USE OF STABLE ISOTOPE ANALYSIS TO DESCRIBE FISH FOOD WEBS IN A HYDROELECTRIC RESERVOIR

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USE OF STABLE ISOTOPE ANALYSIS TO DESCRIBE FISH FOOD EBS IN A HYDROELECTRIC RESERVOIR

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ABSTRACT

Hydroelectric reservoirs are regulated systems that can sometimes experience extreme fluctuations in seasonal water level. These fluctuations can result in low biodiversity and productivity in littoral areas, which may have major impacts on reservoir ecosystem structure and functioning. Understanding reservoir ecosystem structure and function is especially relevant to the management of fish production in these systems. For instance, knowledge of fish diet is necessary in order to implement appropriate management actions to maintain or increase fish production, because if food for fish is mainly produced in the reservoir, this has quite different implications than if the main food supply is brought in from outside via streams. Using stable isotope analysis, I investigated fish food webs in Carpenter reservoir, a hydroelectric reservoir that experiences extreme seasonal fluctuation and is located on the Bridge River, British Columbia. I sampled fish tissues and macroinvertebrates from the reservoir, the mainstem river, and three major tributaries. I also sampled pelagic zooplankton and terrestrial leaf litter. I found that fish stable isotope signatures were most similar to those of macroinvertebrate drift from the mainstem river and Chironomidae from the reservoir littoral zone, while pelagic zooplankton, tributary macroinvertebrate drift and terrestrial vegetation have stable isotope signatures that are different from those of fish tissues. These findings seem to indicate that production from the mainstem river and reservoir littoral benthos is utilised more by fish than that from other sources. This is contrary to former beliefs that reservoir food webs are primarily driven by pelagic energy sources, and supports recent work describing the importance of benthic-pelagic coupling in lacustrine systems.

DEDICATION

To Megan and Dan,

because you are just that special

To Alice Cooper, who said it first and said it best:

"School's out forever"

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CHAPTER 1

REGULATED RIVERS

Until recently, river systems in North America have been modified by humans with insufficient understanding of the importance of ecological processes, which has resulted in cumulative impacts that have degraded aquatic environments considerably. Coupled with terrestrial transformations that affect natural disturbance regimes and spatial patterning, the anthropogenic alteration of rivers has important and lasting consequences for the character and productivity of aquatic ecosystems (Naiman and Turner 2000).

Human demographics, patterns of water consumption and resource use, technological development, and social organisation have been identified as the five major categories of anthropogenically-induced change for freshwater systems (Naiman *et al.* 1998). Working singly or in concert, these agents can result in the physical restructuring of freshwater ecosystems, exotic invasions, release of toxins, and overexploitation of resources (Rapport and Whitford

1999). Such pervasive and severe impacts on river ecosystems may be exemplified through recent trends in dam construction.

Historically, humans caused little change to rivers through dam building, because structures were generally small and reflected the abilities and needs of pre-industrial, agrarian societies (Poff and Hart 2002). However, during the 19th and 20th centuries, advances in technology led to the construction of large and sophisticated structures that were developed to control floods, provide water for agriculture and consumption, improve navigation, and generate hydroelectric power (McCully 2001). Once viewed as a testament to engineering science, these structures have become the object of increasing global controversy.

By definition, the construction of a dam has an impact on the natural function of a river. Scientists, managers, and society now widely recognize the extent to which those impacts pervade the natural environment. Dams elicit biological and physical impacts on both local and landscape scales, altering the downstream movements of water and sediments, changing water temperatures, and creating barriers to movement of organisms and nutrients, all of which have profound consequences to the operation of these ecosystems (Poff and Hart 2002).

The damming of a river changes the environment through fragmentation and isolation not only of animal communities, but also of the physical processes which occur in unregulated rivers. Control or cessation of flows in a river results in an artificial hydrograph with reduced flows and sediment transport to downstream habitats, causing large alterations to downstream food webs and productivity through loss of nutrients and habitat (Wootton *et al.* 1996). Both

riparian and aquatic habitats are decreased in area or degraded as recruitment of terrestrial plants is hampered by fragmentation or increased desiccation of soils though loss of natural flooding patterns. Downstream from dams, riverbeds become narrow and deep with steep banks and hard substrates, affecting benthic community composition and abundance (Poff and Hart 2002). Dams also present a barrier to fish migration. In the Pacific Northwest, the cumulative impacts of isolation, fragmentation, and habitat loss caused by large dams has contributed to the decline of numerous anadromous fish stocks (Slaney *et al.* 1996).

In British Columbia, Canada, over 90% of the province's electricity is generated by hydroelectric facilities, most of which are operated by B.C. Hydro. In response to growing concerns regarding the environmental impacts of large dams on aquatic systems, this crown corporation has placed increased emphasis on reducing impacts by determining how power is actually generated within the province and assessing how to best make the trade-off between supplying adequate power and minimising environmental impacts (B.C. Hydro 2003*a*).

One of the greatest environmental challenges facing B.C. Hydro today is the mitigation of damage to fish and wildlife habitat caused by the development and operation of hydroelectric facilities. Thus, B.C. Hydro has embarked on a major venture with provincial and federal governments and special interest groups to develop Water Use Plans for each hydroelectric facility in the province.

Water Use Plans are technical documents created through a multi-stakeholder planning process that defines operating parameters to be used by

managers of hydroelectric and other water control facilities within B.C.. These plans provide clarification on how rights to provincial water resources should be exercised, explicitly recognizing existing legal and constitutional rights and responsibilities, and taking into account multiple uses for water resources, including ecological functions.

At present, B.C. Hydro has completed three Water Use Plans, while another 17 are currently in progress. One project is the Water Use Plan for the Bridge River, a large system that flows southeast from the Coast Range to join the Fraser River near Lillooet (Figure 1). The Bridge/Seton Hydroelectric facility is on this river, which is the third largest generating facility in the province and generates about 3 000 GW.h annually (B.C. Hydro, 2003*b*).

Established in 1934, the system initially diverted about 1 $m^3 \cdot s^{-1}$ of flows from the Bridge River. In 1946, work commenced on the construction of the Mission Dam to create the Carpenter reservoir. This dam eliminated all access for anadromous fish species to the upper Bridge River watershed. Upon completion of the dam in 1948, the La Joie Dam and power facility were added upstream of Mission Dam to form Downton reservoir, and within seven years diverted flows were increased to 62 $m^3 \cdot s^{-1}$. The Mission Dam was replaced in 1960 by the Terzaghi Dam and diverted flows increased to 153 $m^3 \cdot s^{-1}$ seven years later. Water from Carpenter reservoir is shunted to Seton Lake located to the south of the Bridge River. Additional generation results from the diversion of water from Seton Lake directly to the Fraser River via a 20 km power canal which terminates with the Seton generating facility (Komori 1997).

The establishment of hydroelectric activity on the Bridge River has resulted in the decline of salmon populations through barred access to available

spawning and rearing areas, because anadromous and migratory resident stocks have been excluded from or trapped within the Bridge system above the Terzaghi Dam site for over 50 years (Bridge Coastal Restoration Program 2002). Permanent or seasonal loss of habitat has also occurred through the dewatering and flooding of the reservoir and tributaries, and the alteration of flow regimes which affect sediment flows and recruitment of large woody debris (Bridge Coastal Restoration Program 2002). Also, spills and other periodic releases of high flows have resulted in increased sediment loads, loss of spawning gravels, and degradation of riparian habitat (Komori 1997). These impacts further emphasise the need for research to ensure effective mitigation and enhancement projects may be undertaken.

Due to the nature of the preparatory and ongoing work undertaken by the Water Use Plan's Fisheries Technical Committee, data already exist for the Bridge River from physical and biological models. This previous work has indicated that there is uncertainty about the relative contribution of alternative energy sources to fish food webs in this system from riparian, littoral, and pelagic sources. In the present study, I use stable isotope analysis to clarify food web dependence on alternative energy sources. I then make general recommendations as to how this information may be incorporated into scenarios for operating the flows from the dam, and comment on the efficacy of stable isotope analysis in describing food web linkages in regulated systems.

CHAPTER 2

FISH FOOD WEBS IN A HYDROELECTRIC RESERVOIR DESCRIBED USING STABLE ISOTOPES

INTRODUCTION

Hydroelectric reservoirs are regulated systems that can sometimes experience extreme fluctuations in seasonal water level. Such artificial systems often exhibit low biodiversity and productivity in littoral areas, which may have major impacts on such reservoirs' ecosystem structure and functioning (Wetzel 1990). Aquatic plants that colonize the littoral zone are soon shaded out by the increased light scattering and absorption associated with increased water depth and dissolved and suspended matter that occurs as the reservoir fills (Kimmel *et al.* 1990). Instability and loss of littoral habitat occurs during draining of the reservoir, also preventing macrophyte colonization. As aquatic macrophytes are an important substrate for periphyton (Sze 1993), which are potential energy source for aquatic food webs (Hecky and Hesslein 1995), the inability of

macrophytes to colonize littoral areas further decreases levels of primary production within reservoirs.

