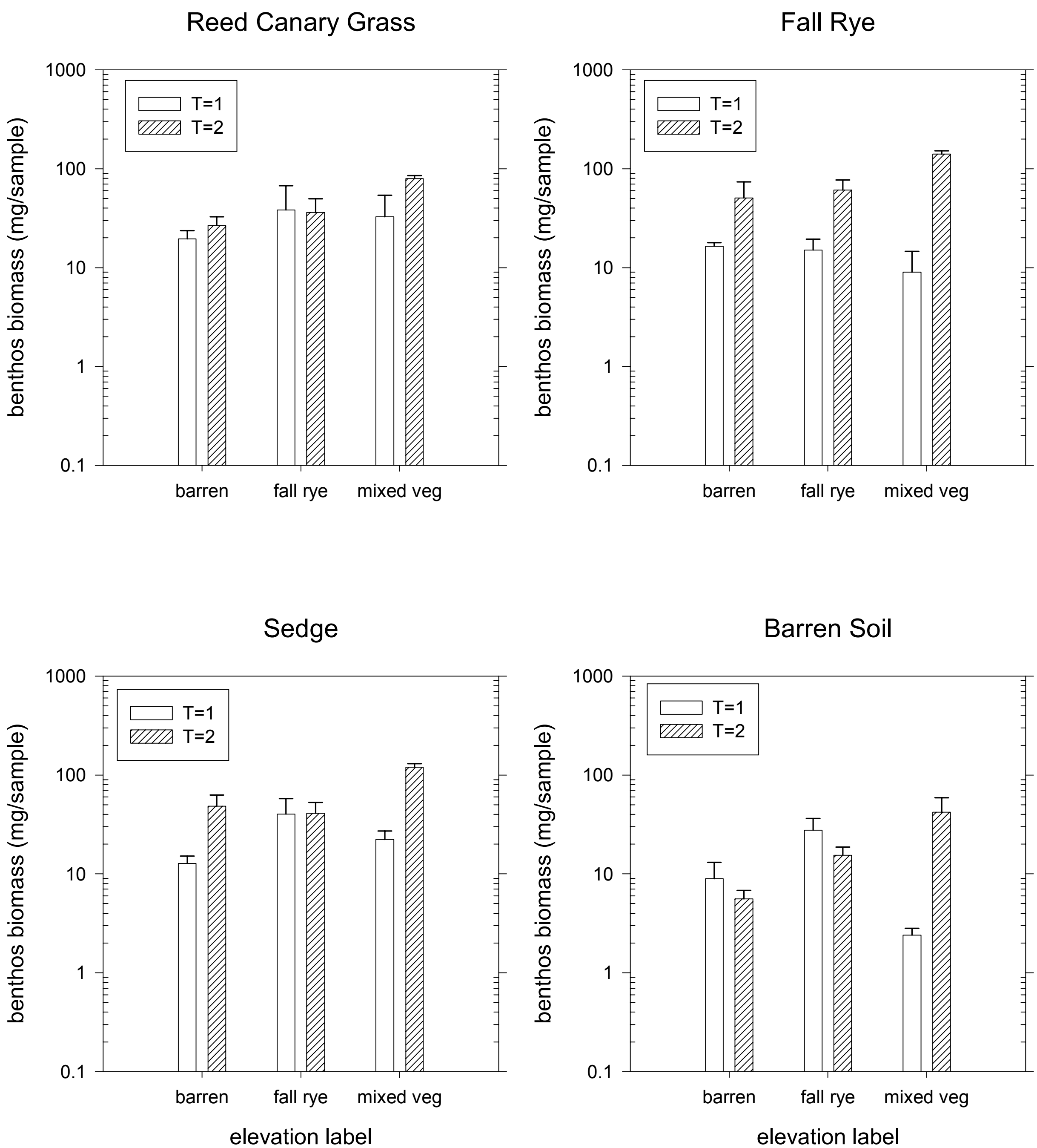


Figure 6. Mean benthos biomass (±SE) in combined above-ground and below-ground plant samples among all time and elevation combinations.

Table 8. Probabilities of time effects on benthos biomass and plant-specific benthos biomass measured on all combinations of plant species and sites. Values were determined by ANOVA on $\log_{10}(x+1)$ transformed biomass data.

Site	Plant species	time effect on benthos biomass (*p*)	Time effect on plant-specific benthos biomass (*p*)
Mixed vegetation (high elevation)	reed canary grass	0.132	0.274
	fall rye	0.008	<0.001
	sedge	0.001	0.007
	barren	0.005	
Fall Rye (low elevation with fall rye)	reed canary grass	0.604	0.936
	fall rye	0.038	0.036
	sedge	0.777	0.646
	barren	0.232	
Barren (low elevation)	reed canary grass	0.370	0.075
	fall rye	0.362	0.146
	sedge	0.043	0.027
	barren	0.578	

Plant surfaces may provide a source of nutrients as exudates (if the epiphyte matrix has damaged cuticle structure of the macrophyte) or leachates to support growth of algae and other components of the benthic biofilm on plant surfaces. That biofilm may then provide a food source that can be directly used by benthic invertebrates. Exudates or leachates from roots may also increase availability of food in the vicinity of plant roots, although literature is very scarce to determine if this is true or not. Given that some plant species may show different strategies for survival under water and other species may not survive under water, it is conceivable that the nutritional quality and quantity of plant biomass and its associated biofilm may also differ between plant species. One way to examine this “plant effect” on benthos biomass was to calculate the ratio of benthos biomass to plant biomass and track results over time. We called this term *plant-specific benthos biomass* (B_r) having units of $mg{\cdot}g^{-1}$. We calculated B_r as total mass of benthos (B) found in roots and leaves of a plant sample divided by the total mass of leaves and roots in that same plant sample (S):

$$B_r = B/S \qquad (1)$$

B_r may be sensitive to three processes associated with subaqueous survival of emergent plants. One may be species-specific differences in nutrient leaching or exudation rates. These differences may produce variation in invertebrate food quality and quantity associated with species-specific differences in nutrients supplying the epiphytic biofilm. Thus, B_r may differ between submersed plants having different nutrient leaching or exudation rates. Alternatively, loss of nutrients from a submersed plant may be negligible, in which case development of a biofilm would be related to nutrient supply from the ambient water column, not the plant substrata. In this case, B_r may be similar between samples from different plant species despite potential differences in benthos biomass between the same samples. Plants that do not survive under water will decompose, providing a direct source of organic matter and nutrients for use by bacteria, algae, and fungi that are food for detritivores. In this case, plant biomass may decline while benthos biomass increases, producing a rise in B_r over time.

Measures of time course change in plant biomass after inundation contributed to evidence of which process had greatest influence on B_r determined for benthos found in association with each of the three plant species. Figure 7 shows that fall rye decomposed after inundation, losing mass according to the model shown in Table 9. Fall rye B_r responded to a transition from standing plant biomass at time of inundation to detritus some time later. Both reed canary grass and lenticulate sedge did not lose or gain mass over time (Figure 7 and Table 9), indicating that change in B_r associated with those species was related to biofilm development on plant biomass after inundation and not to loss or gain of plant biomass over time.

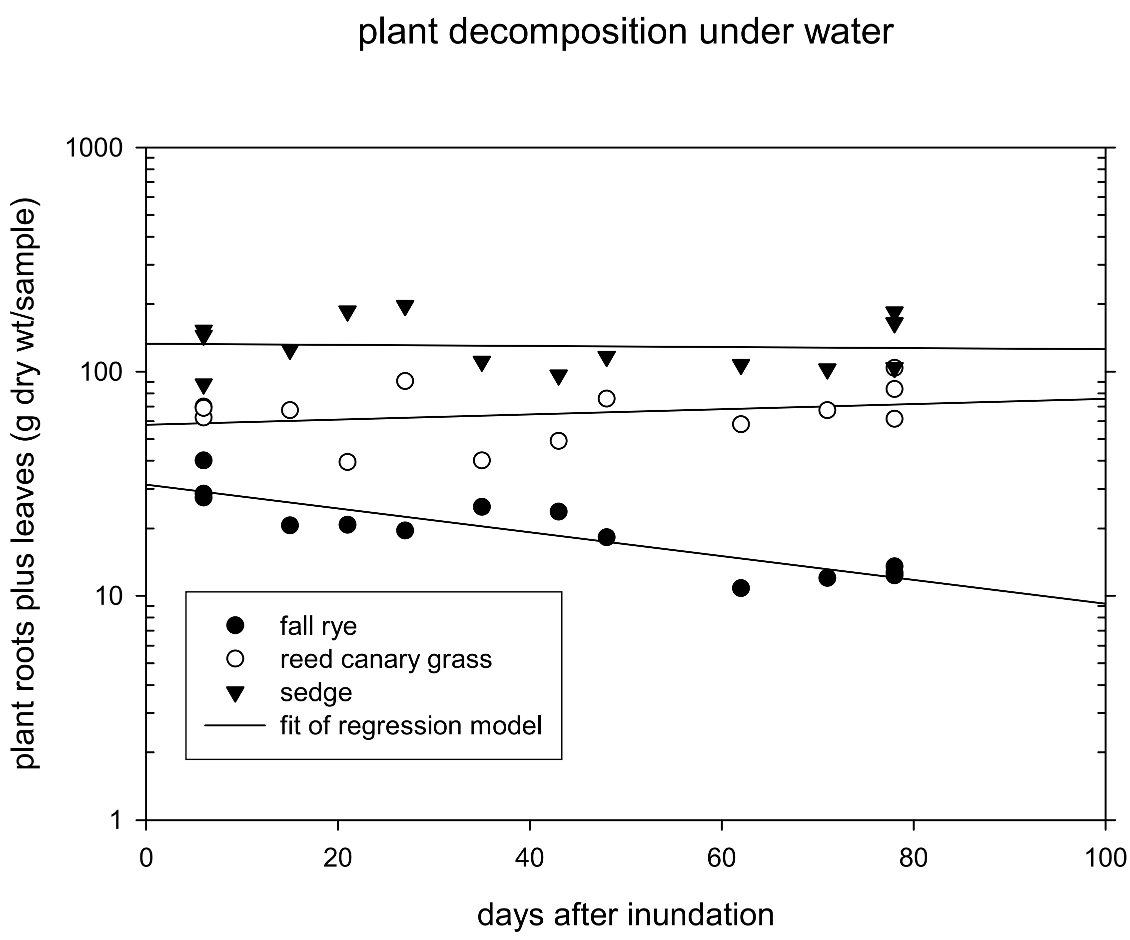


Figure 7. Time course change in plant biomass after inundation during sampling at the high elevation mixed vegetation site.

Table 9. Regression models fit to time course change in plant biomass, by species, after inundation at the high elevation mixed vegetation site.

Species	Regression equation*	r^2	*p*
fall rye	$Log_{10}(S_f+1)=1.508 - 0.005(t)$ or $S_f=(32.21 * 10^{-0.005(t)})-1$	0.78	<0.001
lenticulate sedge	No significant regression model		
reed canary grass	No significant regression model		

*S_f is biomass of fall rye

Differences in B_r between T=1 and T=2 (Figure 8) were examined by ANOVA among all combinations of plant species and elevation. A separate ANOVA was run on each combination of site and plant species to examine time effects as was done with the benthos biomass data. A Bonferroni correction to remove random effects of multiple ANOVA's was not applied and a significant probability level of p=0.05 was assigned to each analysis.

There were no significant time effects on B_r associated with reed canary grass at any elevation (p>0.08, Table 8). Since there was no change in biomass of reed canary grass after inundation (Figure 7), this result indicated no change in benthos biomass after initial colonization on reed canary grass. Similarly, there was no time effect on fall rye B_r at the barren site. But, in the presence of other plants at the fall rye site and at the high elevation mixed vegetation site, large time effects were found (p<0.04, Table 8). The difference in fall rye B_r between T=1 and T=2 was 10.7 $mg \cdot g^{-1}$ at the mixed vegetation site and up to 13 $mg \cdot g^{-1}$ at the fall rye site (Figure 8). This increase in B_r over time indicated an increase in use by benthos of fall rye substrata as decomposition proceeded. Time effects were also apparent on lenticulate sedge B_r at the barren and mixed vegetation sites (p<0.03), but differences between T=1 and T=2 were <0.7 $mg \cdot g^{-1}$ or only 5% of the time effects on fall rye B_r. Again these results indicate little biomass-specific accrual of benthos on lenticulate sedge after initial colonization. Lenticulate sedge B_r was in the range of reed canary grass B_r suggesting little change in biomass-specific use of these two substrata by benthos over time. The fact that time effects were apparent, albeit small on lenticulate sedge may suggest marginal preference of lenticulate sedge over reed canary grass by benthos over time.

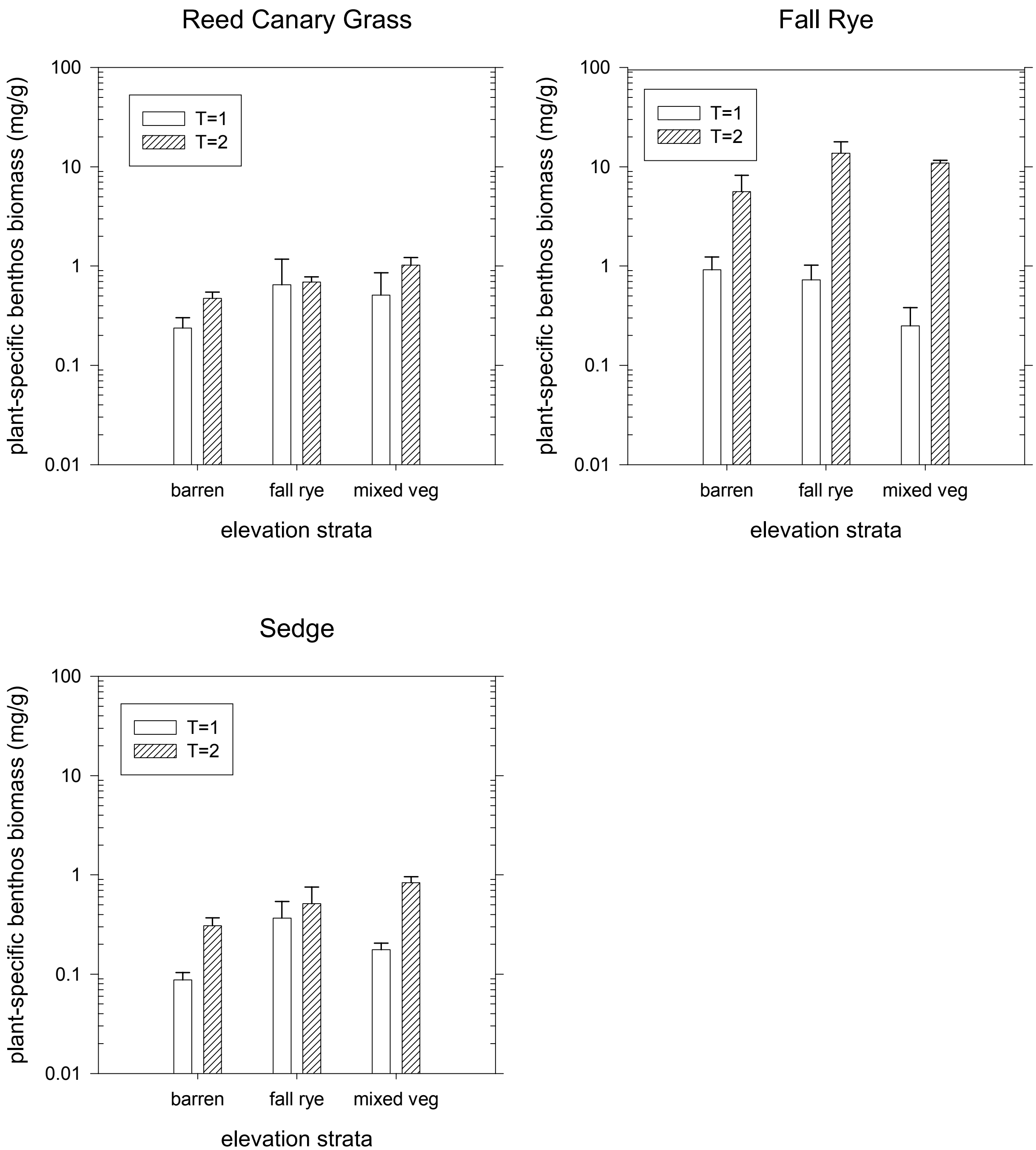


Figure 8. Average plant-specific benthos biomass (±SE) in combined aboveground and belowground plant samples among all time and elevation combinations.

Time series regressions from the high elevation mixed vegetation site supported these time effects on benthos. Significant regression models were found to describe benthos biomass accrual between T=1 and T=2 (Figure 9 and Table 10) in barren soil (p=0.003), and in association with fall rye (p<0.001) and lenticulate sedge (p=0.004). At the start of the time series, mean biomass was lowest in the absence of vegetation in barren soil samples (<4 mg/sample or <88.9 mg·m^{-2}) and greatest in association with reed canary grass (32.6 mg/sample or 724 mg·m^{-2}). No significant biomass accrual was found in association with reed canary grass (p=0.064). Although regression models were significant in describing biomass accrued in barren soil and in association with lenticulate sedge, the models only moderately fitted the data (r^2=0.53 and 0.5 respectively). Biomass increased logarithmically by approximately 10 times between T=1 and T=2 in both barren soil and in association with lenticulate sedge. A highly significant logarithmic model (p<0.001) provided a better fit to the biomass accrual on fall rye (r^2=0.67) on which mean benthos biomass increased from 9 mg/sample (200 mg·m^{-2}) at T=1 to reach 140.6 mg/sample (3,124 mg·m^{-2}) at T=2.

Accrual of plant-specific biomass showed even greater differences between plant species (Figure 10). Again no significant regression was found to describe time course accrual of plant-specific biomass on reed canary grass and only a very weak relationship was found in association with lenticulate sedge (Table 11). These results indicated that plant-specific biomass changed little or not at all over the time series between T=1 and T=2 on reed canary grass and lenticulate sedge. In contrast, a highly significant logarithmic regression (p<0.001) fit well to plant-specific biomass in association with fall rye (r^2=0.72, Table 11). Fall rye B_r started at values approaching zero but increased to values well over 10 at T=2. This result indicated that invertebrate biomass eventually exceeded plant biomass as the time series of plant decomposition progressed, a process that was not observed on lenticulate sedge and reed canary grass that remained alive while submersed.

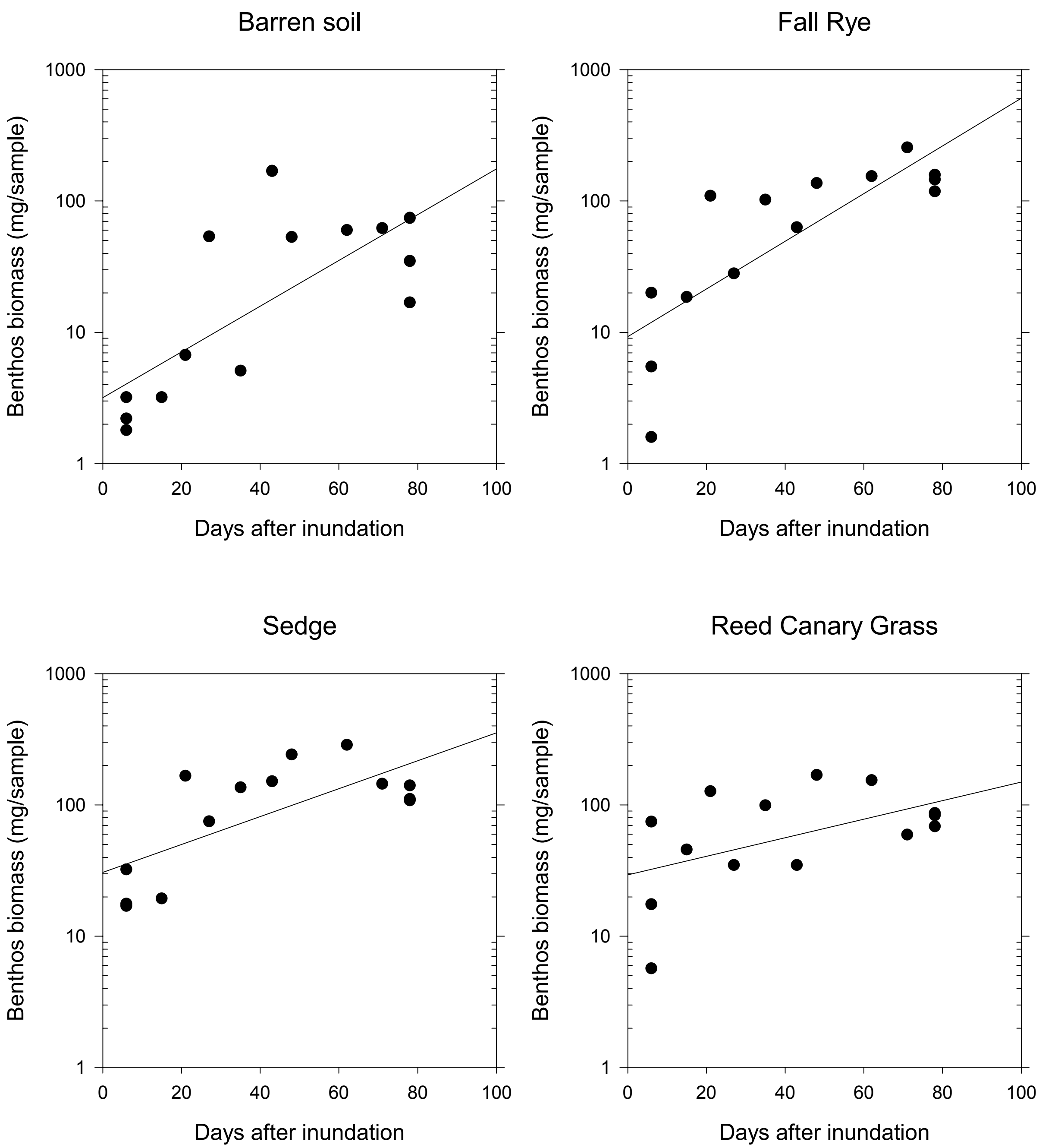


Figure 9. Scatterplot and regression line describing a linear model fit to $\log_{10}(x+1)$ transformed benthos biomass accruing in barren soil and in association with fall rye, lenticulate sedge, and reed canary grass planted at the high elevation, mixed vegetation site.

Table 10. Regression models fit to $\log_{10}(x+1)$ transformed benthos biomass on each plant species and barren soil determined over the time series between T=1 and T=2.

Species	Regression equation	r^2	p
barren soil	$Log_{10}(B+1)=0.636 + 0.016(t)$ or $B=(4.33 * 10^{0.016(t)})-1$	0.53	0.003
fall rye	$Log_{10}(B+1)=1.039 + 0.017(t)$ or $B=(10.94 * 10^{0.017(t)})-1$	0.67	<0.001
lenticulate sedge	$Log_{10}(B+1)=1.504 + 0.01(t)$ or $B=(31.92 * 10^{0.01(t)})-1$	0.50	0.004
reed canary grass	No significant regression model		

Table 11. Regression models fit to plant-specific benthos biomass on each plant species determined over the time series between T=1 and T=2.

Species	Regression equation	r^2	p
fall rye	$B_r = 0.192(t) – 1.357$	0.72	<0.001
lenticulate sedge	$B_r = 0.015(t) + 0.35$	0.3	0.04
reed canary grass	No significant regression model		

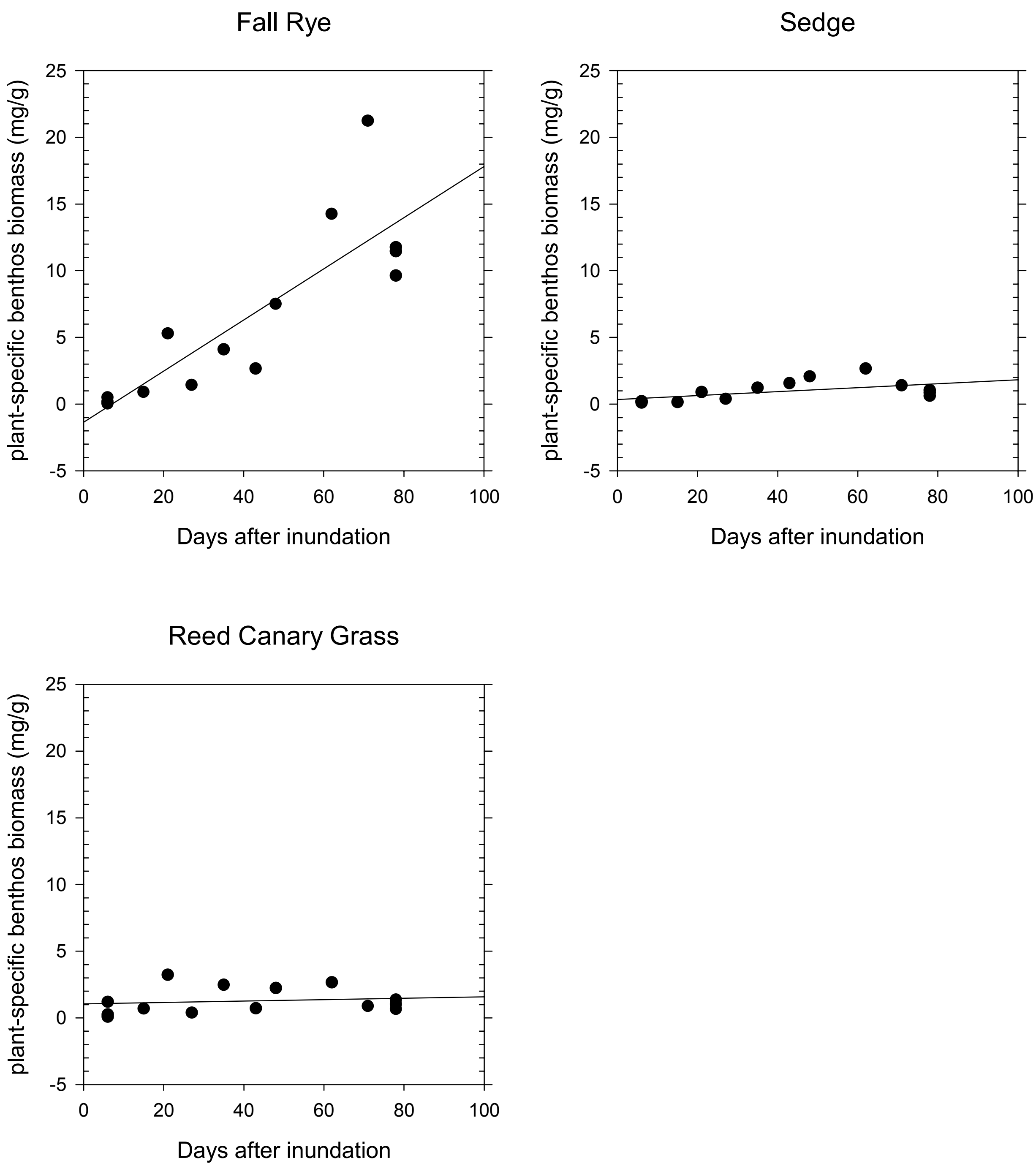


Figure 10. Scatterplot and regression lines describing a linear model fit to plant-specific benthos biomass (benthos biomass rated to plant biomass) accruing in association with each plant species planted at the high elevation, mixed vegetation site.