Low littoral primary production may have major impacts on how hydroelectric reservoirs operate as ecosystems. Depending on trophic transfer efficiencies within food webs, the organic carbon that contributes to fish production may be supplemented by allochthonous energy inputs (i.e. terrestrial plant material), as opposed to only autochthonous sources (i.e. aquatic plant material) (Adams *et al.*, 1983). In natural lacustrine systems, fish production is dependent on carbon from littoral autochthonous inputs, as well as benthic and pelagic inputs (Vander Zanden and Vadenboncoeur 2002). In these systems, benthic and pelagic food webs are linked to each other by numerous methods, including the broad foraging behaviour of piscivorous fish, which will link benthic and pelagic food chains through consumption of smaller pelagic and benthic fishes and benthic and terrestrial insects (Schindler *et al.* 1996).

Reservoirs can be shallow and may potentially operate as small lakes, where a significant proportion of primary production is attributed to littoral algae or macrophytes. The importance of benthic and allochthonous energy inputs to aquatic food webs compared to those of pelagic inputs is situation-dependent. Littoral production may dominate in shallow, clear lakes, whereas phytoplankton production may be more important in deep, oligotrophic lakes (Wetzel 1983).

Investigation into the nature of autochthonous and allochthonous inputs, the biological availability of these inputs, and the actual trophic transfer efficiencies of reservoir food webs is required to describe relative contributions

of various organic matter sources to fish production in reservoirs (Adams and Kimmel 1983). Understanding which energy sources drive reservoir food webs is especially relevant to the management of fish production in these systems because production of consumers tends to be limited by energy at the level of their food, and not by levels of available dissolved nitrogen and phosphorus in the water (Elser and Urabe 1999). Therefore, knowledge of fish diet is necessary in order to implement reservoir operations that accommodate the production of those energy sources (Johnson *et al.* 2002). The present study addresses this requirement by using stable isotope analysis to investigate the use of different potential energy sources by fish food webs within a regulated reservoir, and describe foraging behaviour within and among fish species across time and space within this system.

Increasingly, ecologists are using stable isotope analysis to describe energy pathways in food webs. This is done by comparing stable isotope ratios in animal tissues to those in their diet (DeNiro and Epstein 1978; DeNiro and Epstein 1980; Tieszen *et al.* 1983; Tieszen and Boutton 1989). This technique may allow for the tracking of material flow from energy sources through to higher consumers (Peterson and Fry 1987; Fry 1991). This technique offers a unique insight into diet, because animal tissues reflect diet integrated over time. This integrated measure is not easy to determine with more traditional forms of diet reconstruction such as gut content analysis (DeNiro and Epstein 1978; Tieszen *et al.* 1983), due to logistic difficulties associated with these techniques.

Food web analyses most often use stable isotope ratios of carbon and nitrogen. Stable nitrogen ratios ($^{15}N:^{14}N$) show a predictable increase of 3 - 5 ‰

with increasing trophic position, primarily due to the excretion of isotopically light nitrogen (Minagawa and Wada 1984). Stable carbon ratios (^{13}C:^{12}C) are conserved within 0 - 1 ‰ and do not exhibit significant changes with trophic position, thus reflecting energy sources (Peterson and Fry 1987). Frequently the ratios are used in combination (Roth and Hobson 2000) with $\delta^{15}N$ values reflecting an organism's trophic position (Hobson and Welch 1992) and $\delta^{13}C$ values offering a signature to trace the flow of energy through the food web (Roth and Hobson 2000).

Using the Carpenter reservoir, a hydroelectric reservoir in the Cariboo-Chilcotin region of British Columbia, Canada, I investigated the feasibility of using stable isotope analysis on a regulated river system with the primary objective of describing the use of potential carbon inputs by fish food webs in that reservoir. I sampled from three different habitat areas linked to the reservoir that I speculated could provide prey to fish: the mainstem river, the reservoir, and three major tributaries. I collected samples over five months to describe what seasonal trends, if any, were present in stable isotope signatures of fish tissues, prey items (i.e. macroinvertebrates and zooplankton), terrestrial leaves, and dissolved inorganic carbon.

Secondary objectives of this study included (1) determining if and how use of potential carbon sources by fish species changed seasonally and over their life history, and (2) how use of carbon sources by fish may change between fish of different size classes captured from the middle Bridge River, the reservoir, and the three major tributaries. To address both of these objectives, I explored the relation between fish body length and stable isotope signatures, and the effect of body size and geographic area on isotope ratios within fish

species. The results of these investigations were then used to address a third secondary objective: (3) describing the feeding ecology of fishes within and among species. To determine relative trophic levels and identify ecological linkages, I compared stable isotope signatures among fish species. I then used the information obtained through the above analyses and predicted outcomes for several key performance measures from a quantitative model developed by BC Hydro to make broad qualitative statements regarding appropriate operating scenarios given the objective of maintaining or increasing fish production in this system.

Understanding how facility operations may affect fish production requires an understanding of how carbon energy sources contribute to fish production. Depending on fish utilisation of these prey sources, effective operating scenarios could be very different. For instance, if fish production is more dependent on carbon inputs from the Bridge River than those from the reservoir or major tributaries, then operating scenarios must recognise the importance of the river and maintain as much high quality river habitat as possible through decreased reservoir filling rates and lower storage capacity. Conversely, if either the reservoir or tributaries are found to be the primary contributor to fish production, then reservoir operations must similarly conserve and/or promote these habitats through variations in flooding and dewatering rates, storage capacity, and retention time. Appropriate actions would necessarily become more complex if more than one habitat area was found to contribute strongly to fish food webs, because different strategies have to be employed to promote production in each area.

CHAPTER 3

METHODS

STUDY AREA

The Bridge River is 120 km long and flows southeast from the Bridge Glacier in the Coast Mountain Range to join the Fraser River near Lillooet, British Columbia (Figure 1). Over the last half century, the Bridge River has been extensively altered for the purpose of hydroelectric generation. Historically, anadromous salmonids migrated into the upper reaches of this system and spawned in tributaries (Nielson and Shepherd 1983). This migration was blocked with the construction of the Mission Dam in 1948 (Komori 1997), and continues to be blocked to the present day.

In 1960, the Mission Dam was incorporated into the upstream toe of the Terzaghi Dam to form Carpenter reservoir, the focus area of the present study (Figure 2). This impoundment reservoir has a storage capacity of 1 011 million m^3, and an area of 4 900 ha. Elevation of the reservoir is measured at 609 to 651 m above sea level, and water levels vary approximately 45 m in

vertical elevation. Mean depth of the reservoir is 23 m. Mean water retention time is 3.8 months (Bridge Coastal Restoration Program 2002).

Within the Bridge River basin, snow and glacial melt cause high inflows from May through August, while inflow from September through April is low. Natural lakes in the watershed are relatively insignificant with respect to additional storage capacity. The Carpenter reservoir is one of three storage facilities built on this river system for hydroelectric generation. Directly upstream of Carpenter reservoir is Downton reservoir, formed by the La Joie Dam. The portion of the river between La Joie and Terzaghi Dams is referred to as the middle Bridge River. Water from Downton reservoir passes through the La Joie generating station into Carpenter reservoir, is shunted through penstocks under Mission Mountain to Seton Lake, and is eventually released to the Fraser River.

At maximum storage capacity, 112 km of shoreline is present in the Carpenter reservoir, creating a perimeter-to-area ratio of 2.28 ($km:km^2$). Much fish habitat was lost with the completion of impoundment and the subsequent flooding of the mainstem river. About 92 km of mainstem river habitat and 552 ha of associated riparian habitat, as well as 55 km of tributary streams and 165 ha of associated riparian habitat were inundated by the reservoir, as were 46 ha of productive wetlands (Bridge Coastal Restoration Program 2002).
Perrin and MacDonald (1999) found that Carpenter reservoir experiences seasonal stratification, whereby waters are isothermal in the winter, but become stratified in spring and remain so through the fall. During periods of stratification, the cooler, denser water of the Bridge River travels along the bottom of the reservoir, entraining many of the nutrients and contributing little

to pelagic production due to isolation near the reservoir bottom. Throughout the summer, the thermocline exists at a depth of 10 to 12 m. Epilimnetic temperatures range from 17 to 21°C, while hypolimnetic temperatures are 10 to 12°C. The reservoir is well oxygenated during stratification. Nutrient conditions in the Carpenter reservoir are most similar to those of an oligotrophic lake. Soluble reactive phosphorus concentrations range from 6.0 to 4.8 $\mu g \cdot L^{-1}$, while NO_3^- loads range from 18.3 to 26.5 $\mu g \cdot L^{-1}$ and NH_4^- concentrations range from 7.4 to 10.1 $\mu g \cdot L^{-1}$. The reservoir is turbid, with a downstream gradient of 21.7 to 4.9 NTU from the confluence of the Bridge River with the reservoir to Terzaghi Dam.

The Bridge River system upstream of Terzaghi Dam supports populations of bridgelip sucker (*Catastomus macrocheilus*), coastrange sculpin (*Cottus aleuticus*), redsided shiner (*Richardsonius balteatus*), rainbow trout (*Oncorhynchus mykiss*), bull trout (*Salvelinus confluentus*), kokanee (lacustrine sockeye, *O. nerka*), and mountain whitefish (*Prosopium williamsoni*) (Higgins and Bradford 1996). Prior to the building of the Terzaghi dam, sockeye (*O. nerka*) and chinook (*O. tswatschya*) salmon had been sporadically sighted in this section of the Bridge River and in Fergusson and Tyaughton Creeks (Atkinson 1947). It is also likely that coho (*O. kisutch*) populations were present in this section of river as well, although the secretive behavior and small group size typical of coho spawners may be why these species were unreported in this large, turbid system (Cartwright 1978).