Elevation and plant effects on benthos biomass were examined in a two-way ANOVA (3 levels of elevation and 4 levels of plant species). Two endpoints were examined; one was $\log_{10}(x+1)$ transformed biomass found in the combination of aboveground and belowground samples and the other was plant-specific biomass determined from the same combination of aboveground and belowground samples. All data were from T=2 when maximum biomass was achieved on all substrata. No significant interaction between factors was found in either of the two ANOVA's, indicating that site and plant species effects could be examined independently. Results indicated a strong location and plant species effect on benthos biomass ($p<0.001$, Tables 12 and 13). Biomass was similar between the two low elevation sites (fall rye and barren) but it was more than two times greater at the high elevation mixed vegetation site. Biomass was significantly lower in barren soil (21 $mg \cdot g^{-1}$) than in association with any of the plant species (>47 $mg \cdot g^{-1}$). Among the plant species, benthos biomass was greatest in association with fall rye (84.1 $mg \cdot g^{-1}$) and lowest in association with reed canary grass (47.5 $mg \cdot g^{-1}$). Fall rye also supported more than 10 times the plant-specific benthos biomass than did reed canary grass or lenticulate sedge ($p<0.001$). Lenticulate sedge supported the lowest plant-specific biomass (0.55 $mg \cdot g^{-1}$). No site effect on plant-specific biomass was found ($p=0.121$), with all values ranging between 2 $mg \cdot g^{-1}$ and 5 $mg \cdot g^{-1}$).

Table 12. Mean invertebrate biomass and plant-specific invertebrate biomass (±SE) by elevation in roots and leaves of all plant samples.

Metric	Mean value among sites at T=2 in aboveground and belowground samples of all plant species (± SE)			Elevation effect (*p*)
	Mixed vegetation	Fall rye	Barren	
Benthic invertebrate biomass (mg dry wt/sample)	95.5 ± 12.5	38.4 ± 7.1	32.9 ± 8.1	<0.001*
Plant-specific benthos biomass ($mg \cdot g^{-1}$)	4.27 ± 1.68	4.98 ± 2.5	2.13 ± 1.15	0.121
*determined from $\log_{10}(x+1)$ transformed data				

Table 13. Mean invertebrate biomass and plant-specific invertebrate biomass (±SE) in roots and leaves, by plant species among all elevations.

Metric	Mean value in roots plus leaves among plant species at T=2 (± SE)				Plant species effect (*p*)
	reed canary grass	fall rye	lenticulate sedge	barren soil	
Benthic invertebrate biomass (mg dry wt/sample)	47.5 ± 9.3	84.1 ± 16.7	69.8 ± 14.0	21.0 ± 7.4	<0.001*
Plant-specific benthos biomass ($mg \cdot g^{-1}$)	0.73 ± 0.1	10.1 ± 1.86	0.55 ± 0.11	N/a	<0.001
*determined from $\log_{10}(x+1)$ transformed data					

5.3 Fish

5.3.1 Gill Net Collections

In total, 222 fish, representing nine species were captured using gill nets in September 1999 (Table 14). Species captured, listed in order of decreasing abundance in the catch included peamouth, mountain whitefish, northern pikeminnow, kokanee, largescale sucker, longnose sucker, rainbow trout, bull trout, and lake whitefish.

Sportfish contributed 40.1% to the total gill net catch. Mountain whitefish (43.8% of the sportfish catch) and kokanee (37.1% of the sportfish catch) were the most abundant sportfish species in gill net catches. Other sportfish species including rainbow trout, bull trout, and lake whitefish contributed 7.9%, 5.6%, and 5.6% to the sportfish catch, respectively.

Non-sportfish contributed 59.9% to the total gill net catch. Peamouth was the most common non-sportfish species captured in gill nets (48.9% of the non-sportfish catch). Northern pikeminnow, largescale sucker, and longnose sucker made up the remainder of the non-sportfish catch and represented 25.6%, 19.5%, and 6.0% of the non-sportfish catch, respectively.

Table 14. Total gill net catch of fish species in each of the vegetation strata sampled in Upper Arrow Reservoir, September 1999.

Fish Species	Number of Fish Caught			Total Catch
	Barren Sites (*n*=10)	Fall Rye Sites (*n*=10)	Mixed Vegetation Sites (*n*=8)	
Sportfish				
Rainbow trout	3	2	2	**7**
Bull trout	1	1	3	**5**
Kokanee	17	2	14	**33**
Mountain whitefish	10	14	15	**39**
Lake whitefish	1	2	2	**5**
Non-Sportfish				
Peamouth	13	12	40	**65**
Northern pikeminnow	4	8	22	**34**
Largescale sucker	2	5	19	**26**
Longnose sucker	0	2	6	**8**
Total All Species	**51**	**48**	**123**	**222**

The greatest number of fish (n=123) was caught in the mixed vegetation stratum (Table 14). Lesser numbers of fish were captured in the barren (n=51) and fall rye strata (n=48). Of the total sportfish catch, 40.4% were captured in mixed vegetation sites, 36.0% were captured in barren sites and 23.6% were captured in fall rye sites. For all sportfish species except kokanee, similar numbers were captured in each vegetation stratum. However, the total numbers of rainbow trout, bull trout, and lake whitefish captured were very small. Only two kokanee were captured in fall rye sites, while 14 were captured in mixed vegetation sites and 17 were caught in barren sites. Collectively, the majority (65.4%) of all non-sportfish captured by gill nets was from mixed vegetation sites. The catches of each non-sportfish species were also greatest in mixed vegetation sites. Fall rye sites contributed 20.3% and barren sites contributed 14.3% to the total gill net catch of non-sportfish.

Sampling effort was not identical in each of the vegetation strata because the duration of gill net sets varied and fewer nets were set in mixed vegetation sites than in barren or fall rye sites. As a result, comparisons of relative abundance of fish among the three vegetation strata were based on standardised CPUE data. Gill net CPUE statistics (mean, median, minimum, and maximum) for each of the vegetation strata are provided in Table 15. For all species, a wide range of CPUE values was observed; the minimum CPUE was zero for each species and the maximum for any one species (kokanee in barren sites) was 8.00 fish/net/hour. The overall average CPUE (all species and all sites combined) was 2.22 fish/net/hour and the CPUE ranged from 0.00 to 16.67 fish/net/hour. The mean gill net CPUE for all species combined was greatest in mixed vegetation sites, less in barren sites, and lowest in fall rye sites (3.53, 2.33, and 1.06 fish/net/hour, respectively). In most cases, the median CPUE value was much less than the mean CPUE, and the median was often zero. This occurred because the catch of a given species was usually very low or zero for most of the gill net sets. Exceptions to this were kokanee, mountain whitefish, northern pikeminnow, and largescale sucker in mixed vegetation sites.

Statistical comparisons of CPUE among the vegetation strata were performed for individual species if the numbers of fish captured were sufficient to warrant such an analysis. If the total number of fish captured for a particular species was 30 or greater, the CPUE data for that species were analyzed using the Kruskal-Wallis procedure (Zar 1984) to test for differences in CPUE among the different vegetation types. The Kruskal-Wallis test is a nonparametric test that is analogous to analysis of variance. Sucker species were combined for the purpose of this analysis.

Results of the Kruskal-Wallis tests for kokanee, mountain whitefish, peamouth, northern pikeminnow, and sucker spp. are provided in Table 16. Graphical representations of the distributions of CPUE values for each species in each vegetation stratum are also included in Table 16. Statistically significant ($p<0.05$) differences in CPUE among vegetation type strata were noted for kokanee, mountain whitefish, and sucker spp. Differences in CPUE of peamouth and northern pikeminnow among the different vegetation strata were not significant.

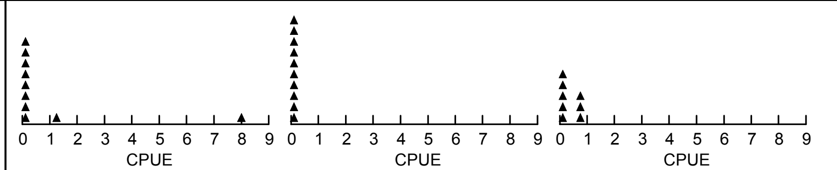
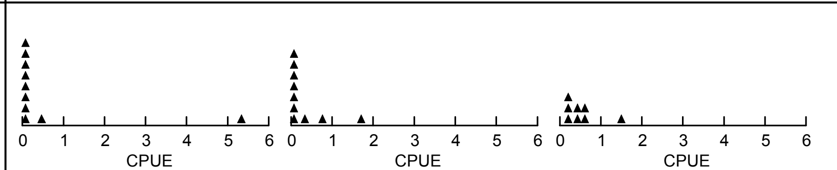
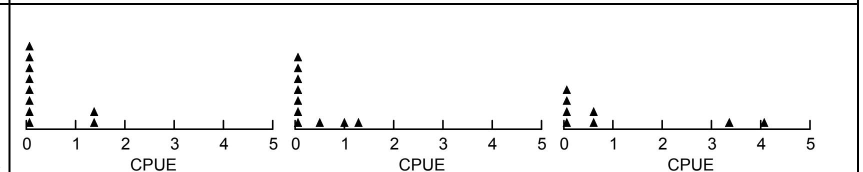
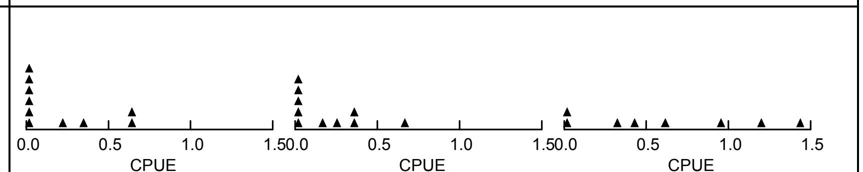
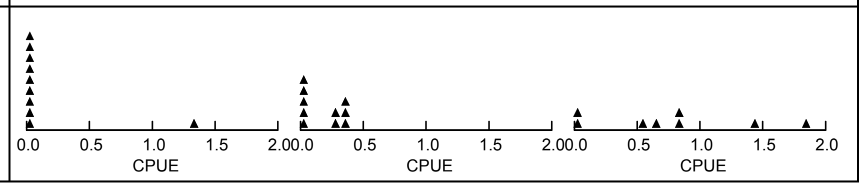
The CPUE data for kokanee, mountain whitefish, and sucker spp. were analyzed further using a multiple comparisons procedure (Dunn 1964, as described by Zar 1984) to determine what specific differences between pairs of the vegetation strata were statistically significant. The significance level, α, used for these tests was 0.10. In the case of multiple comparisons, α represented an experiment-wise error rate; it was therefore appropriate to use a value for α that was larger than is typically used in single-comparison statistical tests (Daniel 1978).

Results of the multiple comparisons tests are provided in Table 17. The CPUE of kokanee was significantly greater in mixed vegetation sites than in fall rye sites, but not significantly different between mixed vegetation and barren sites. Mountain whitefish CPUE was significantly greater in mixed vegetation sites than in either fall rye sites or barren sites but not significantly different between fall rye and barren sites. The CPUE of sucker spp. was significantly greater in mixed vegetation sites than in barren sites but not significantly different between mixed vegetation and fall rye sites.

Table 15. Catch-per-unit-effort (CPUE) of fish captured with gill nets in each of the vegetation strata sampled in Upper Arrow Reservoir, September 1999.

Fish Species	CPUE (number of fish/net/hour)															
	Barren Sites (*n*=10)				Fall Rye Sites (*n*=10)				Mixed Vegetation Sites (*n*=8)				All Sites (*n*=28)			
	Mean	Median	Min.	Max.	Mean	Median	Min.	Max.	Mean	Median	Min.	Max.	Mean	Median	Min.	Max.
Sportfish																
Rainbow trout	0.06	0.00	0.00	0.44	0.05	0.00	0.00	0.28	0.04	0.00	0.00	0.21	0.05	0.00	0.00	0.44
Bull trout	0.07	0.00	0.00	0.67	0.02	0.00	0.00	0.17	0.11	0.00	0.00	0.47	0.06	0.00	0.00	0.67
Kokanee	0.96	0.00	0.00	8.00	0.04	0.00	0.00	0.25	0.36	0.32	0.00	0.72	0.46	0.00	0.00	8.00
Mountain whitefish	0.58	0.00	0.00	5.33	0.28	0.00	0.00	1.71	0.48	0.34	0.14	1.50	0.44	0.02	0.00	5.33
Lake whitefish	0.07	0.00	0.00	0.67	0.05	0.00	0.00	0.28	0.05	0.00	0.00	0.21	0.05	0.00	0.00	0.67
Non-Sportfish																
Peamouth	0.26	0.00	0.00	1.33	0.30	0.00	0.00	1.29	1.09	0.35	0.00	4.07	0.51	0.00	0.00	4.07
Northern pikeminnow	0.19	0.00	0.00	0.67	0.18	0.08	0.00	0.67	0.62	0.52	0.00	1.44	0.31	0.19	0.00	1.44
Largescale sucker	0.13	0.00	0.00	1.33	0.11	0.00	0.00	0.34	0.60	0.60	0.00	1.85	0.26	0.00	0.00	1.85
Longnose sucker	0.00	0.00	0.00	0.00	0.05	0.00	0.00	0.28	0.17	0.00	0.00	0.72	0.07	0.00	0.00	0.72
All Species	**2.33**	**0.41**	**0.00**	**16.67**	**1.06**	**0.95**	**0.00**	**2.91**	**3.53**	**3.48**	**0.93**	**8.14**	**2.22**	**1.14**	**0.00**	**16.67**

Table 16. Results of Kruskal-Wallis tests comparing catch-per-unit-effort (CPUE) data among the different vegetation strata for kokanee, mountain whitefish, peamouth, northern pikeminnow, and sucker spp. captured with gill nets in Upper Arrow Reservoir, September 1999. Graphs on the right side of the table illustrate the distributions of CPUE values, with each triangular symbol representing one gill net collection.