SAMPLING

To address the objectives of this study, which were to describe how fish food webs utilize different carbon inputs, to determine if and how use of carbon sources by fish may change temporally and spatially, and to describe the feeding ecology of different fish species, I collected terrestrial plant material, zooplankton, macroinvertebrate drift and muscle tissues from six fish species from three areas within the Carpenter reservoir. These areas were the middle Bridge River (the mainstem river between La Joie Dam and the confluence with the reservoir), three major tributaries (Gun, Marshall, and Tyaughton Creeks upstream of their confluences with Carpenter reservoir or the middle Bridge River), and the reservoir (the waters downstream of the confluence with the middle Bridge River). Samples were collected monthly between May through September to examine possible changes over time, as well as across habitat types.

The three major areas correspond to different inputs of potential carbon sources available to fish food webs in the system. Within these areas, I selected eleven sites (Figure 2), which were chosen to represent the diversity of habitat available to fish in the system. Four sites were established along the middle Bridge River, two sites near or at the confluence of the river with the reservoir, and two sites within the littoral area of the reservoir. For two major tributaries (Gun Creek and Tyaughton Creek), a site was established both within the tributary just upstream of its confluence with the reservoir, and within the middle Bridge River or the reservoir directly upstream of the tributary confluence. Due to infilling of the reservoir, these sites changed from lotic to lentic waterbodies as the summer progressed. A third tributary,

Marshall Creek, was sampled only within the tributary, as the reservoir could not be accessed due to the steep, unstable banks in this vicinity.

Monthly samples were collected from May through September 2001. Conditioned deciduous leaf litter (decaying leaves), larval aquatic insects, and dissolved inorganic carbon (DIC) were collected during each trip. Fish tissues and pelagic zooplankton were acquired from two concurrent studies conducted on the reservoir. The sampling times of these studies were within one week of the present study, to ensure confounding effects of tissue turnover on stable isotope signatures would be negligible.

Conditioned leaf litter was collected by hand from the stream channel. Macroinvertebrates in drift from tributaries and the middle Bridge River were collected using drift samplers (Mundie 1964), as well as by hand-sorting through substrate material and brushing from cobble to supplement drift samples. Macroinvertebrates from sites on the middle Bridge River upstream of Gun and Tyaughton Creeks, and at the confluence of the middle Bridge River with the reservoir were collected by hand only because drift sampling was not feasible in these areas due to water depth and soft sediments. Drift samplers were set for 24 hours and used 253 μm nets. I attempted to set up three samplers per site, however, due to high flows and depths, often only two samplers, and on occasion only one sampler could be safely placed. These in-stream conditions prevented me from setting up samplers across the width of each channel. With the exception of Marshall Creek where nets could be established in a transect across the stream width, all samplers were set up within 3 to 5 meters of the bank.

I sorted the collected drift material and hand-collected macroinvertebrates by washing through a series of two sieves such that macroinvertebrates were separated into large (> 1.2 mm) and small (0.5 to 1.2 mm) size classes. Because prey size can be related to fish body length (Keeley and Grant 2001), only the large size class was utilized for the present study. Assuming the relation between prey size and fish body length presented in Keeley and Grant (2001) for salmonids may also be applied to other fish, prey between approximately 1 and 10 mm in length would be utilized by fish with a body length of approximately 5 to 20 cm, the size of the fish captured in this study.

Various methods were used for gathering data on other components of this system. Fish were collected using angling as well as backpack- and boat-electrofishing. For each sampling trip, attempts were made to collect five individuals from both large and small size classes (Table 1) of each species from each site, although this was not always possible. Tissue samples were taken either as whole body, dissected dorsal muscle tissue, or dorsal muscle tissue plugs (from salmonid species). Zooplankton were collected monthly from the pelagic zone of the reservoir near Bighorn Creek using a Wisconsin Tow. A 64 μm mesh was used when collecting plankton, and 1000 L of water were filtered (equivalent of two tows) from the water column to an average depth of 20 m. I collected DIC samples from each site by injecting 5 ml of unstirred water into an Exetainer™ vial containing 0.5 ml of Phosphoric acid.

With the exception of fish tissues and zooplankton, I froze all samples for subsequent lab analysis. I preserved fish tissues in ethanol, while zooplankton were kept at 4°C for up to two weeks. I washed fish muscle tissues

with water and removed any scales or skin tissue. I cleaned plant samples liberally with water to remove as much dirt and extraneous debris as possible. I dried all samples at 60°C for 48h. Following drying, I ground samples to a fine powder using a mortar and pestle, and subsampled for stable isotope analysis. For fish and macroinvertebrates, I used 1 mg samples, while for plant material I used 3 mg samples. Because of small body sizes, most invertebrate taxa had to be pooled in order to meet the required sample weights. Up to 11 sample replicates were used for each taxon from each site, with the majority of samples consisting of 1 to 5 replicates due to low abundance of individual taxa.

All samples were analysed at the Stable Isotope Facility of the University of California, Davis using a Europa 20/20 continuous-flow isotope-ratio spectrometer. Standard delta notation (‰, parts per mil) is used to express isotope ratios relative to international standards (Equation 1):

$$(1) \qquad \delta X = \frac{R_{sample} - R_{standard}}{R_{standard}} \times 1000$$

Where X is either ^{13}C or ^{15}N, R_{sample} is $^{13}C/^{12}C$ or $^{15}N/^{14}N$ of the samples and $R_{standard}$ is the isotope ratio of an international standard (Pee Dee Belemnite limestone for $\delta^{13}C$, atmospheric N_2 for $\delta^{15}N$).

CHAPTER 4

DATA ANALYSIS

Prior to my analyses, I processed the raw data extensively to obtain a manageable dataset. This processing included correcting for preservation effects in fish tissues and weighting of macroinvertebrate drift to account for differences in biomass across taxa, differences in flows through drift nets, and differences in discharge from each tributary into the reservoir. Detailed explanations of these procedures follow.

MACROINVERTEBRATE DRIFT

I estimated the stable isotope signatures of potential food items from tributaries and the middle Bridge River by the following methods. I assumed that invertebrates >1.2 mm obtained from drift nets were potentially available as fish food. I then used the biomass of individuals to weight the stable isotope signatures to account for variations in body size among taxa.

Macroinvertebrate density estimates for drift (#/100 m^3) were calculated using methods outlined in Smock (1996). Also, when determining macroinvertebrate isotopic signature for combined tributary input to the

reservoir, individual tributary values were weighted by relative discharges from each sub-watershed.

To estimate the biomass of macroinvertebrate taxa, I obtained Ash Free Dry Mass (AFDM, mg) for individual organisms from Korman (unpublished data), and Benke *et al.* (1999), and used the following steps:

- Korman collected AFDM data from drift samples in my study area in 2000, but only sorted his collections into five groups (Mayflies, Stoneflies, Caddisflies, Chironomidae, or Simuliidae). I reclassified my data to correspond to these categories.
- Korman's individual weights were point estimates based on weighing bulk samples of known numbers, using insects from both Carpenter and Downton reservoirs. Collection alternated monthly between the two sites over four months, however, no seasonal trends were present in macroinvertebrate biomass over time ($p < 0.05$). I pooled biomass data for each category to obtain a single seasonal value for use in my study.
- The Dipteran families Orthorrhapha and Cyclorrhapha were not included in Benke *et al.* (1999), nor could I find any length-mass relationships for these taxa. Therefore, I used the overall length-mass relationship for all Diptera to approximate the AFDM for these taxa and used the length data for Chironomidae for these families given their similarity in size. The published length range for Blephariceridae in Benke *et al.* (1999) was too small for the insects I collected, and I used a visually estimated length for this family that was about double that of the published value.

To calculate the average stable isotope signatures of macroinvertebrate input to the reservoir, isotope signatures of individual taxa were weighted by

their biomass. I also calculated the total numerical abundance of invertebrate taxa in drift input from the middle Bridge River, Gun Creek, Marshall Creek, and Tyaughton Creek. I assumed that the composition of drift samples were representative of total drift composition in each watercourse. I also accounted for differences in total volume of water sampled among drift nets placed in each watercourse and for relative differences in discharge among streams using the following steps:

- For each drift net sample, I multiplied the count of a taxonomic group by its AFDM per individual to obtain the total mass of that taxon.
- To calculate the total macroinvertebrate mass within each drift net, I summed the total taxonomic masses within that drift net.
- The ratio of taxon mass to total macroinvertebrate mass was calculated by dividing the total taxonomic mass by the total macroinvertebrate mass for each drift net.
- To correct for differences in the volume sampled by each drift net, I weighted the invertebrate data by the proportion of total volume sampled by each net. This correction was made for each sampling period. I calculated the volume sampled by each net using methods outlined in Smock (1996).
- The total volume of water sampled by the drift nets was summed for each month and the entire season for the middle Bridge River and for tributaries, so as to facilitate different analyses.
- I corrected for differences in discharge ($m^3 \cdot s^{-1}$) from each watercourse prior combining Gun, Marshall, and Tyaughton Creeks into one 'tributaries' region, using Equation 2 to estimate discharge. Using Tyaughton Creek as

the base, the estimated relative discharge was 1.0:0.54:0.0004 for Tyaughton, Gun, and Marshall Creeks, respectively.

(2) $$Q = a(\text{Area})^b$$

where Q = discharge ($m^3 \cdot sec^{-1}$), a = 2.1 x 10^{-6} and b = 2.44 (from Korman, unpublished data), a and b are constants, and watershed area is measured in km^2 (Wisler and Brater 1959).

- To calculate the overall weighting factor needed to estimate stable isotope signatures of drift input into the reservoir, the mass ratio and flow ratio for each drift net and relative discharge for each tributary were multiplied together. This step incorporates differences in biomass across taxa, differences in through-flow of drift nets within watercourses, and differences in discharge across tributaries.
- When performing analyses, all models involving macroinvertebrate data were built such that the weighting factor was used to determine relative contribution of each taxa in each region (i.e. middle Bridge River or tributaries) when calculating stable isotope signatures.

To further describe macroinvertebrate drift from the middle Bridge River and tributaries, I examined stable isotope signatures of known prey items in the drift by taxa and functional group, as defined by Merritt and Cummins (1996). I also determined the numerical density of macroinvertebrate functional groups (# insects$\cdot 100\ m^{-3}$), and functional group biomass densities ($mg \cdot 100\ m^{-3}$) in drift. I described these attributes as probabilities of occurrence within macroinvertebrate drift from the middle Bridge River and from tributaries.

RESERVOIR MACROINVERTEBRATES

Macroinvertebrates in the reservoir were not found in numbers sufficient for stable isotope analysis. Therefore, I used $\delta^{13}C$ and $\delta^{15}N$ values for Chironomidae collected from the reservoir littoral zone upstream from Bighorn Creek during a pilot study for this project conducted October 2000. No other macroinvertebrate taxa were collected from the reservoir. Chironomidae were gathered by washing of bottom substrate in basins, which was not sampled in a quantitative manner.

ZOOPLANKTON

I used modified kokanee (*Oncorhynchus nerka*) stable isotope signatures as a proxy for zooplankton signatures in all food web reconstructions. Because zooplankton can exhibit wide seasonal variations in stable isotopes due to changes in community composition and abundance (Branstrator *et al.* 2000), using an integrated measure such as a predator of zooplankton is preferable to using actual zooplankton signatures. Planktivore signatures will more accurately reflect the overall seasonal signature of zooplankton than relatively infrequent sampling. Kokanee are predominately planktivorous (Scott and Crossman 1973), so their $\delta^{13}C$ signature should reflect that of zooplankton. However, when I compared kokanee $\delta^{13}C$ signatures with zooplankton $\delta^{13}C$ signatures, I found that kokanee $\delta^{13}C$ signatures were more enriched than those of the zooplankton I collected (Student-Neuman-Keul's test: $t_{1,\,15} = 5.06$, $p < 0.01$) (Figure 3). Therefore, I used kokanee as an inferred diet signature for zooplankton in all food web analyses. Because $\delta^{13}C$ signatures increase by a maximum of 1 ‰, and $\delta^{15}N$ signatures increase by 3 - 5 ‰ with each increase

in trophic level, I subtracted 1 ‰ from kokanee $\delta^{13}C$ signatures, and 3 ‰ from kokanee $\delta^{15}N$ signatures prior to substituting them for zooplankton signatures. For reference purposes, in food web constructions I plotted both the inferred zooplankton stable isotope signatures and the actual measured zooplankton stable isotope signatures, and qualitative comparisons are made using both the actual and inferred zooplankton signatures.

FISH STABLE ISOTOPE SIGNATURES

All stable isotope signatures for fish were corrected for ethanol preservation effects as suggested by (Arrington and Winemiller 2001). I increased $\delta^{13}C$ values by 1.12‰ and decreased $\delta^{15}N$ values by 0.62‰. These correction factors are most appropriate in situations where $\delta^{13}C$ signatures of different primary producers are separated by at least 2 ‰, because longer preservation might increase variation in signatures caused by preservatives. This requirement was met in the present study, although my fish tissue samples were only preserved for a maximum of 4 weeks, so concerns surrounding increased variation with extended periods of preservation (i.e. several months or years) are not applicable here.

SITE AND AGE EFFECTS ON STABLE ISOTOPE SIGNATURES OF FISH TISSUES

To describe possible variation in prey choice and mobility of different species and size classes of fish, I investigated whether differences in stable isotope signatures existed within species captured from the middle Bridge River, tributaries or the reservoir, or between size classes within species. These

area and size effects for each of the 6 fish species and for large and small size classes were determined using 1-way and 2-way ANOVAs on stable isotope signatures. Size classes were not analyzed for bull trout because too few samples of small fish were collected. Kokanee were not included in the site effects analysis because samples were collected from the middle Bridge River only. Within species, if no significant effects were found across area or age, I pooled data across that attribute and re-analyzed the pooled data to determine the effects of the remaining attribute on stable isotope signatures of fish tissues.

SEASONAL TRENDS IN FISH STABLE ISOTOPE SIGNATURES

To assess whether stable isotope signatures changed over the growing season, and the extent to which that change occurred, I fit a linear regression of stable isotope signatures of individuals of each species of fish on sampling date. For each regression, fish were grouped within species according to the presence of significant area effects, as investigated previously. If no area effects were present, fish stable isotope signatures within species were pooled across space prior to regression analysis. If area effects were present, regression analyses were performed separately on fish captured from the middle Bridge River, tributaries, and the reservoir.

RELATIONS BETWEEN FISH STABLE ISOTOPE SIGNATURES AND BODY LENGTH

To identify any trends of stable isotope signatures with fish size, I fit linear regressions of stable isotope signatures of individual fish on body size. For each regression, fish were grouped within species in accordance to the

presence of significant area effects, as investigated previously. If no area effects were present, fish stable isotope signatures within species were pooled across space prior to regression analysis. If area effects were present, then regression analyses were performed by area, specifically the middle Bridge River, tributaries, and the reservoir.

CONSTRUCTION OF FISH FOOD WEBS WITHIN THE CARPENTER RESERVOIR

Differences in stable isotope signatures between the five potential carbon inputs I measured (i.e. middle Bridge River macroinvertebrate drift, tributary macroinvertebrate drift, reservoir Chironomidae, zooplankton, and terrestrial leaves) were analyzed using a 1-way ANOVA. Post-hoc comparisons of means were conducted using the Student-Neuman-Keul's test (hereafter referred to as the SNK-test), which makes individual pair-wise comparisons of means with unequal sample sizes, and is appropriate for comparisons in small 1-way layouts (Sall and Lehman 1996).

For all food web constructions I used stable isotope values pooled over time within each food web component. I was unable to use a mixing model approach to quantitatively determine the proportion of energy source contribution to fish diet because significant separation in $\delta^{13}C$ and/or $\delta^{15}N$ signatures among all sources could not be obtained. Therefore, I qualitatively compared stable isotope signatures (mean ± 2SE) of fish, grouped by significant area and/or size effects within species, with those of the five potential carbon inputs. I then visually compared the signatures to determine which energy sources were most likely being used by fish.

I compared fish with energy sources in two ways. First, I used fish data pooled over size and area within species. Here I used a 1-way ANOVA to obtain the mean ± 2SE for fish tissue stable isotope signatures. For the second method, I performed separate comparisons of fish tissues by area with signatures of energy sources, and kept within-species size-effects explicit. Here I included variation in fish tissue signatures as mean ± 2SE obtained through the area and size analyses.

CHAPTER 5

RESULTS

TRENDS OF STABLE ISOTOPES OF FOOD WEB COMPONENTS

Seasonal trends in fish stable isotope signatures

For bull trout, no significant changes in $\delta^{13}C$ or $\delta^{15}N$ signatures were present over the period of sampling for fish caught in the middle Bridge River, tributaries, or reservoir. Rainbow trout, coastrange sculpin, redsided shiners caught in the reservoir, large bridgelip suckers, and small mountain whitefish from the middle Bridge River and tributaries all showed significant enrichment in $\delta^{13}C$ values between June and September ($p \leq 0.05$) (Table 2). Significant seasonal trends in $\delta^{15}N$ signatures were found for small rainbow trout, coastrange sculpin from the reservoir and tributaries, and small mountain whitefish from tributaries. In all cases $\delta^{15}N$ became more depleted with time ($p \leq 0.05$).

Fish stable isotope signatures vs. length

Only one of 27 regression analyses between fish stable isotope signatures and body length was significant ($p = 0.05$, Table 3). Also, no general patterns for either direction of correlation or strength of those relations were evident. Thus, I interpret these analyses as showing no definitive relations between fish stable isotope signatures and body size for any species of fish.

Seasonal trends in energy sources available to reservoir food webs

Of the five potential carbon sources I sampled (i.e. conditioned terrestrial leaves, zooplankton, reservoir Chironomidae, middle Bridge River macroinvertebrate drift, and tributary macroinvertebrate drift), only terrestrial leaves, middle Bridge River drift, and zooplankton showed seasonal trends in stable isotope signatures. Terrestrial leaf stable isotope signatures became more enriched with time, as did the $\delta^{13}C$ values for middle Bridge River drift. Zooplankton $\delta^{13}C$ became more depleted over the 4 months I sampled, while zooplankton $\delta^{15}N$ and tributary drift signatures showed no seasonal trends (Table 4).

Seasonal trends in $\delta^{13}C$ signatures of DIC

Middle Bridge River DIC $\delta^{13}C$ signatures became more depleted with time but no seasonal trends were found in the tributaries or for the reservoir (Table 5). When averaged over the season, no significant differences were found between mean $\delta^{13}C$ signatures of DIC from each area (1-way ANOVA: $F_{2, 80} = 2.94$, $p = 0.06$). However, post-hoc comparisons using the SNK-test showed that $\delta^{13}C$ of DIC of the middle Bridge River was significantly more depleted than that of tributaries ($p < 0.05$), but the reservoir $\delta^{13}C$ signature was intermediate

and could not be differentiated from either the middle Bridge River or tributary $\delta^{13}C$ DIC signatures ($p > 0.05$) (Table 5).