Fish Species	Vegetation Strata	Rank Sum	Count	Kruskal-Wallis Statistic	P[a]	Distribution of CPUE Values: Barren Sites / Fall Rye Sites / Mixed Vegetation Sites
Kokanee	Barren	144.0	10			
	Fall Rye	106.0	10			
	Mixed Vegetation	156.0	8	6.395	0.041 *	
Mountain whitefish	Barren	118.5	10			
	Fall Rye	124.5	10			
	Mixed Vegetation	163.0	8	6.556	0.038 *	
Peamouth	Barren	123.0	10			
	Fall Rye	140.0	10			
	Mixed Vegetation	143.0	8	2.702	0.259 n.s.	
Northern pikeminnow	Barren	123.5	10			
	Fall Rye	127.5	10			
	Mixed Vegetation	155.0	8	4.383	0.112 n.s.	
Sucker spp.	Barren	102.5	10			
	Fall Rye	137.5	10			
	Mixed Vegetation	166.0	8	9.056	0.011 *	

[a] * indicates a significant difference (*P*<0.05) in CPUE among the vegetation strata; n.s. indicates differences in CPUE among the vegetation strata were not significant.

Table 17. Results of Dunn's multiple comparisons tests for differences in catch-per-unit-effort between pairs of vegetation strata for kokanee, mountain whitefish, and sucker spp. captured with gill nets in Upper Arrow Reservoir, September 1999.

Fish Species	Vegetation Strata Comparisons	Mean Rank Difference	Q Statistic[a]	Significance[b]	Significant Differences[c]			
Kokanee	mixed vegetation vs. fall rye	8.90	2.528	*	Vegetation Type:	Fall Rye	Barren	Mixed
	mixed vegetation vs. barren	5.10	1.449	n.s.	Mean Ranks:	10.60	14.40	19.50
	barren vs. fall rye	not tested	--					
Mountain whitefish	mixed vegetation vs. barren	8.70	2.384	*	Vegetation Type:	Barren	Fall Rye	Mixed
	mixed vegetation vs. fall rye	8.10	2.219	*	Mean Ranks:	11.80	12.40	20.50
	fall rye vs. barren	0.60	0.174	n.s.				
Sucker spp.	mixed vegetation vs. barren	10.50	2.983	*	Vegetation Type:	Barren	Fall Rye	Mixed
	mixed vegetation vs. fall rye	7.00	1.989	n.s.	Mean Ranks:	10.25	13.75	20.75
	fall rye vs. barren	not tested	--					

[a] Q statistics for Dunn's multiple comparisons were computed as described by Zar (1984). The critical value ($Q_{0.10,3}$) was 2.128 for all comparisons.
[b] * indicates a significant difference (P<0.10) in CPUE between the two groups; n.s. indicates the difference between the two groups was not significant.
[c] Groups overlapped by the heavy line are considered to be not significantly different.

One of the barren sites and one of the fall rye sites had abundant submersed stumps. A comparison of the total numbers of fish captured with gill nets in barren and fall rye sites with and without stumps is provided in Table 18. These data were from eight gill net sets in barren sites without stumps, two in barren sites with stumps, six in fall rye sites without stumps, and four in fall rye sites with stumps. Equal numbers of fish (n=34) were captured in each of the barren and fall rye sites without stumps. In barren sites with stumps, 17 fish were captured, and in fall rye sites with stumps, 14 fish were captured. Rainbow trout, peamouth, and northern pikeminnow were the only species captured in barren and fall rye sites with stumps, and rainbow trout were not captured in sites without stumps. However, the total number of rainbow trout captured was very small (three in barren sites with stumps and two in fall rye sites with stumps). Except for a single fish, all peamouth were captured in sites with stumps. Most of the northern pikeminnow (10 out of 12 fish) were captured in sites without stumps. Kokanee and mountain whitefish were captured only in sites without stumps.

Table 18. Total number of fish captured with gill nets in barren and fall rye sites, with and without submersed stumps, Upper Arrow Reservoir, September 1999.

Fish Species	Number of Fish Captured			
	Barren Sites Without Stumps (*n*=8)	Barren Sites With Stumps (*n*=2)	Fall Rye Sites Without Stumps (*n*=6)	Fall Rye Sites With Stumps (*n*=4)
Sportfish				
Rainbow trout	0	3	0	2
Bull trout	1	0	1	0
Kokanee	17	0	2	0
Mountain whitefish	10	0	14	0
Lake whitefish	1	0	2	0
Non-Sportfish				
Peamouth	0	13	1	11
Northern pikeminnow	3	1	7	1
Largescale sucker	2	0	5	0
Longnose sucker	0	0	2	0
All Species	**34**	**17**	**34**	**14**

Gill net CPUE statistics (mean, median, minimum, and maximum) for barren and fall rye sites with and without stumps are provided in Table 19. The distributions of CPUE values for each of these habitat categories for the six most abundant fish species captured are illustrated in Figure 11. The mean gill net CPUE for all species combined was greater in barren sites without stumps (2.47 fish/net/hour) than in barren sites with stumps, fall rye sites without stumps, and fall rye sites with stumps (1.75, 1.21, and 0.85 fish/net/hour, respectively). The mean and maximum CPUE values for mountain whitefish were greater in barren sites without stumps than in fall rye sites without stumps. The mean CPUE for peamouth was greater in barren sites than in fall rye sites.

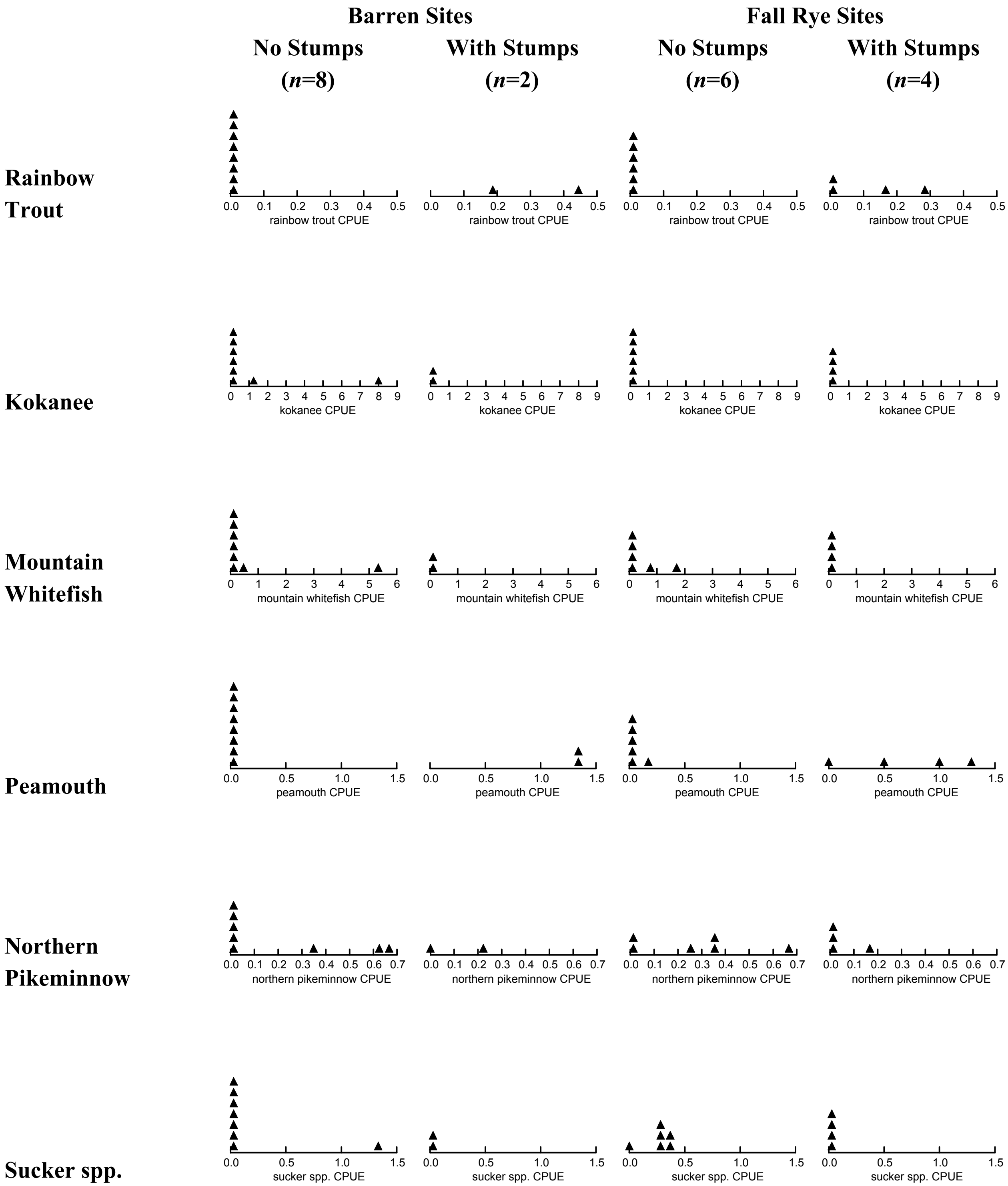


Figure 11. Distributions of catch-per-unit-effort (CPUE) values for selected fish species captured with gill nets in barren and fall rye sites, with and without submerged stumps. Each triangular symbol represents one gill net collection.

Table 19. Catch-per-unit-effort (CPUE) of fish captured with gill nets in barren and fall rye sites, with and without submerged stumps, in Upper Arrow Reservoir, September 1999.

Fish Species	CPUE (number of fish/net/hour)															
	Barren Sites Without Stumps (*n*=8)				Barren Sites With Stumps (*n*=2)				Fall Rye Sites Without Stumps (*n*=6)				Fall Rye Sites With Stumps (*n*=4)			
	Mean	Median	Min.	Max.	Mean	Median	Min.	Max.	Mean	Median	Min.	Max.	Mean	Median	Min.	Max.
Sportfish																
Rainbow trout	0.00	0.00	0.00	0.00	0.32	0.32	0.19	0.44	0.00	0.00	0.00	0.00	0.11	0.08	0.00	0.28
Bull trout	0.08	0.00	0.00	0.67	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.17	0.00	0.00	0.00	0.00
Kokanee	1.20	0.05	0.00	8.00	0.00	0.00	0.00	0.00	0.07	0.00	0.00	0.25	0.00	0.00	0.00	0.00
Mountain whitefish	0.73	0.00	0.00	5.33	0.00	0.00	0.00	0.00	0.47	0.17	0.00	1.71	0.00	0.00	0.00	0.00
Lake whitefish	0.08	0.00	0.00	0.67	0.00	0.00	0.00	0.00	0.08	0.00	0.00	0.28	0.00	0.00	0.00	0.00
Non-Sportfish																
Peamouth	0.00	0.00	0.00	0.00	1.32	1.32	1.31	1.33	0.03	0.00	0.00	0.17	0.70	0.75	0.00	1.29
Northern pikeminnow	0.21	0.00	0.00	0.67	0.11	0.11	0.00	0.22	0.27	0.30	0.00	0.67	0.04	0.00	0.00	0.17
Largescale sucker	0.17	0.00	0.00	1.33	0.00	0.00	0.00	0.00	0.19	0.22	0.00	0.34	0.00	0.00	0.00	0.00
Longnose sucker	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.08	0.00	0.00	0.28	0.00	0.00	0.00	0.00
All Species	2.47	0.32	0.00	16.67	1.75	1.75	1.50	2.00	1.21	1.12	0.00	2.91	0.85	0.92	0.28	1.29

5.3.2 Boat Electroshocking Collections

In total, 809 fish, representing 11 species, were captured and observed by boat electroshocking (Table 20). Species encountered, in order of decreasing abundance in the catch were mountain whitefish, sucker spp., redside shiner, northern pikeminnow, largescale sucker, kokanee, peamouth, rainbow trout, bull trout, lake whitefish, sculpin spp., and longnose sucker. Sportfish contributed 60.9% to the total number of fish recorded during boat electroshocking surveys.

Table 20. Total numbers of fish captured and observed by boat electroshocking in each of the vegetation strata sampled in Upper Arrow Reservoir, September 1999.

Fish Species	Number of Fish Captured and Observed			
	Barren Sites (*n*=3)	Fall Rye Sites (*n*=3)	Mixed Vegetation Sites (*n*=2)	Total Catch
Sportfish				
Rainbow trout	4	13	0	**17**
Bull trout	2	9	0	**11**
Kokanee	4	28	2	**34**
Mountain whitefish	87	189	152	**428**
Lake whitefish	1	2	0	**3**
Non-Sportfish				
Redside shiner	28	36	35	**99**
Peamouth	0	20	5	**25**
Northern pikeminnow	13	21	7	**41**
Largescale sucker	3	0	33	**36**
Longnose sucker	0	0	2	**2**
Sucker spp.[a]	12	4	94	**110**
Sculpin spp. [a]	0	3	0	**3**
All Species	**154**	**325**	**330**	**809**

[a] Denotes fish observed that were identified as sucker or sculpin spp. but could not be identified to species.

Mountain whitefish, the most abundant sportfish species encountered, contributed 86.8% to the total sportfish catch. Kokanee, rainbow trout, bull trout, and lake whitefish, the other sportfish encountered, represented 6.9%, 3.4%, 2.2%, and 0.6% of the total sportfish catch, respectively. Non-sportfish contributed 39.1% to the total number of fish recorded by boat electroshocking. Sucker spp. (34.8% of the non-sportfish catch) and redside shiner (31.3% of the non-sportfish catch) were the most abundant non-sportfish encountered. The other non-sportfish species were northern pikeminnow, largescale sucker, peamouth, sculpin spp., and longnose sucker, which represented 13.0%, 11.4%, 7.9%, 0.9%, and 0.6% of the non-sportfish catch, respectively.