FOOD-WEB CHARACTERISTICS

Although some seasonal time trends were present in fish tissues and potential prey, I disregarded these seasonal trends and used data pooled over time for all food web constructions. Data were pooled under the assumption that the rate of muscle signature dilution in fish tissues is slow and requires long time periods to attain isotopic equilibrium with a new prey source with different isotopic signatures. This assumption is supported by findings from controlled feeding experiments on broad whitefish (*Coregonus nasus*), where $\delta^{13}C$ of tissues did not reach equilibrium with a new prey source that differed by –5 ‰ within 1 year, and most of the observed change in tissue signature was due to muscle growth, not tissue turnover (Hesslein *et al.* 1993). Thus, it is reasonable to assume that fish tissue stable isotope signatures reflect a long-term average of seasonal changes in prey signatures, as opposed to exhibiting similar seasonal changes in isotopic signatures within the same time frame, and that trends observed were not biologically significant.

Characteristics of potential carbon inputs to Carpenter Reservoir food webs

Differences in stable isotope signatures among potential energy sources were present for both $\delta^{13}C$ (1-way ANOVA: $F_{4, 264} = 55.24$, $p < 0.01$) and $\delta^{15}N$ (1-way ANOVA: $F_{4, 264} = 103.82$, $p < 0.01$). The SNK-test showed that terrestrial leaf $\delta^{13}C$ was more depleted than middle Bridge River drift, reservoir Chironomidae, and inferred zooplankton signatures ($p < 0.05$), but showed no

difference from tributary macroinvertebrate drift signatures ($p > 0.05$). Leaf $\delta^{15}N$ signatures were more depleted than all other potential energy sources ($p < 0.05$) (Figure 4). Middle Bridge River drift $\delta^{13}C$ signatures were more enriched than tributary macroinvertebrate drift and actual and inferred zooplankton signatures, but could not be separated from reservoir Chironomidae. For $\delta^{15}N$, reservoir Chironomidae were significantly more enriched than middle Bridge River drift, but could not be separated from tributary drift or actual and inferred zooplankton nitrogen signatures. Middle Bridge River drift, tributary drift, and actual and inferred zooplankton $\delta^{15}N$ signatures showed no differences from each other.

Within middle Bridge River drift, differences in stable isotope signatures of functional groups were present for both $\delta^{13}C$ (1-way ANOVA: $F_{3, 52} = 36.11$, $p < 0.01$) and $\delta^{15}N$ (1-way ANOVA: $F_{3, 52} = 4.20$, $p = 0.01$). The SNK-test showed that collectors were more enriched in $\delta^{13}C$ than any other functional group ($p < 0.05$) (Figure 5). Predator $\delta^{13}C$ signatures were more enriched than scraper signatures ($p < 0.05$), but neither predators nor scrapers could be differentiated from the intermediate signature of shredders ($p > 0.05$). For $\delta^{15}N$ signatures, collectors were significantly more depleted than scrapers and predators ($p < 0.05$). These latter two functional groups could not be differentiated by $\delta^{15}N$ signatures ($p > 0.05$). No functional group from middle Bridge River macroinvertebrate drift could be separated from shredders ($p > 0.05$), which showed an intermediate $\delta^{15}N$ signature (Figure 5).

In tributaries, $\delta^{13}C$ signature patterns of functional groups were different from those seen in the middle Bridge River, but still showed significant differences from each other (1-way ANOVA: $F_{3, 143} = 35.19$, $p < 0.01$). The SNK-

test showed that predators and shredders were most enriched ($p < 0.05$) but could not be differentiated from each other ($p > 0.05$), while collectors showed a unique intermediate signature and scrapers were significantly depleted from all other functional groups ($p > 0.05$) (Figure 5). Differences also existed among $\delta^{15}N$ signatures for tributary functional groups (1-way ANOVA: $F_{3, 143} = 11.67$, $p < 0.01$). The SNK-test showed that, using $\delta^{15}N$, collectors, predators, and scrapers could not be differentiated from each other ($p > 0.05$), but all were significantly more enriched than shredders ($p < 0.05$) (Figure 5).

The proportion of functional groups in drift follows the same general pattern of abundance in both the middle Bridge River and tributaries, but with actual proportions of occurrence being quite different (Figure 6). In the middle Bridge River, collectors comprise the majority of macroinvertebrates (about 90%) while the remainder is composed of predators, shredders, and scrapers, in that order. However, in tributaries, collectors account for only half of the macroinvertebrates in the drift, while predators make up over a quarter of the insects. Scrapers and shredders comprise the remaining 20% of tributary drift.

In contrast, about half of the functional group biomass in the middle Bridge River is attributed to collectors, while predators and scrapers each comprised about 20% of the drift biomass, and shredders made up the remainder (Figure 7). Biomass of macroinvertebrate drift in tributaries was predominately collectors and scrapers (75%), while shredders and predators comprise only a quarter of the tributary drift biomass.

Effects of body size and area on stable isotope signatures of fish tissues

Area effects observed in stable isotope signatures of fish tissues were consistent across species, with the exception of rainbow trout (Table 6 and Table 7, Figure 8). Generally, $\delta^{13}C$ signatures of tissues from fish captured from the middle Bridge River were more enriched, and $\delta^{15}N$ signatures were more depleted than those of fish from the reservoir. Signatures of fish captured from tributaries did not show any consistent pattern of enrichment or depletion in either carbon or nitrogen relative to fish captured from the middle Bridge River or the reservoir. Tributary signatures were rarely different from those of the middle Bridge River or reservoir. Small bridgelip suckers displayed a different pattern in $\delta^{13}C$ signatures, where fish captured from the middle Bridge River had more depleted $\delta^{13}C$ than those fish of the same size class from the reservoir. No small bridgelip suckers were captured from tributaries. Rainbow trout signatures were only affected by size, where large rainbow trout had more depleted $\delta^{13}C$ and more enriched $\delta^{15}N$ signatures than smaller rainbow trout.

Bridgelip sucker and mountain whitefish showed differences in stable isotope signatures between size classes as well as between areas, but only in some instances (Figure 8). In large fish, only $\delta^{15}N$ signatures of bridgelip sucker were affected by area; fish captured from tributaries displayed heavier nitrogen signatures relative to all other bridgelip suckers. No differences in nitrogen signatures were observed for large mountain whitefish, and no effect of area on carbon signatures was found for either large bridgelip sucker or large mountain whitefish.

Within an area, small fish tended to show $\delta^{13}C$ signatures that were more enriched than signatures of large fish (Figure 8). The exception was small

bridgelip suckers from the middle Bridge River, which had more depleted $\delta^{13}C$ signatures than large bridgelip suckers from this area. For $\delta^{15}N$, small bridgelip suckers and mountain whitefish had similar or more depleted signatures than large fish.

Comparison of stable isotope signatures of fish tissues with those of potential energy sources

Using data pooled over size and area, fish tissue $\delta^{13}C$ signatures were most similar to $\delta^{13}C$ signatures of middle Bridge River macroinvertebrate drift and reservoir Chironomidae (Figure 9). No fish species showed any similarity in $\delta^{13}C$ signatures with those of actual zooplankton, tributary macroinvertebrate drift, or terrestrial leaves. Bull trout and coastrange sculpin showed $\delta^{13}C$ signatures that were enriched relative to other fish species and reservoir Chironomidae, but these signatures were not distinct from those of middle Bridge River macroinvertebrate drift. All fish excluding bull trout formed a single trophic group, where $\delta^{15}N$ signatures of all fish are within 3 ‰ of each other. Bull trout had the most enriched $\delta^{15}N$ signatures relative to all other taxa.

Further comparisons were performed between fish tissue signatures and signatures of macroinvertebrate functional groups within the middle Bridge River (Figure 10). These analyses showed that scrapers were >1 ‰ more depleted in $\delta^{13}C$ than all fish species, indicating this carbon source was not utilized by fish. Collectors showed an enriched $\delta^{13}C$ signature that was similar only to coastrange sculpin and bull trout, but was < 5 ‰ more depleted in $\delta^{15}N$ than sculpin signatures. Middle Bridge River predators showed a $\delta^{13}C$

signature that was similar to all fish species, as were $\delta^{15}N$ signatures. This similarity in stable isotope signatures between middle Bridge River predators and all fish species indicates that this functional group may be of primary importance to fish foraging in the middle Bridge River.

Area-specific relationships between fish species and energy sources are similar to those at the whole-system level. However, some exceptions are present. In the middle Bridge River (Figure 11), small bridgelip sucker displayed depleted $\delta^{13}C$ signatures relative to all other fish species except kokanee. These depleted signatures showed greater similarity with both actual and inferred zooplankton $\delta^{13}C$ signatures, but were not distinct from the $\delta^{13}C$ of middle Bridge River or tributary macroinvertebrate drift, except for middle Bridge River collectors. When compared to middle Bridge River functional groups, small bridgelip suckers show some similarity with the depleted $\delta^{13}C$ signatures of scrapers and shredders, as well as the intermediate signatures of predators. Also, small bridgelip suckers show $\delta^{15}N$ signatures that are within 3 - 5 ‰ of $\delta^{15}N$ signatures of middle Bridge River shredders and predators. These results for carbon and nitrogen signatures indicate that small bridgelip suckers may be foraging more on either middle Bridge River scrapers and shredders and/or drift inputs from tributaries, as well as other food inputs with more enriched carbon signatures.

Conversely, coastrange sculpin and small mountain whitefish showed a much more enriched $\delta^{13}C$ signature relative to all other fish species. Coastrange sculpin signatures were most similar to those of middle Bridge River collectors, but were more than 5 ‰ enriched in $\delta^{15}N$ than this functional group, so collectors are likely not preyed upon by sculpin in the middle Bridge River.

Sculpin signatures are likely the result of some other, unmeasured prey item that has a carbon signature similar to middle Bridge River collectors but has a more enriched nitrogen signature.

Small mountain whitefish $\delta^{13}C$ signatures were not different from those of middle Bridge River collectors but were relatively more enriched than this prey item. Small mountain whitefish had $\delta^{15}N$ signatures about 5 ‰ more enriched than middle Bridge River collectors. These results for small mountain whitefish and collectors indicate that this fish species may be feeding in part on this functional group, but is also dependent on some unknown prey source with a carbon signature more enriched than middle Bridge River collectors.

For fish captured in the reservoir, small bridgelip suckers showed enriched $\delta^{13}C$ signatures relative to other fish species, while large mountain whitefish tended to be more depleted in $\delta^{13}C$ and showed signatures similar to that of inferred zooplankton (but not actual zooplankton) and predators and shredders from the middle Bridge River (Figure 12). However, $\delta^{13}C$ signatures for large mountain whitefish were indistinct from those of other fish species with intermediate carbon signatures. Large mountain whitefish $\delta^{15}N$ signatures were within 3 - 5 ‰ of $\delta^{15}N$ signatures of inferred zooplankton and predators and shredders from the middle Bridge River. Again, these data suggest that large mountain whitefish may be foraging on components of middle Bridge River drift, and possibly zooplankton as well.

Collectors from the middle Bridge River drift were most similar in $\delta^{13}C$ signatures small bridgelip suckers but these fish were more enriched in $\delta^{15}N$ than collectors by over 5 ‰, so middle Bridge River collectors are unlikely to be a part of small bridgelip sucker diet.

Coastrange sculpin from the reservoir showed $\delta^{13}C$ signatures that were more similar to reservoir Chironomidae than sculpin from the middle Bridge River and tributaries, which were distinctly enriched relative to reservoir Chironomidae.

No extremes in $\delta^{13}C$ signatures were seen among fish captured in tributaries (Figure 13), where all fish displayed $\delta^{13}C$ signatures that were most similar to $\delta^{13}C$ signatures of middle Bridge River collectors, predators and shredders and reservoir Chironomidae. However, only middle Bridge River predators and reservoir Chironomidae are likely prey items for these fish, because differences in $\delta^{15}N$ between this food source and fish with relatively depleted nitrogen signatures (i.e. sculpin, whitefish, and small rainbow trout, which are all predominately insectivorous or benthic foragers) were less than 5 ‰, while differences in nitrogen signatures between middle Bridge River collectors and shredders and the most depleted fish species were greater than 5 ‰.

Patterns in $\delta^{15}N$ signatures of fish species among regions were similar (Figures 10 - 13), with coastrange sculpin, and large and small mountain whitefish displaying $\delta^{15}N$ signatures which, at 4 - 6 ‰, were more depleted relative to other fish species. Large and small rainbow trout and small bridgelip sucker showed intermediate $\delta^{15}N$ signatures of about 6 - 7 ‰, while $\delta^{15}N$ signatures of redsided shiners were enriched relative to other fish species (other than bull trout) with nitrogen signatures of about 7 - 8 ‰. In all three areas, bull trout displayed $\delta^{15}N$ values between 9 - 10 ‰. Within tributaries, fish $\delta^{15}N$ values were more spread out from each other, as compared to the tighter groupings seen in the reservoir and the middle Bridge River.

CHAPTER 6

DISCUSSION AND CONCLUSION

The major finding of this study is that stable isotope signatures of fish in the Carpenter system were most similar to those of reservoir Chironomidae and middle Bridge River macroinvertebrate drift. Inferred zooplankton signatures also showed similarity with the stable isotope signatures of some fish species, but not to the extent of the former energy sources. Terrestrial and tributary macroinvertebrate drift, and actual zooplanton signatures appeared to make minimal contributions to fish stable isotope signatures. These patterns in signatures between fish and potential energy sources indicate a greater use by fish of secondary production in the reservoir and middle Bridge River compared with other inputs. This benthic and lotic dependence is contrary to other findings for regulated reservoirs with similar bathymetry, turbidity, and water elevation fluctuations where food webs are primarily driven by pelagic carbon sources (Kimmel *et al.* 1990; Martinez and Wiltzius 1995). These findings do, however, support recent work that describes the importance of benthic-pelagic coupling in lacustrine systems (Vander Zanden and Vadenboncoeur 2002;

Johannsson *et al.* 2000; Hecky and Hesslein 1995). These latter three studies have found that benthic secondary production plays a central role in contributing to production at higher trophic positions, because extensive zoobenthivory has been found to partially support even pelagic fish species. In fact, it is a common feature of temperate lakes in North America that benthic energy pathways account for more than half of total fish consumption (Vander Zanden and Vadenboncoeur 2002).

Stable isotope analysis proved to be an effective tool for describing these food web linkages in the Carpenter reservoir. It provided a more complete description of food source utilization than would be possible using traditional diet study techniques such as gut content analysis. Drift from the middle Bridge River and tributaries and samples from the reservoir were comprised of the same invertebrate taxa. Because it is not possible to visually identify where insects may have originated, use of stable isotopes was essential to identifying different energy sources available to and utilized by fish. Also, traditional diet analyses cannot provide an understanding of diet integrated over time, nor can they ascertain true assimilation of prey into animal tissues, whereas stable isotopes provided this information easily in the present study.

STABLE ISOTOPE SIGNATURES OF PREY SOURCES

Zooplankton versus kokanee signatures

The discrepancy I observed in seasonal mean $\delta^{13}C$ signatures between kokanee and zooplankton may be due to selective foraging by kokanee on zooplankton taxa that had relatively enriched $\delta^{13}C$ signatures compared to other

taxa. Differences in stable isotope signatures between various zooplankton taxa exist due to variations in foraging behaviour (Grey and Jones 1999; Meili *et al.* 1996). It is also possible that sizes of zooplankton selected by kokanee differed from those caught by the mesh size of the plankton net I used, resulting in kokanee only foraging from a subset of the zooplankton community that I captured. Planktivorous fish feed preferentially on zooplankton larger than 500 µm (O'Brien 1979), whereas I sampled zooplankton taxa as small as 63 µm. If large zooplankters displayed a more enriched $\delta^{13}C$ signature than all sizes of zooplankton as a whole, then this selectivity could be a contributing factor to the disparity in carbon signatures between kokanee and sampled zooplankton. I did not identify zooplankton by taxa or size, so the signature I obtained from my samples was representative of all zooplankton greater than 63 µm and not necessarily the $\delta^{13}C$ signature of zooplankton taxa or size classes utilized by planktivorous fish.

Characteristics of energy sources available to fish

The depleted stable isotope signatures of tributary macroinvertebrate drift compared to middle Bridge River macroinvertebrate drift may be attributed to differences in numerical abundance and biomass densities of the various functional groups between these inputs, and to differences in stable isotope signatures of those functional groups within these watercourses. It is unlikely that differences in carbonate rock weathering, presence of mineral springs, or differences in respiration of organic matter, all of which can influence the $\delta^{13}C$ signatures of DIC available to aquatic communities (Peterson and Fry 1987) would have caused the different $\delta^{13}C$ signatures of drift from these

watercourses, because DIC signatures from the middle Bridge River and tributaries were not significantly different from each other.

Tributary macroinvertebrate drift numerical abundances and biomass densities were more heavily weighted to functional groups with depleted $\delta^{13}C$ signatures (e.g. scrapers and shredders). Functional group numerical abundances and biomass of middle Bridge River macroinvertebrate drift were more weighted towards groups that had $\delta^{13}C$ signatures much more enriched than those of terrestrial leaves (e.g. collectors). This gradient in $\delta^{13}C$ signatures is typical of streams of various sizes within the same watershed. In watersheds, smaller streams exhibit more depleted $\delta^{13}C$ signatures than larger streams due to greater influences from groundwater inputs, as well as differences in stream metabolism and other in-stream processes involving carbon cycling that are presently not well understood (Finlay 2002).

The apparent dependence on allochthonous inputs to tributary macroinvertebrate production, while middle Bridge River macroinvertebrate production apparently uses some other, likely autochthonous, primary energy source, is consistent with the tenets of the River Continuum Concept, where low-order streams in temperate forests are thought to be more dependent on terrestrial carbon inputs while medium- to high-order streams, which lack a closed forest canopy, are more dependent on autochthonous production (Vannote *et al.* 1980).

The difference observed between carbon signatures of reservoir Chironomidae and zooplankton is expected. Although the signatures of profundal benthos cannot be differentiated from pelagic zooplankton due to the importance of settling zooplankton as a food source for profundal benthic

communities (Vander Zanden and Vadenboncoeur 2002), littoral benthos will display a different, more enriched signature than pelagic zooplankton because of the importance of algae and macrophytes (which have more enriched carbon signatures than phytoplankton due to boundary layer effects and differences in fractionation (Keeley and Sanquist 1992; Osmond *et al.* 1981)) to that community (France 1995).