The total numbers of all fish captured and observed while boat electroshocking were similar in the fall rye and mixed vegetation sites (325 and 330 fish, respectively, Table 20), with substantially fewer fish encountered in barren sites (154 fish). Although only two mixed vegetation sites were sampled by boat electroshocking, the highest total number of fish was encountered in this stratum. Three sites were sampled in each of the fall rye and barren strata, with the total number of fish encountered being greater in fall rye sites than in barren sites.

Of the total number of sportfish recorded by boat electroshocking, 48.9% were recorded in fall rye sites, 31.2% in mixed vegetation sites, and 19.9% in barren sites. Mountain whitefish occurred in all vegetation strata, but greater numbers were encountered in fall rye and mixed vegetation sites than in barren sites. The only other sportfish species encountered in mixed vegetation sites was kokanee (n=2). Greater numbers of all sportfish species were encountered in fall rye sites than in barren sites. The majority (55.7%) of non-sportfish recorded by boat electroshocking occurred in mixed vegetation sites. Fall rye sites contributed 26.6% and barren sites contributed 17.7% to the total number of non-sportfish encountered.

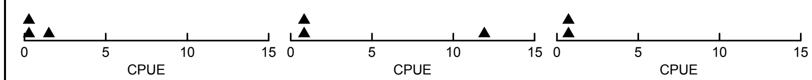
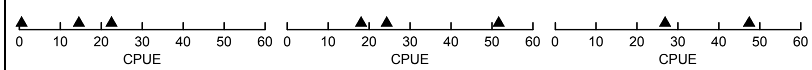
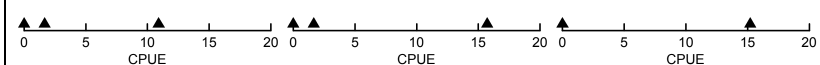
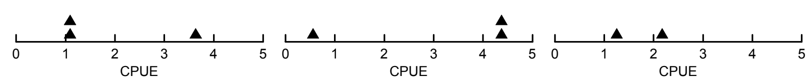
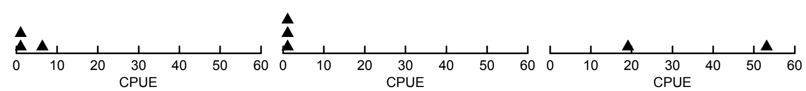
Comparisons of relative abundance of fish species among the three vegetation strata were based on CPUE values calculated as the number of fish per kilometre. The CPUE statistics (mean, median, minimum, and maximum) for sampling by boat electroshocking in each of the vegetation type strata are provided in Table 21. A wide range of CPUE values was recorded for all species. The minimum CPUE was zero for all species except mountain whitefish and northern pikeminnow, and the maximum CPUE for any one species (mountain whitefish in fall rye site) was 51.7 fish/km. The average CPUE for all fish species and all sites combined was 49.0 fish/km; the range of CPUE values was 4.5 to 86.5 fish/km. The mean CPUE for all species combined was greatest in mixed vegetation sites, lower in fall rye sites, and lowest in the barren sites (84.2, 52.0, and 22.6 fish/km, respectively).

Where the numbers of fish recorded by boat electroshocking were sufficient (i.e., n greater than 30), statistical comparisons of CPUE among vegetation strata were carried out for individual fish species using Kruskal-Wallis tests. Sucker species were combined for the purpose of this analysis. Results of the Kruskal Wallis tests for kokanee, mountain whitefish, redside shiner, northern pikeminnow, and sucker spp. are provided in Table 22. Graphical representations of the distributions of CPUE values for each species and vegetation stratum are also provided in Table 22. Differences in CPUE among vegetation strata were not significant for any of these species. These results are in contrast to those based on gill net collections, where significant differences were noted for kokanee, mountain whitefish, and sucker spp. However, the boat electroshocking sample sizes were small (three collections in each of the barren and fall rye strata and two in the mixed vegetation stratum) making it more difficult to have confidence in the outcome of the statistical tests.

Table 21. Catch-per-unit-effort (CPUE) of fish captured and observed by boat electroshocking in each of the vegetation strata in Upper Arrow Reservoir, September 1999.

Fish Species	CPUE (number of fish/km)															
	Barren Sites (*n*=3)				Fall Rye Sites (*n*=3)				Mixed Vegetation Sites (*n*=2)				All Sites (*n*=8)			
	Mean	Median	Min.	Max.	Mean	Median	Min.	Max.	Mean	Median	Min.	Max.	Mean	Median	Min.	Max.
Sportfish																
Rainbow trout	0.58	0.50	0.00	1.25	1.94	1.90	1.11	2.80	0.00	0.00	0.00	0.00	0.95	0.81	0.00	2.80
Bull trout	0.33	0.00	0.00	1.00	1.25	0.95	0.00	2.80	0.00	0.00	0.00	0.00	0.59	0.00	0.00	2.80
Kokanee	0.64	0.42	0.00	1.50	4.42	0.80	0.56	11.90	0.53	0.53	0.43	0.63	2.03	0.59	0.00	11.90
Mountain whitefish	12.52	14.55	0.50	22.50	31.32	24.29	18.00	51.67	37.13	37.13	26.88	47.39	25.72	23.39	0.50	51.67
Lake whitefish	0.14	0.00	0.00	0.42	0.32	0.40	0.00	0.56	0.00	0.00	0.00	0.00	0.17	0.00	0.00	0.56
Non-Sportfish																
Redside shiner	4.19	1.67	0.00	10.91	5.79	1.67	0.00	15.71	7.61	7.61	0.00	15.22	5.65	1.67	0.00	15.71
Peamouth	0.00	0.00	0.00	0.00	2.82	2.86	0.00	5.60	1.09	1.09	0.00	2.17	1.33	0.00	0.00	5.60
Northern pikeminnow	1.96	1.25	1.00	3.64	3.08	4.29	0.56	4.40	1.71	1.71	1.25	2.17	2.32	1.71	0.56	4.40
Largescale sucker	0.45	0.00	0.00	1.36	0.00	0.00	0.00	0.00	8.70	8.70	7.39	10.00	2.34	0.00	0.00	10.00
Longnose sucker	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.53	0.53	0.43	0.63	0.13	0.00	0.00	0.63
Sucker spp.	1.81	0.42	0.00	5.00	0.66	0.56	0.00	1.43	26.90	26.90	11.30	42.50	7.65	0.99	0.00	42.50
Sculpin spp.	0.00	0.00	0.00	0.00	0.40	0.00	0.00	1.20	0.00	0.00	0.00	0.00	0.15	0.00	0.00	1.20
All Species	**22.62**	**27.92**	**4.50**	**35.45**	**52.00**	**56.67**	**36.00**	**63.33**	**84.20**	**84.20**	**81.88**	**86.52**	**49.03**	**46.33**	**4.50**	**86.52**

Table 22. Results of Kruskal-Wallis tests comparing catch-per-unit-effort (CPUE) data among the different vegetation strata for kokanee, mountain whitefish, redside shiner, northern pikeminnow, and sucker spp. sampled by boat electroshocking in Upper Arrow Reservoir, September 1999. Graphs on the right side of the table illustrate the distributions of CPUE values, with each triangular symbol representing one boat electroshocking sample.

Fish Species	Vegetation Strata	Rank Sum	Count	Kruskal-Wallis Statistic	P[a]	Distribution of CPUE Values		
						Barren Sites	Fall Rye Sites	Mixed Vegetation Sites
Kokanee	Barren	10.0	3					
	Fall Rye	18.0	3					
	Mixed Vegetation	8.0	2	1.889	0.389 n.s.			
Mountain whitefish	Barren	7.0	3					
	Fall Rye	16.0	3					
	Mixed Vegetation	13.0	2	4.028	0.133 n.s.			
Redside shiner	Barren	12.5	3					
	Fall Rye	14.5	3					
	Mixed Vegetation	9.0	2	0.118	0.943 n.s.			
Northern pikeminnow	Barren	11.5	3					
	Fall Rye	16.0	3					
	Mixed Vegetation	8.5	2	0.597	0.742 n.s.			
Sucker spp.	Barren	10.5	3					
	Fall Rye	10.5	3					
	Mixed Vegetation	15.0	2	4.048	0.132 n.s.			

[a] * indicates a significant difference (P<0.05) in CPUE among the vegetation strata; n.s. indicates differences in CPUE among the vegetation strata were not significant.

5.3.3 Sizes and Ages of Fish Utilizing Different Vegetation Strata

The lengths and weights of fish using each of the vegetation strata are summarised in Tables 23 and 24. These tables are based on all fish measured, from both gillnetting and boat electroshocking collections. Length measurements were taken for 500 fish and weights were obtained for 483 fish. The majority of these measurements were obtained from a few of the most abundant species. Among the sportfish species, fork lengths were measured for 221 mountain whitefish, 45 kokanee, 16 rainbow trout, 13 bull trout, and 6 lake whitefish. Length measurements of non-sportfish species were taken for 71 peamouth, 61 largescale sucker, 43 northern pikeminnow, 13 redside shiner, and 11 longnose sucker. Ages were determined for 17 fish, including 14 rainbow trout and 3 bull trout.

Rainbow trout fork lengths ranged from 135 to 377 mm and weights ranged from 30 to 605 g. Mean lengths and weights were similar for rainbow trout captured from barren sites and fall rye sites. Rainbow trout captured in mixed vegetation sites were larger (mean fork length=363 mm; mean weight=498 g) than those captured in either barren sites (mean fork length=263 mm; mean weight=208 g) or fall rye sites (mean fork length=231 mm; mean weight=215 g). However, this comparison is based on a sample size of only two fish from mixed vegetation sites. Ages of rainbow trout ranged from two to seven years, and ages of fish among the three vegetation strata were not obviously different. Seven rainbow trout from barren sites included two fish of age-2, two of age-3, two of age-7, and one of age-6. Five rainbow trout collected from fall rye sites included two fish of age-2 and one fish each of age-4, age-5, and age-6. Only two rainbow trout were captured in mixed vegetation sites, one was six years old and one was seven years old.

Bull trout fork lengths ranged from 202 to 625 mm and weights ranged from 75 to 3490 g. Mean lengths of bull trout were similar in barren sites, fall rye sites and mixed vegetation sites (423, 383, and 425 mm, respectively). The difference in mean weights among sites (735 g in barren sites, 1077 g in fall rye sites, and 802 g in mixed vegetation sites) was not particularly meaningful due to the small sample size. Only 13 bull trout were collected, and both the smallest and largest fish were from fall rye sites.

Fork lengths of kokanee ranged from 68 to 343 mm and weights ranged from 5 to 410 g. The mean lengths and weights of kokanee were slightly less in fall rye sites (222 mm; 202 g) than in barren sites (275 mm; 303 g) or mixed vegetation sites (272 mm; 299 g), but the ranges of kokanee lengths and weights recorded in each of the vegetation strata were similar.

Mountain whitefish ranged from 51 to 323 mm fork length and from 5 to 330 g in weight. Mean lengths and weights of mountain whitefish were slightly less in mixed vegetation sites (139 mm; 59 g) than in fall rye sites (169 mm; 76 g) or barren sites (185 mm; 83 g).

Only six lake whitefish were captured and measured. They ranged in length from 375 to 417 mm and in weight from 665 to 1010 g. Two lake whitefish were collected from each of the vegetation strata and differences in lengths of fish using each stratum were not apparent.

Redside shiner fork lengths ranged from 53 to 78 mm and weights were all 5 g or less. All redside shiner weights were recorded as less than 5 g because the balance used was not capable of measuring weights less than 5 g. Differences in lengths of redside shiner in different vegetation strata were not apparent.

Fork lengths of all peamouth ranged from 63 to 262 mm and weights ranged from 10 to 165 g. Mean lengths and weights of peamouth were similar in the barren and fall rye sites and were only slightly less in mixed vegetation sites.

A broad range of sizes of northern pikeminnow was collected. Fork lengths ranged from 96 to 516 mm and weights ranged from 15 to 1590 g. Mean lengths and weights of northern pikeminnow were less in mixed vegetation sites than in either fall rye or barren sites.

Largescale sucker collected also represented a broad range of sizes. Fork lengths ranged from 111 to 489 mm and weights ranged from 15 to 1525 g. The smallest mean lengths and weights of largescale sucker were in fall rye sites and the largest were in mixed vegetation sites. However, a broad range of sizes was present in each of these vegetation strata and most of the largescale sucker (52 of 61 fish) were collected from mixed vegetation sites.

Only 11 longnose sucker were collected. Fork lengths ranged from 242 to 384 mm and weights ranged from 180 to 616 g. Although longnose sucker were larger in fall rye sites than in mixed vegetation sites, this observation was based on very small sample sizes. Longnose sucker were not captured in barren sites.

Table 23. Fork lengths of fish using each of the vegetation strata, based on data from gill net sampling and boat electroshocking in Upper Arrow Reservoir, September 1999.