SEASONAL SHIFTS IN DIET AND STABLE ISOTOPE SIGNATURES OF FISH TISSUES

Shifts in temporal foraging behavior of fish may be reflected through changes in stable isotope signatures. Different signatures over time may indicate changes in diet in response to differential resource availability, such as plankton blooms, pulses in fish recruitment, and emergence of insects in spring and summer. However, I found that stable isotopes were not particularly effective at discerning the presence of seasonal diet shifts in the various fish species of Carpenter reservoir. Although trends in fish tissue signatures with time were present, the lack of pattern in trends across species, the disparities between signatures in potential prey and fish, differences in direction of trends in stable isotope signatures with time of potential prey items compared to those of fish, and dilution of tissue signatures, especially in large fish, make it unlikely that the trends seen in fish tissues were caused by diet shifts in fish foraging behaviour, and therefore are not biologically significant.

If a shift in diet should occur, stable isotope signatures of larger fish are much less likely than smaller fish to reach the stable isotope signature of the new prey source within a growing season given the lower growth and metabolic rates of larger fish compared to smaller fish (Vander Zanden *et al.* 1998). Thus,

it was surprising to see that seasonal trends in stable isotope signatures were present not only in small rainbow trout and whitefish, but also in large rainbow trout and bridgelip sucker. Redsided shiners from the reservoir and coastrange sculpins throughout the Carpenter reservoir also showed significant seasonal trends, even though mature fish were present in these datasets. This is contrary to the findings of Johnson *et al.* (2002), where no seasonal trends were found in natural fish populations from a similar regulated river system in Colorado, USA.

It would be expected that if small rainbow trout and mountain whitefish were foraging from one food source only (rather than shifting over the season) and if that food source underwent seasonal changes in stable isotope signatures, then the direction of seasonal trends in stable isotope signatures of small rainbow trout and mountain whitefish would match those of the food source. However, trends were not similar between these fish and macroinvertebrate drift from either the middle Bridge River or from tributaries (seasonal trends for inferred zooplankton signatures and reservoir Chironomidae are unknown because only point estimates of stable isotope signatures for these energy sources exist). Thus, it is unlikely that seasonal trends in stable isotope signatures of macroinvertebrate drift were responsible for the observed seasonal trends in small rainbow trout and mountain whitefish tissues.

Small rainbow trout and whitefish can also be planktivorous (Scott and Crossman 1973). Zooplankton were significantly more depleted than middle Bridge River drift, so a positive trend in fish tissues would be seen if fish switched from feeding from zooplankton to middle Bridge River drift. However,

at no point did small rainbow trout and mountain whitefish exhibit $\delta^{13}C$ signatures similar to those of zooplankton, so it is unlikely that these fish underwent a diet shift between prey items during the sampling season.

It is also unlikely that small rainbow trout and mountain whitefish tissues switched foraging arenas at some point during the sampling period. Because the $\delta^{13}C$ trend in small rainbow trout and mountain whitefish was positive, any dietary shift that did occur would have to be from a more depleted $\delta^{13}C$ source to a more enriched $\delta^{13}C$ source. Given this constraint, these fish would have to undergo a diet shift from feeding on the more depleted tributary macroinvertebrate drift to feeding on reservoir Chironomidae or middle Bridge River macroinvertebrate drift, which are more enriched. However, small rainbow trout and mountain whitefish tissues at the start of the growing season did not display carbon signatures depleted enough to indicate that tributaries had been a preferred food source at that time, although it is possible that these small fish were feeding from these sources and had not yet reached isotopic equilibrium between their muscle tissues and food source. But, if small rainbow trout and mountain whitefish had switched to feeding on tributary drift, then over the growing season their new tissues would have exhibited a negative trend in carbon signatures with time, and not the positive trend I observed.

Because of the disparities in direction of trends and carbon signatures between small fish and their prey, and because large fish should not readily reflect diet changes over the course of a season due to low tissue turnover rates and low growth rates, the observed seasonal trends in fish tissue $\delta^{13}C$ and $\delta^{15}N$ signatures are likely due to some unmeasured process as opposed to seasonal

changes in foraging behavior. The middle Bridge River, tributaries, and the reservoir cover large geographic areas. I conducted all sample collection under the assumption that distribution and movement of fish within the system was random over time and space, and as such individual fish from each species were being sampled from a single large population.

However, differences in stable isotope signatures across space may operate on smaller scales than these broad regions. Local signatures may be more reflected in fishes that display higher site fidelity than fishes that are more mobile. Thus, the temporal trends in fish stable isotope signatures may be, in part, an artifact of local stable isotope signatures as opposed to actual seasonal trends. Conversely, seasonal patterns in fish movement may be such that certain groups within a species may have been sampled more heavily than others. If these groups displayed unique signatures, then this greater representation may have biased the isotope signatures for a species within a particular month.

Lastly, I did not extract lipids from fish tissues prior to spectroanalysis, so it is possible that decreasing lipid content over time in fish tissues caused the observed seasonal trends in stable isotopes. Because lipids contain less ^{13}C than muscle tissue, lower lipid content may result in a more depleted whole tissue $\delta^{13}C$ signature (Degens *et al.* 1968; McConnaughy and McRoy 1979; DeNiro and Epstein 1977). If fish tissue lipid content decreased during the season, then this event may have resulted in an overall depletion of $\delta^{13}C$ signatures with time. However, due to increased availability of macroinvertebrate prey, it is more likely that body condition of fish (and

therefore lipid content) increased over the summer, which would result in an overall increase of $\delta^{13}C$ signatures with time.

LIFE HISTORY SHIFTS IN DIET AND STABLE ISOTOPE SIGNATURES OF FISH TISSUES

Stable isotope analysis can be useful in determining diet over the life history of fish by using size as a proxy for time. This use is based on the expectation that stable isotope signatures in fish tissues may change over the life history of fish, given the major assumption that as fish grow their larger gape allows for foraging upon larger prey items which would have more enriched $\delta^{15}N$ values than smaller prey items.

However, the assumption that larger fish will eat larger prey is not necessarily the true state of nature, because larger fish may simply forage from a broad range of prey sizes (Trippel and Beamish 1993), and this opportunistic behavior will obscure relations between stable isotope signatures and body size. Due to broad feeding habits, trophic position of an animal does not tend to increase with body size despite ontogenetic diet shifts (Vander Zanden *et al.* 2000), so it is difficult to investigate how stable isotopes may or may not change with increasing fish body size.

Regardless of this theory, I found no evidence of any significant trends in either $\delta^{13}C$ or $\delta^{15}N$ with body length for any of the species of fish collected in 2001. These findings are comparable with those of Johnson *et al.* (2002) and Vander Zanden *et al.* (2000). Even fish that undergo ontogenetic diet shifts, such as rainbow trout and bull trout, showed no significant relations between $\delta^{15}N$ and body length. Although the lack of any trend in bull trout signatures

may be due to the absence of small size classes in my samples, Vander Zanden (2000) found that for a particular taxon, the trophic position indicated by $\delta^{15}N$ signatures does not increase with body size for that taxon, but increases in trophic position will occur across multiple taxa with increasing consumer order.

SIZE AND AREA EFFECTS IN STABLE ISOTOPE SIGNATURES OF FISH TISSUES

The consistent across-species differences in stable isotope signatures of fish tissues collected from different areas suggests that fish from the middle Bridge River may have utilized prey with enriched $\delta^{13}C$ signatures slightly more than prey with depleted $\delta^{13}C$ signatures, while fish from the reservoir were slightly more dependent on prey with depleted signatures over prey with enriched signatures. Given that fish from tributaries showed no patterns in $\delta^{13}C$ or $\delta^{15}N$ signatures relative to those of fish from other areas, it is possible that fish captured in tributaries may be more mobile or less likely to be dependent on one foraging arena over another.

Even with these slight regional differences in stable isotope signatures, the majority of fish exhibit $\delta^{13}C$ signatures that are most similar to middle Bridge River macroinvertebrate drift or reservoir Chironomidae. Because the carbon signatures of these two input sources cannot be separated, it is impossible to discern whether fish are feeding from middle Bridge River inputs, reservoir littoral inputs, or both. However, it is likely that some site fidelity exists in the foraging behaviour of fish caught from the middle Bridge River and the reservoir, especially with respect to smaller, less mobile fish such as sculpin or small size classes of other fish species. Of these fish, those caught in the

upper reaches of the middle Bridge River are unlikely to be feeding several kilometers away in the reservoir, and vice versa. Larger fish may be more mobile, and it is possible that these fish may be able to forage from any and all habitats, but this cannot be determined based solely on the stable isotope results of my study.

COMPARISON OF STABLE ISOTOPE SIGNATURES OF FISH WITH THOSE OF ENERGY SOURCES

Generally, fish stable isotope signatures were most similar to those of middle Bridge River predators and reservoir Chironomidae. Most fish species displayed carbon signatures that were within 1 ‰ of these prey sources, and those fish with the most depleted nitrogen signatures were within 3 to 5 ‰ of reservoir Chironomidae and middle Bridge River predators. Fish species that were enriched by more than 5 ‰ than these two prey items had some element of piscivory in their known foraging behaviour (Scott and Crossman, 1973). If these fish preyed upon reservoir Chironomidae and middle Bridge River predators, and also preyed on smaller fish that were also dependent on these macroinvertebrates, then fish predation would account for the much more enriched nitrogen signatures of these fish relative to these particular prey items, while retaining similar carbon signatures.