Fish Species	Fork Length (mm)																			
	Barren Sites					Fall Rye Sites					Mixed Vegetation Sites					All Sites				
	Mean	Media	Min.	Max.	*n*	Mean	Media	Min.	Max.	*n*	Mean	Media	Min.	Max.	*n*	Mean	Median	Min.	Max.	*n*
Sportfish																				
Rainbow trout	263	268	165	372	7	231	219	135	359	7	363	363	349	377	2	262	274	135	377	16
Bull trout	423	423	379	467	2	383	353	202	625	8	425	481	300	494	3	399	450	202	625	13
Kokanee	275	301	76	325	20	222	295	68	326	9	272	300	70	343	16	263	298	68	343	45
Mountain whitefish	185	181	73	323	38	169	156	55	299	108	139	132	51	272	75	161	153	51	323	221
Lake whitefish	407	407	398	415	2	406	406	394	417	2	389	389	375	402	2	400	400	375	417	6
Non-Sportfish																				
Redside shiner	64	65	57	68	4	59	59	57	60	3	65	62	53	78	6	63	60	53	78	13
Peamouth	197	199	160	260	13	191	183	160	238	13	172	175	63	262	45	180	183	63	262	71
Northern pikeminnow	312	285	195	516	11	278	261	185	422	8	233	235	96	316	24	261	254	96	516	43
Largescale sucker	343	317	279	444	5	302	347	111	402	4	384	394	118	489	52	375	384	111	489	61
Longnose sucker	--	--	--	--	--	365	365	347	384	3	298	299	242	351	8	316	308	242	384	11

Table 24. Weights of fish using each of the vegetation strata, based on data from gill net sampling and boat electroshocking in Upper Arrow Reservoir, September 1999.

Fish Species	Weight (g)																			
	Barren Sites					Fall Rye Sites					Mixed Vegetation Sites					All Sites				
	Mean	Median	Min.	Max.	*n*	Mean	Median	Min.	Max.	*n*	Mean	Median	Min.	Max.	*n*	Mean	Median	Min.	Max.	*n*
Sportfish																				
Rainbow trout	208	148	55	470	6	215	130	30	605	7	498	498	445	550	2	250	220	30	605	15
Bull trout	735	735	475	995	2	1077	493	75	3490	8	802	998	229	1180	3	961	825	75	3490	13
Kokanee	303	330	5	410	21	202	290	5	380	8	299	340	5	410	16	284	325	5	410	45
Mountain whitefish	83	65	5	305	38	76	40	5	330	103	59	25	5	270	75	71	40	5	330	216
Lake whitefish	803	803	795	810	2	915	915	820	1010	2	700	700	665	735	2	806	803	665	1010	6
Non-Sportfish																				
Redside shiner	5	5	5	5	4	5	5	5	5	3	5	5	5	5	6	5	5	5	5	13
Peamouth	93	100	50	105	6	85	74	50	165	13	74	70	10	160	45	78	73	10	165	64
Northern pikeminnow	422	245	85	1590	11	358	295	65	965	6	164	163	15	376	24	262	205	15	1590	41
Largescale sucker	505	375	275	995	5	370	430	15	665	3	771	783	20	1525	52	728	724	15	1525	60
Longnose sucker	--	--	--	--	--	596	596	575	616	2	339	333	180	515	8	390	363	180	616	10

5.3.4 Remote Underwater Video Observations

Remote underwater video observations were conducted at three locations in Upper Arrow Reservoir, one in each of the vegetation strata. The durations of RUV observations were approximately 60 minutes in the barren site, 72 minutes in the fall rye site, and 52 minutes in the mixed vegetation site. Only nine fish were observed and those observations are documented in Table 25, which identifies the location of the observation and the time on the video tape (supplied separately) for each fish observation.

Table 25. Fish observed at remote underwater video sites in Upper Arrow Reservoir, September 1999.

Site	Date	Time on Tape	Comments
UVBR0-S	22-Sep	10:00:00PM-11:00:05PM	beginning and end of site footage
		10:15:50PM	possible fish at bottom left of screen
		10:19:16PM	unidentified fish crosses screen from right to left
		10:48:05PM	unidentified fish at vertical movement on right side of screen
UVFR1	23-Sep	7:48:40PM-9:00:55PM	furrows and some stubble from fall rye are visible
		7:57:23PM	whitefish at bottom of screen
		8:34:16PM	whitefish at bottom of screen
		8:34:30PM	unidentified fish at bottom right corner of screen
		8:36:20PM	unidentified sucker at bottom of screen
		8:52:10PM	longnose sucker crosses screen from right to left
		8:55:23PM	largescale sucker at bottom right corner of screen
UVMV1	22-Sep	11:24:30PM-12:15:55AM	good visual documentation of mixed vegetation and algae growing on it; fish were not observed

5.4 Fish Stomach Contents

Stomachs from 15 rainbow trout and 3 bull trout were examined to determine the composition of food that was ingested in the study area.

Close to 80 different taxa were found in the 18 stomachs. Adults stages of terrestrial and aquatic were present including caddisflies, moths (Lepidoptera), true flies of terrestrial and aquatic origin, terrestrial and aquatic beetles, aphids, two families of ants including carpenter ants, mites, other wide ranging aquatic and terrestrial insects, and zooplankton. The complete taxonomic list of stomach contents is provided in Table 26. None of the most abundant and common invertebrates that were found in aboveground and belowground material from the outplanting experiment (oligochaete worms, nematodes and ostracods) were encountered in fish stomachs.

Table 26. List of fish food organisms encountered in stomach contents analysis of fish caught in gill net and electroshocking sampling.

Order or Suborder	Family or Genera	Habitat	Stage*	sp#
Trichoptera	Unr. Trichoptera	aquatic	L	sp1
	Unr. Trichoptera	aquatic	PU	sp2
	Unr. Trichoptera	aquatic	AD	sp3
Lepidoptera	Tortricidae	Moths (terrestrial)	AD	sp4
	Unr.Lepidoptera	Moths (terrestrial)	AD	sp5
	larvae		L	sp6
Diptera	Anthomyidae	terrestrial	AD	sp7
	Asilidae	terrestrial	AD	sp8
	Bibionidae	terrestrial	AD	sp9
	Ceratopogonidae	terrestrial	AD	sp10
	Chironomidae	aquatic	AD	sp11
	Chironomidae	aquatic	EM	sp12
	Chironomidae	aquatic	PU	sp13
	Chironomidae	aquatic	L	sp14
	Dryomyzidae	terrestrial	AD	sp15
	Empididae	terrestrial	AD	sp16
	Heleomyzidae	terrestrial	AD	sp17
	Muscidae	terrestrial	AD	sp18
	Sarcophagidae	terrestrial	AD	sp19
	Sciomyzidae	terrestrial	AD	sp20
	Syrphidae	terrestrial	AD	sp21
	Tachinidae	terrestrial	AD	sp22
	Tephritidae	terrestrial	AD	sp23
	Tipulidae	terrestrial	AD	sp24
Coleoptera	Buprestidae	terrestrial (on surface of plants)	AD	sp25
	Carabidae	terrestrial (on surface of plants)	AD	sp26
	Cerambycidae	horned beetles	AD	sp27
	Chrysomelidae	terrestrial	AD	sp28
	Coccinellidae	terrestrial	AD	sp29
	Cucujidae	terrestrial	AD	sp30
	Curculionidae	terrestrial	AD	sp31
	Dytiscidae	aquatic	AD	sp32
	Elateridae	semi-aquatic	AD	sp33
	Melandryidae	terrestrial	AD	sp34
	Phalacridae	terrestrial	AD	sp35
	Scarabidae	terrestrial	AD	sp36
	Scolytidae	terrestrial	AD	sp37

Order or Suborder	Family or Genera	Habitat	Stage*	sp#
	Staphylinidae	semi-aquatic	AD	sp38
	Tenebrionidae		AD	sp39
Hymenoptera	Andrenidae	terrestrial	AD	sp40
	Apidae	terrestrial	AD	sp41
	Braconidae	aquatic	AD	sp42
	Chalcididae	aquatic	AD	sp43
	Diprionidae	aquatic	AD	sp44
	Formicidae(Ants)	terrestrial	AD	sp45
	Formicidae(Carpenter Ants)	terrestrial	AD	sp46
	Ichneumonidae	terrestrial	AD	sp47
	Pompilidae	terrestrial	AD	sp48
	Proctotrupidae	aquatic	AD	sp49
	Scollidae	terrestrial	AD	sp50
	Sphecidae	terrestrial	AD	sp51
	Tenthredinidae	terrestrial	AD	sp52
	Vespidae	terrestrial	AD	sp53
Hemiptera	Achilidae	terrestrial	AD	sp54
	Aphididae	terrestrial	AD	sp55
	Cercopidae	terrestrial	AD	sp56
	Cicadellidae	terrestrial	AD	sp57
	Cicadidae	terrestrial	AD	sp58
	Cixiidae	terrestrial	AD	sp59
	Coreidae	terrestrial	AD	sp60
	Corixidae	aquatic	AD	sp61
	Gerridae	aquatic	AD	sp62
	Hebridae	aquatic	AD	sp63
	Membracidae	terrestrial	AD	sp64
	Miridae	terrestrial	AD	sp65
	Pentatomidae	terrestrial	AD	sp66
	Rhopalidae	terrestrial	AD	sp67
	Scutelleridae	terrestrial	AD	sp68
Neuroptera	Hemerobiidae	terrestrial	AD	sp69
	Corydalidae	terrestrial	AD	sp70
	Raphidiidae	terrestrial	AD	sp71
Ephemeroptera	unrec. Ephemeroptera	aquatic	AD	sp72
Odonata(Zygoptera)		aquatic	AD	sp73
Odonata(Anisoptera)		aquatic	AD	sp74
Orthoptera	Gryllacrididae	crickets	AD	sp75
	Acrididae	crickets	AD	sp76
Aranae	Araneidae	terrestrial		sp77

Order or Suborder	Family or Genera	Habitat	Stage*	sp#
	Salticidae	terrestrial		sp78
	Tetragnathidae	terrestrial		sp79
Cladocera	Daphnia	aquatic		sp80
Cladocera	Eurycersus	aquatic		sp81
Copepoda	Diaptomus	aquatic		sp82
		Aquatic subtotal		sp83
		Terrestrial subtotal		sp84
		Total		sp85

*codes are L (larvae), PU (pupae), AD (adult), EM (emerging)

Counts of individual food items, by taxa, are listed in Appendix C. Most taxa occurred incidentally, however, the Muscidae (terrestrial flies) were consistently found in low numbers and the ants were found in high numbers in most rainbow trout. *Daphnia* sp. was found in high numbers in four of the 15 rainbow trout. In contrast, stomachs from the three bull trout were empty except for one fish that had one chironomid pupae in its stomach.

While the incidence of terrestrial and aquatic invertebrates in stomachs indicated feeding in the water column and on the water surface, the larger number of terrestrial taxa in most rainbow trout stomachs suggested they were feeding mostly at the water surface, taking adult invertebrates caught in the water surface tension. There was no evidence of feeding on taxa common to substrata and abundant in vegetated strata of the flooded drawdown zone.

5.5 Creel Survey

The low relative catch rates of rainbow trout and bull trout using gill nets and electroshocking techniques in the fish survey raised questions about the real abundance of these sport fish and the real size of the fishery that they support. Based on local information at the start of the project that an active rainbow fishery was present in the Revelstoke Reach, there was anticipation that capture rates from gill netting and electroshocking would be very high. The fact that large numbers of rainbow trout were not found in the fish sampling suggested that rainbow trout abundance and the fishery was not as large as originally perceived.

The creel survey revealed that the size of the fishery was indeed very small (Appendix C). A total of 63 responses were received from the card distribution but these came from only 8 anglers. Other inquiries through Brian Gadbois (BC Hydro, pers. comm.) and local anglers who were consulted as part of the selection of fish sampling sites, confirmed that only a few anglers were active in the Revelstoke Reach. During sampling activities for this project, field crews reported few and on many days no anglers in the study area. It appeared that the 8 respondents in the creel survey might have made up most of the active anglers. All were expert fly fishers and members of the local fly fishing club. There did not appear to be a fishery in Revelstoke Reach from large numbers of participants having wide ranging skills.

Participating anglers achieved average catch rates of 1.06 fish/rod hr. with a range of no catch to 4.29 fish/rod hr (Appendix C). The high catch rates were achieved by fishing specific "feed lines" that were laminar concentrations of particles on the water surface that were formed at the boundary layer between different water flows (e.g. between slack water margins and the faster thalweg). All fish caught by anglers were reported to have only terrestrial organisms in their stomachs, a consequence of feeding off the water surface at the various "feed lines".

6.0 DISCUSSION

6.1 General Conclusions

The factorial design used in this study was very effective in showing that vegetation establishment can increase the areal biomass of benthic invertebrates by two to four times over that found in barren soils. The submersed vegetation greatly increased the areal extent of substrata for colonization by benthos, allowing a moderately diverse and abundant fauna to flourish. Results clearly showed that while the simple presence of plants increased benthic invertebrate biomass, invertebrates favoured dead and decaying plant matter (fall rye) over submersed living plants (lenticulate sedge and reed canary grass). We show later in this discussion that the plant-benthos link was mediated by the epilythic biofilm in which benthic diatoms were a major component. Direct feeding on dead and decaying plant matter was a major process contributing to the association between benthos and fall rye. It was here that further links to the aquatic ecosystem appeared truncated. Sucker species that are mainly detritivous feeders may have responded to increased benthos in association with dead and decaying fall rye but we could find no link between the plant – benthos association and sport fish that are mainly visual predators. All sportfish were eating mainly terrestrial invertebrates that landed on the water surface. There was no evidence of these fish eating taxa found in association with the plant substrata. Later in this discussion we argue that one reason for this outcome was that benthos were generally not available to visual feeding habits of those species. In this respect, the establishment of vegetation in the drawdown zone of Revelstoke Reach greatly increased the capacity of the reach to host a diverse and abundant benthic community but it did not directly lead to an equal change in abundance of sportfish.

Notwithstanding this finding, we cannot ignore the fact that a small fishery is now present in the reach where it was not present before vegetation establishment. Clearly, cover is available in shallow habitat for fish to use as they mainly feed on surface organisms. An abundance of terrestrial invertebrates may use the vegetation in the spring and become inundated with rising water. These invertebrates may not be directly associated with plant substrata after flooding (and thus not found in our samples) but may provide an abundance of food for sportfish in the water column and on the water surface when the water surface elevation is rising. Detection of this process was not included in our experimental design but may be an important factor explaining the presence of surface-feeding sportfish and the presence of a fishery based mainly on fly gear.

Fish may move in and out of vegetation cover, potentially confounding our ability to distinguish effects of location on fish presence, absence, and abundance. If this project is pursued further, the focus must clearly be placed on improving ways to quantitatively resolve this link between the strong association of benthos and plants with higher trophic levels. One technique that can provide insight into the extent of any fish movement is to radio tag several fish and examine movements by radio tracking over summer months. This approach could substantially improve insight into fish use of discrete elevation and plant substrata. Other techniques such as tracking stable isotopes between trophic levels may also be useful in showing clear links or lack of links in the food web.

A substantial benefit of this study is that we now have functional responses describing plant decomposition and benthos accrual. We also have very good estimates of plant-specific benthos biomass and several measures of benthos abundance. Along with descriptions of the algal biofilm and other very good descriptive data, all these endpoint measurements are suitable for direct input to simulation modeling. This modeling is the next phase of the existing project. It will help in showing spatial and temporal dynamics of vegetation establishment and the associated benthic community in Revelstoke Reach. It may also be used to examine time course change in carbon flux in Revelstoke Reach. Output from this modeling will be a valuable tool to explore the benefits of similar planting treatments in other large reservoirs managed by BC Hydro and other power utilities.

Some of the field techniques could be improved if this type of study is repeated. The vertical retrieval of outplanted samples from a boat was logistically simple but it may have caused some silt resuspension and settlement on plant substrata. While sedimentation of silt and glacial flour, particularly from the Illecillewaet River was one source of deposits on substrata that is a natural occurrence in Revelstoke Reach, some disturbance of sediment around the submersed sack as it was pulled free of the bottom potentially added to particles settling on leaf substrata. Particle settlement made the biofilm analysis particularly difficult and likely introduced errors in that analysis. Certainly, cell densities were underestimates of actual values.

One way to improve on the technique would be to sample using SCUBA. Although diver movement may also cause unwanted disturbance of silt substrata, it may be possible to minimize this problem with a carefully designed sampling protocol. If SCUBA is not possible, use of a different type of sampling container (e.g rigid walls) may avoid bottom disturbance during sampling. In this way, the same retrieval technique employed in this study could again be used.

6.2 Biofilm Observations

Average diatom densities measured at the mixed vegetation site were extremely low compared to densities reported in other rivers/streams and lake littoral zone communities in BC. For example, densities of diatoms in littoral zones of ultra-oligotrophic coastal lakes are 30-40,000 cells/cm^2, and in oligotrophic streams and lakes they can be 78,000 to >1,000,000 cells/cm^2 (Stockner and Shortreed 1976, Shortreed and Stockner 1978). In dimictic lakes on the Canadian Shield, littoral densities can be 40,000 to 300,000/cm^2, and in more eutrophic situations, e.g. Lake Winnipeg, densities of periphytic diatoms are reported to be >3 million/cm^2 (Stockner and Armstrong 1971, Evans and Stockner 1972).

Given that densities reported on leaves in this study were <18,000 cells/cm^2 and most were <6000 cells/cm^2, a question is raised as to why densities were so low. Nutrient concentrations were low but not unlike other oligotrophic rivers and lakes that can support higher periphyton densities. Heavy siltation/sedimentation of the upper surface of the blades of all three plant types was possibly from sediment transport from inflow rivers or from the actual process of sample recovery as mentioned above (Section 6.1). Turbidity caused by sediment transport may severely reduce available light, limit growth rates, and produce constant scour. Nearly all samples from the mixed vegetation stratum contained a heavy burden of silt-sized particles. Fall rye samples were particularly affected by the sediment burden. They appeared to lack sufficient strength in stem and blade architecture to remain upright, although much of this structural failure was due to decomposition of the plants under water. Epipelic (sediment surface living) diatoms may be rapidly occluded by clay and silt and become light limited. In contrast, lenticulate sedge and reed canary grass were found to have the stem strength to remain upright after inundation, mainly because they remained alive under water. Although these plants also received and retained some burden of clay and silt, accumulations appeared less than that found on the fall rye. In this respect, the reed canary grass and lenticulate sedge provided a better substratum for periphyton colonization than fall rye.

Another explanation for low cell densities is grazing pressure from benthic invertebrates. We have shown that high densities of aquatic insect larvae, naidid and enchytrid worms, nematodes, and ostracods plus a wide diversity of other benthic taxa were present in association with plant substrata. Densities on plant leaves at the mixed vegetation site were up to 47,000 animals/m^2, which is higher than densities commonly found below the sediment – water interface in oligotrophic lakes. All of the common taxa found on the plants use surface biofilms as a food resource, potentially inducing a grazing pressure that may strongly limit the accrual of algal, bacterial, and fungal biomass on the leaf surfaces.

Diatom cells did not become measurable on reed canary grass blades until the last week in July. At that time, either siltation (turbidity) lessened and growth could proceed, or approximately 4 weeks was required before interactions between settlement, growth, and grazing produced measurable cell densities. The same can be said for lenticulate sedge but to a far lesser extent. Given that periphyton accrual can proceed at much faster rates on inert substrata in nutrient-deficient systems (Perrin et al. 1987, Bothwell 1989), the potential influence of silt scour, grazing by the very dense invertebrate fauna or even allelopathic inhibition of colonization and growth may have been important determinants of observed periphyton cell densities on leaf surfaces.

6.3 Factors Determining Benthos Abundance and Biomass

A fundamental reason why invertebrates are associated with plant substrata is to acquire food (Cummins and Merritt 1996). In Revelstoke Reach, aboveground plant surfaces greatly increased the area of substrata for colonization and development of a biofilm and benthic invertebrates. In this study, biomass of invertebrates on the leaf surfaces added to biomass found in belowground soil and sediment. We found that submersed vegetation present at the high elevation site increased benthic invertebrate biomass over that found in submersed barren soil at the lowest elevation site at the end of 78 days under water. Mean invertebrate biomass was 33 mg/sample (733 $mg \cdot m^{-2}$) at low elevations where vegetation was absent, while it was an average of 96 mg/sample (2,133 $mg \cdot m^{-2}$) in association with submersed vegetation at higher elevations.

In nutrient-deficient aquatic ecosystems, like Arrow Lakes Reservoir, soluble phosphorus concentration that limits productivity in the water column is typically less than a part per billion and this was true in the Revelstoke Reach. Similarly, Pieters et al. (1998) reported soluble reactive phosphorus concentrations of <1 $\mu g \cdot L^{-1}$ and average total phosphorus concentrations of 4.8 $\mu g \cdot L^{-1}$ in Arrow Reservoir in 1997. These values are typical of ultra-oligotrophic waters and were part of an assessment by Pieters et al. (1998) that led to nutrient addition to the northern basin of Arrow Lakes for restoration of kokanee populations through increased production of zooplankton.

In contrast, food quality for invertebrates on substrata underlying nutrient-deficient waters can be relatively high. Burkholder (1996) cited evidence that substrata, including leaves of plants, provide an interface for concentration of charged and neutral particles. On this surface, the biofilm typically consists of a three dimensional array of hydrated glycocalyx and other mucopolysaccharide materials that are secreted by colonizing algae and bacteria. At our sites in Revelstoke Reach, very fine sediment potentially originating as glacial flour from the Illecillewaet River was also associated with plant substrata. A biofilm can develop in association with those sediment particles (Lock 1994) that can settle on leaf surfaces. The biofilm can sequester nutrients and dissolved organic matter (Burkholder

1996, Wetzel 1983) via uptake and adsorption processes (Maki and Hermansson 1994) and physically and chemically isolate the surface biofilm from the overlying water column. Uptake of nutrients by the biofilm can be effective in lowering concentrations of several nutrients, including phosphorus, in water transported through areas of macrophyte abundance (Wetzel 1983). Including direct uptake by the macrophytes, this process contributes to effective use of planted macrophytes as a treatment for lowering phosphorus concentrations in nutrient-rich waters (Kadlec and Knight 1996). Dissolved nutrients required to support the biofilm may originate from the water column but cellulolytic bacteria that are part of the surface biofilm can also dissolve the cuticle of host plants, causing additional nutrients to be available to support metabolic needs of the epiphytes (Burkholder 1996). Benthic invertebrates can substantially damage protective cuticle of plant substrata using shredding, boring, and mining feeding strategies (Wallace and Anderson 1996) that result from use of specialized mouth parts for acquiring food (Cummins and Merritt 1996). While some invertebrates directly feed on plants (e.g. some beetles, aquatic Lepidoptera, specialized Diptera, listed by Wallace and Anderson 1996), most taxa found in our study likely grazed on the nutrient-rich matrix of mucopolysaccaride materials, bacteria, and algae. Even though these grazing invertebrates were not direct herbivores on the plant tissue, it is possible that host disturbance occurred during invertebrate grazing, leading to additional secretion of plant-derived nutrients.

Depending on species-specific resistance of plants to surface attack by bacteria and invertebrates, macrophytes may host a wide range of epilythic biomass. In some plants, resistance may be high, resulting in a biofilm supported with nutrients derived mainly from the ambient water column via active transport, uptake, and adsorption processes. At the other extreme, resistance may be low, resulting in a biofilm supported with an abundant pool of nutrients secreted from plant tissue that is damaged by invertebrate grazing and cellulolytic bacteria.

Two other scenarios of plant functioning under water may occur and influence the biomass of an associated benthic community. One is that the plant substrata may be virtually inert. The plant stays alive under water for extended periods, supplying only a surface for an attached biofilm that relies totally on nutrients from the overlying water column (biofilm on leaves) and on nutrients available from surrounding sediment or submersed soil (invertebrates in association with roots). In this case, the plant may be expected to host a benthic community limited by ambient nutrient supply and unrelated to nutrient content of the plant itself. This situation was hypothesized to occur but considered rare by Burkholder (1996) in her review of plant-epiphyte interactions. It was not considered likely by Wetzel (1983) in his discussion of release of nutrients by submersed macrophytes. The other extreme is complete decomposition of a plant that is intolerant to flooding. In this case, plant senescence occurs, completely releasing organic matter and nutrients (Wetzel 1983) for use by decomposer organisms and detritivores.

We propose three hypotheses of plant-biofilm interactions that potentially contributed to the significant elevation and plant species effects on invertebrate biomass in this study:

1. The submersed plant was able to survive for the study period with high resistance to surface damage potentially caused by cellulolysis mediated by bacteria and invertebrate grazing. In this hypothesis, there was little or no loss of nutrients from the plants. The host plants mainly provided surface areas for colonization and development of a biofilm and a community of benthic invertebrates. The biofilm was supplied with nutrients derived mainly from the ambient water column.
2. The submersed plant was able to survive for the study period but with low resistance to surface damage potentially caused by cellulolysis mediated by bacteria and invertebrate grazing. In this hypothesis, nutrient loss from the plant had the potential to substantially supply demand for nutrients by uptake and adsorption processes in the surface biofilm. Nutrients supplied from the water column and the plant provided a relatively rich food supply for benthic invertebrates that could occur in greater biomass than on plants that were relatively resistant to surface damage.
3. Senescence of the submersed plant occurred, resulting in decomposition and complete release of organic matter and nutrients for direct use by detritivores.

Elevation of substrata in Revelstoke Reach was largely distinguished by the presence or absence of assemblages of submersed vegetation. Lenticulate sedge and reed canary grass was generally present where substrata was flooded for <150 days a year (above 435 m) and substrata was barren of vegetation where it was flooded for >150 days a year (<434 m). Fall rye was planted early in the growing season at low elevations that were potential sources for dust storms. These time and elevation marks were not critical thresholds for presence or absence of vegetation but they generally indicated a transition zone between submersed vegetation and barren soils at full pool. Given that areal invertebrate biomass was greater in the presence of any vegetative cover than in barren soils (Table 13), it was clear that the presence or absence of vegetation was an important factor contributing to the elevation effect on invertebrate biomass. Another factor accentuating this plant effect may have been that net photosynthesis was favoured at the mixed vegetation site but net respiration was favoured at the other sites. These metabolic differences may not have affected the macrophytes, in which growth shut down under water, but it may have yielded less of a algal biofilm at the low elevation sites compared to the mixed vegetation site. However, there was no significant interaction between elevation and substrata type, indicating that effects of plant species and barren soil on invertebrate biomass was similar among elevations, suggesting that an irradiance effect was not important. Elevation had no effect on plant-specific biomass, indicating that characteristics of invertebrate accrual on specific substrata were the same in deep and shallow water.

The significant plant species effect on invertebrate biomass suggested that different processes supporting the biofilm and invertebrate community were active in association with the different substrata examined in the study. Barren soil hosted the smallest invertebrate biomass of 21 mg/sample (467 mg·m^{-2}; all elevations combined), which can be explained by the simple lack of plant surfaces for aboveground colonization that was available for invertebrates in all other samples. Fall rye was unique among plant species by not surviving under water. Senescence resulting in loss of erect stems and loss of biomass over the 78 days under water provided nutrients and organic matter for use by fungi, bacteria, and detritivores. Decomposition of leaves essentially removed surface areas for accrual of algae, thus explaining the very low cell counts found on fall rye at the end of 78 days under water. Invertebrate biomass associated with the detrital mass was 84 mg/sample (1,867 mg·m^{-2}; mean across all elevations) or 1.2 times that found in association with lenticulate sedge and 1.8 times that found in association with reed canary grass. Plant-specific invertebrate biomass was more than 10 times greater on the decomposed fall rye than on the other plant species. These two metrics clearly showed that benthic invertebrates favoured dead and decaying plant biomass compared to living and erect plants.

Both lenticulate sedge and reed canary grass survived under water for the 78 day study period and they hosted a biofilm comprised of bacteria, micro-flagellates, protozoans, ciliates, and rotifers. Lenticulate sedge hosted a greater areal biomass of invertebrates than reed canary grass. But, lower plant-specific biomass on lenticulate sedge suggested that it was mainly providing a larger surface area for colonization while reed canary grass may have hosted a higher quality biofilm as food for invertebrates. The higher algal cell counts, in fact, inferred a richer biofilm on reed canary grass compared to that on lenticulate sedge. However, little or no time effects on invertebrate biomass associated with lenticulate sedge and reed canary grass suggested that community development on those species was limited to animals initially colonising the plants within the first 10 days after inundation. Our microscopic evidence showed that a complex biofilm was achieved within 6 days of inundation, indicating the presence of a rich food supply to support invertebrates at that time. It also showed limited time course accrual of diatoms on lenticulate sedge but greater accumulation of algal cells on reed canary grass, although counts were generally small. This difference was additional evidence of somewhat richer conditions in the epiphyte community on reed canary grass compared to that on lenticulate sedge.

Burkholder (1996) indicated that submersed plants can release chemicals that limit algal accrual on plant substrata. This allelopathic response is not known in submersed lenticulate sedge and reed canary grass, but it may be a factor contributing to the relatively low algal cell counts and very low plant-specific biomass of invertebrates on those plants.

The unique sampling method used in this study made comparison of areal invertebrate densities with other studies equally unique. Generally, one would expect greater numbers in the present samples than those occurring in benthic grabs from lakes or surber-type or kick samples from rivers mainly because the sample volumes were generally greater than is typical from conventional grab techniques. Perrin (1996) reported invertebrate densities in the littoral zone of the Revelstoke Reservoir, upstream of the present study site, of 1,010 – 69,212 animals/m^2. These densities were similar to those found to date at the higher elevation sites in the present study. There were more chironomids than worms in Revelstoke Reservoir while the inverse was true in Revelstoke Reach. Perrin and Richardson (1997) reported aquatic insect densities of 15,000 – 26,000 animals/m^2 in fertilisation experiments in the Nechako River. Deegan et al. (1997) found aquatic insect densities of 5,000 – 15,000 animals/m^2 in the Kuparuk River, Alaska. Wipfli et al. (1998) reported densities of 1,000 – 11,000 animals/m^2 in another Alaskan stream but these densities increased up to 40,000 individuals/m^2 in the presence of decomposing salmon carcasses. This finding corroborates our evidence that animals preferred dead and decaying plant matter over living erect plant substrata. There is a greater amount and quality of food associated with the decomposition of a whole plant compared to food available only from a surface biofilm. These are just a few examples to suggest that the densities found in the belowground samples from vegetated sites in the present study (up to 64,000 individuals/m^2) were high and generally at the top end of values found at other sites. The fact that the presence of animals on the aboveground vegetation essentially doubled those densities, suggests that total densities were some of the highest that are found in oligotrophic systems.

The relative abundance of small individuals produced biomass values that were moderate compared to that in other rivers. Biomass ranged from 2.4 mg/sample (0.053 $g \cdot m^{-2}$) in barren soil at the mixed vegetation site to 140 mg/sample (3.1 $g \cdot m^{-2}$) associated with fall rye at the mixed vegetation site. In recent sampling of the Cheakamus River in southwestern British Columbia, benthos dry weight biomass ranged from 0.3 $g \cdot m^{-2}$ to 25 $g \cdot m^{-2}$. The overall average was approximately 2.5 $g \cdot m^{-2}$. The Cheakamus River hosts very high densities of invertebrates and is considered a productive river (Perrin 2001). Wetzel (1983) listed benthos dry weight biomass ranging between 0.25 $g \cdot m^{-2}$ and 4.4 $g \cdot m^{-2}$ found in oligotrophic lakes of Canada, the United States and Europe. In the absence of plants in Revelstoke Reach, benthos biomass was lower than this range but in the presence of plants, benthos biomass shifted to the high end of the range, clearly indicating that the presence of plants was not trivial but a major change to the functioning of benthic processes. Certainly benthos biomass in Revelstoke Reach infered richer conditions than the ultra-oligotrophic conditions that surface water chemistry implied. These differences are consistent with evidence described above that the biofilm on substrata of an oligotrophic system can be relatively rich, and it can physically and chemically isolate benthic processes from a more nutrient-deficient overlying water column.

6.4 Fish Distribution

The relative abundance of most species was not significantly different among the three vegetation strata examined (barren, planted fall rye, and mixed native grasses). For mountain whitefish and sucker spp., in particular, there was some evidence of preference for areas with mixed vegetation. Small sample sizes, however, did not provide us with confidence that a strong plant effect on abundance of these species was present. Similarly, the low catch rate among rainbow trout, bull trout, and lake whitefish meant that any association with vegetation strata was not clear for these species. Some fish of each of these species were captured by gill nets in each of the barren, fall rye, and mixed vegetation strata. In contrast, electroshocking collections indicated use of the barren and fall rye sites but not the mixed vegetation sites.

Based on gill net collection data, the relative abundance of kokanee was significantly greater in mixed vegetation sites than in fall rye sites. However, difference in relative abundance of kokanee between mixed vegetation sites and barren sites was not significant. In most boat electroshocking collections, the relative abundance of kokanee was similar regardless of the vegetation stratum sampled. The exception was one sample event in a fall rye site, where relatively large numbers of kokanee were encountered. Given these mixed findings, there was no clear evidence to suggest kokanee had a preference for vegetated areas over barren sites.

The relative abundance of mountain whitefish, as determined by gill net sampling, was significantly greater in mixed vegetation sites compared to either the fall rye sites or barren sites. When estimated by boat electroshocking, the mean relative abundance of mountain whitefish was also greatest in the mixed vegetation sites, but the differences among vegetation strata were not statistically significant and the relative abundance in mixed vegetation sites and fall rye sites were similar. These findings suggested there was only a weak association of whitefish with vegetation strata. Relatively large numbers of mountain whitefish were encountered in each of the three vegetation strata during boat electroshocking surveys. In addition, the highest CPUE of mountain whitefish was from gill nets set in a barren site. That catch rate was more than three times the next highest CPUE, which was from a gill net set in a mixed vegetation site.

Sucker spp. had the strongest association with the mixed vegetation stratum. Based on gill net sampling, the relative abundance of sucker spp. was significantly greater in mixed vegetation sites than in barren sites. The mean gill net CPUE for sucker spp. in mixed vegetation areas was almost six times greater than that in barren sites. Relative abundance of sucker spp. in gill net catches in fall rye sites was not significantly different from that in mixed vegetation sites. In boat electroshocking collections, sucker spp. were much more abundant in mixed vegetation sites than in either barren sites or fall rye sites. When tested statistically, however, these differences in boat electroshocking CPUE were not significant. However, the boat electroshocking sample sizes were small (two collections in the mixed vegetation stratum and three collections in each of the barren and fall rye strata), which decreased confidence in the outcome of the statistical tests. The mean boat elecroshocking CPUE for sucker spp. in mixed vegetation sites was almost 15 times greater than the mean CPUE in barren sites and was about 40 times greater than the mean CPUE in fall rye sites.

There was no strong evidence to suggest that different size-classes of fish used different vegetation strata. For most species, differences in mean lengths and weights of fish among the three vegetation strata were not apparent. The mean lengths and weights of mountain whitefish and peamouth were slightly less in mixed vegetation sites than in either barren sites or fall rye sites. Northern pikeminnow in mixed vegetation sites also had mean lengths and weights less than northern pikeminnow in barren sites or fall rye sites. However, in all cases, there was a large amount of overlap in the size-ranges of fish that used the different vegetation strata.

Anecdotal evidence from local residents (B. Gadbois, BC Hydro, pers comm) suggests that rainbow trout were absent from the Revelstoke Reach before grasses invaded the drawdown zone. Rainbow trout started to show up in the local fishery about 10 years ago, which coincided with active invasion of native grasses and initial stabilisation of the substrata, just before the planting of fall rye for dust control was started (B. Gadbois, BC Hydro, pers comm). This coincidence cannot be ignored and may suggest that establishment of vegetation in some way provided cover and extended a range of habitat that the rainbow trout and other species could use. Present data shows there is no obvious preference for the vegetated sites relative to barren sites by most fish species, which suggests that the presence of vegetation is not a present requirement for use of the various strata. The possible exception includes the suckers, which were found in much greater relative abundance in the mixed grasses compared to the fall rye or barren sites. These species may have a greater preference for habitat created by vegetation establishment than the other fish species.

Dominance by microbenthos also did not favour optimum availability of benthic invertebrates as food for fish that are visual predators. While bottom scavengers may take advantage of benthos in the bottom substrata, and particularly in areas of decomposing fall rye, species like rainbow trout may avoid potential food associated with the plants and substrata because it cannot be seen. Stomach contents of fish supported this possibility. Rainbow trout were found to ingest mainly large taxa of terrestrial origin and avoid much smaller aquatic taxa. This selection was not surprising given that rainbow trout are visual and opportunistic predators, targeting largest prey available. Given that more than 95% of the benthos at vegetated sites was <1 mm and associated with leaf and other substratum surfaces, it was generally not available for rainbow trout. Despite the high abundance of benthos at vegetated sites and moderate amount of biomass, this potential unavailability of food from vegetated substrata for rainbow trout may be one reason for the lack of association between catch rates of rainbow trout and presence of vegetation.

6.5 Fishery

Our evidence shows a very small fishery catering mainly to expert fly anglers from local fishing clubs. This observation generally supports the low catch rates of sport fish in this study. It is important, however, that the creel survey was not representative of all anglers potentially using Revelstoke Reach. Results from the creel may be biased by the method of distribution of the creel cards. For ease of distribution, they were only handed out to members of the local fishing clubs. These “experts” may have provided a biased impression of angling success because they had the experience on where and how to catch fish despite what appeared to be low overall abundance. A more objective measure of angling success would be to conduct a routine creel from boat launch areas where anglers of all skill levels could participate. This approach may result in very different responses than were encountered from the experts who were surveyed in this creel. A budget for the effort required to complete this type of creel was not available in this project. Despite potential bias in the creel, the small number of respondents and apparent small size of the fishery is consistent with finding low numbers of rainbow trout throughout the study area using the gill netting and electroshocking techniques.

7.0 RECOMMENDATIONS

While this study was a major step forward in examining potential benefits to the aquatic community to revegetation of a drawdown zone, other tasks can be considered to measure longer-term benefits. Examples are as follows:

- Sampling of lower trophic levels in 1999 followed development of the benthic community over a relatively short period of up to 78 days. In this time period, an abundant fauna was found. Animals were small, however, making them largely unavailable to visual predators. If the opportunity arises to repeat the 1999 experiment, it should include a longer period of sampling to determine if advanced development of the benthic community produces larger individuals and greater biomass than was found in 1999. Larger animals would potentially increase their availability to fish late in the growing season and increase the importance of vegetation establishment as a benefit to fish populations.
- Most surface depressions in the drawdown zone of Revelstoke Reach become dewatered as the water surface elevation of the reservoir declines in winter months. Many fish can be stranded in those depressions and pools as water recedes. In winter, ice forms over these pools but under the ice the water can recede to ground by infiltration, leaving a dry depression in most circumstances. The result is that all fish die that are stranded. Through winter, otter and birds of prey have been observed to dig passages under the ice or through the ice to feed on the fish carcasses and perhaps other organic matter left there from the previous growing season. The result is that either no carcasses remain in the spring or numbers are greatly diminished over what they were at the time of drawdown. These local observations suggest that fish stranding may be closely linked to use of the drawdown zone by wildlife. For this reason, it may be important to link measurements of use of vegetated and non-vegetated areas by

wildlife at different times of the year with measurements of fish stranding and total biomass produced in vegetation strata. Beach seining and electroshocking could be used to recover and enumerate newly stranded fish as soon as a series of pools are isolated from the reservoir at the start of drawdown in the early winter. Plant and benthos biomass estimates and measures of composition could also be completed at the same time. Thereafter, standardized surveys could be used to routinely observe use of pools by wildlife, stratified by type of vegetation that was characteristic of the sites in summer (barren, fall rye, mixed grasses). Measurements of wildlife use could include direct counts of animals observed entering and leaving holes in the ice. They could also include counts of animal sign and analysis of scat to confirm direct feeding on fish by wildlife. These observations should ideally be conducted throughout winter by individuals having knowledge of wildlife sign and wildlife behaviour in the Arrow drawdown zone.

- A potential benefit of vegetation establishment in the spring months is that new and existing biomass may provide extensive habitat for terrestrial invertebrates. While these animals may directly provide food for birds, they may also be trapped with rising water later in the spring and summer. If this process happens, a pulse of food may be available for fish that follow the rising water into Revelstoke Reach. Evidence of the extent of this food supply may be measured with emergence traps or other sampling device capable of catching flying insects at the water surface. If there is interest to continue investigation of potential benefits to fish from revegetation of the drawdown zone, these measurements should be considered as part of future sampling activities.
- A potential consequence of vegetation establishment in drawdown zones is creation of a carbon sink. That sink may be in the form of permanent vegetation and associated soils or if plants die under water, it may be in the form of carbon taken up in vegetation and then translocated to the aquatic ecosystem to be fixed in other organic matter. Either of these processes or the combination of these processes may represent a significant carbon sink. Creation of large carbon sinks is desirable as a means to limit carbon loss to the atmosphere. The magnitude of such a sink may be determined with calculation of a carbon budget for the aquatic component of the Revelstoke Reach in which the fate of downstream transport of carbon is measured. These data may be coupled with existing work on development of a carbon budget for soils of the Revelstoke Reach.

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