It is also possible that fish carbon signatures were an intermediate mixture of enriched and depleted prey items, as would be the case if fish were feeding from middle Bridge River collectors and scrapers and/or shredders, respectively. While these macroinvertebrate functional groups were more depleted in $\delta^{15}N$ than predators and therefore the change in nitrogen signatures

between these prey items and fish is larger than that seen between predators and fish, recent work has shown that, especially in nitrogen limited systems, the degree of change in nitrogen signatures between a predator and its prey can be quite variable, encompassing ranges that traditionally have been thought to represent an increase of two trophic levels (Adams and Sterner 2000). However, the extent of this variation is relatively small between a secondary or tertiary consumer and their prey compared to a primary consumer and its plant food source, and is a minor source of error to trophic position estimates, especially in qualitative analyses (Vander Zanden and Rasmussen 2001) such as those in my study. Collectors, shredders and scrapers did represent the majority of the numerical abundance and biomass of macroinvertebrates found in the middle Bridge River drift, and so are likely foraged upon by fish residing in the river as often or more than are predators, assuming fish do not display selective foraging behaviour on the different macroinvertebrate functional groups available to them as prey.

While I had difficulty obtaining samples of reservoir Chironomidae in the field due to their rarity, this inability to find Chironomidae in the littoral zone is more likely attributed to problems associated with access than with actual abundances of Chironomidae in the littoral zone. Due to unstable substrates and water depth, I was unable to sample the reservoir littoral zone beyond a distance of one to two meters from the water's edge. Because of the rapid infilling rate experienced by the reservoir, macroinvertebrate colonization of recently inundated accessible areas would have been negligible. Deeper areas of the littoral zone that had been inundated for longer time periods would more than likely have greater numbers of Chironomidae present in the benthos, and

would therefore be available for fish, which may explain the apparent discrepancy between scarcity of reservoir Chironomidae and reliance of fish on this prey item given similarity in stable isotope signatures. However, it is possible that reservoir Chironomidae were actually rare, but it is not possible to determine how important they were to fish as a food source, given their similarities in carbon signature with middle Bridge River drift.

While most fish species had isotope signatures similar to those of middle Bridge River drift and reservoir Chironomidae, some fish species displayed signatures that were more similar to other potential energy sources, although these similarities may or may not be attributed to foraging upon these alternate energy sources.

Small bridgelip suckers in the middle Bridge River showed depleted $\delta^{13}C$ signatures that were intermediate to those of zooplankton (actual and inferred), and tributary and middle Bridge River drift. When macroinvertebrate functional groups from the middle Bridge River drift were considered, these fish signatures were also found to be intermediate to shredders and predators.

However, note that the individual fish that comprise the $\delta^{13}C$ signature for small bridgelip suckers were all captured from a small tributary to the middle Bridge River, Fergusson Creek. This small, localized sample is likely a poor representation of how small bridgelip suckers may be foraging within the whole of the middle Bridge River. This sample is non-random and could be biased to reflect attributes particular to stable isotopes of small watersheds, particularly the depleted $\delta^{13}C$ signatures in primary production (Peterson and Fry 1987).

The examination of middle Bridge River drift functional groups provides insight into why some fish species displayed relatively enriched $\delta^{13}C$ signatures compared to other fish species and energy sources. In the middle Bridge River, coastrange sculpin and small mountain whitefish exhibited $\delta^{13}C$ signatures very similar to those of collectors, and displayed an enrichment of about 5 ‰ in $\delta^{15}N$ signatures, indicating that these fish may depend more on this functional group as a food source than other functional groups present in the drift. However, small mountain whitefish displayed $\delta^{13}C$ signatures that were somewhat more enriched than even collectors, indicating that there may be some other, unmeasured carbon source available in the reservoir upon which these fish foraged. Complementary gut content analysis is necessary to ascertain the true diet of these fish and resolve these speculations. Alternatively, the enriched carbon signature of these fish may have been obtained elsewhere (also unmeasured), depending on the mobility of mountain whitefish during the first part of their life history.

Within the reservoir, small bridgelip sucker $\delta^{13}C$ signatures were similar to those of middle Bridge River collectors. However, this direct trophic link cannot explain the $\delta^{13}C$ enrichment seen in these fish. Although the $\delta^{13}C$ signature of small bridgelip sucker is similar to that of collectors in middle Bridge River drift (and is far more enriched than $\delta^{13}C$ signatures for reservoir Chironomidae), the $\delta^{15}N$ enrichment of 7 ‰ between these two taxa precludes any direct foraging of small bridgelip sucker on collectors from middle Bridge River drift.

RESERVOIR MANAGEMENT

Based on these results, it is possible to draw some limited conclusions that are relevant to the management of Carpenter reservoir. Fish stable isotope signatures within the Carpenter system are most similar to those of middle Bridge River macroinvertebrate drift (or components thereof) and reservoir Chironomidae and are not similar to those of pelagic zooplankton and tributary drift. Because of this similarity between fish and invertebrate production in the middle Bridge River and reservoir, managers who wish to promote fish production should favor operations that ensure high rates of macroinvertebrate production within the middle Bridge River and the littoral areas of the reservoir, as opposed to operations that promote pelagic or tributary production. However, because the stable isotope signatures for the middle Bridge River drift and reservoir Chironomidae cannot be separated, stable isotope analysis cannot be used to understand to what extent fish utilize each of these food sources. Because of this problem, it is also impossible to choose between scenarios that make tradeoffs between production levels in the middle Bridge River and the reservoir.

As part of the ongoing Water Use Planning process for the Bridge-Seton hydroelectric system, and Integrated Response Model (IRM) has been developed for BC Hydro. The IRM simulates the dynamics of different performance measures for 27 alternative operating scenarios by quantifying the hydrodynamics of the system and their potential effects on various food sources in the overall carbon budget of the reservoir. These alternative scenarios cover a range of management options that differ by reservoir elevation and ponding/draw down rates, littoral and pelagic reservoir productivity, river

productivity and riparian habitat benefits, annual discharge, and power gerneration, among others.

The main purpose of the IRM is to help managers understand how different measures perform under various operating scenarios and the nature and extent of trade-offs that must occur between performance measures among these regimes. For example, if managers want to increase river production, the maximum elevation of the reservoir could be lowered, thus increasing the length of non-inundated riverbed. This action comes at the expense of reduced water surface area and water clarity in the lentic area of the reservoir, which may decrease pelagic and littoral production. Managers must understand the system's ecological dynamics in order to implement those operating scenarios which have trade-offs with the least impact on ecosystem productivity. In the example above, if river production contributed little to reservoir carbon budget relative to production from the lentic zone in the reservoir, it would not be advisable for managers to adopt that strategy which increases river production if the goal was to increase overall aquatic production in the system.

The IRM functions as a series of sub-models, each simulating a different component of the Bridge-Seton system. There are seven sub-models in total:

1. A *water-routing module* where the surface area, volume, and turnover time of water in each reach in the reservoir is predicted as a function of water surface elevation and discharge.
2. A *sediment-routing module* that predicts the input of suspended sediment and its fate within the reservoir based on assumed settling and resuspension rates and predictions of turnover time from the water-routing module.

3. A *pelagic productivity module* which uses predictions of solar insolation at depth to estimate the mean photosynthetic rate of phytoplankton over the growing season. Zooplankton productivity is computed as a function of a mean photosynthetic rate and an assumed production-to-biomass rate (i.e. P/B or turnover rate). This estimate is scaled to the entire reservoir based on predicted surface area.
4. A *littoral productivity module* predicts the biomass of benthic invertebrates per unit area (primarily Chironomidae) as a function of solar insolation accrued over the growing season and the biomass of flooded vegetation. Reservoir-wide estimates of production are computed by scaling up the per unit area biomass values derived from a Digital Elevation Model and multiplying by an assumed P/B ratio. Predictions of the biomass of flooded vegetation are derived from the riparian vegetation model.
5. A *river productivity module* predicts the biomass of benthic invertebrates in flowing reaches of the reservoir as a function of water velocity, using a P/B ratio for Chironomidae in flowing water.
6. A *drift module* predicts the input of macroinvertebrates from tributaries as a function of observed drift densities and local inflows predicted from the water-routing module.
7. A *riparian vegetation module* predicts the response of multiple types of vegetation to variations in water surface elevation based

on the specific biology of those vegetation types and their response to different flooding durations under different operating regimes.

From the 27 possible operating scenarios developed for the Bridge River Water Use Plan, I have chosen to assess four scenarios with respect to the appropriateness of each action given the findings of current study and a goal of maintaining or increasing fish productivity in the Carpenter reservoir. These scenarios are as follows:

- **Alternative B**: Current operating regime (status quo).
    - Under this scenario, reservoir operations do not change from the present regime.
- **Alternative G**: Stabilize Carpenter reservoir at 643.3 above sea level.
    - No seasonal drawdown is associated with this scenario, and discharge rates are equal to infilling rates, creating a stable water surface elevation.
- **Alternative M5**: Highest productivity within Carpenter reservoir and the middle Bridge River, without trade-offs for the needs of other parts of the Bridge-Seton system.
    - This scenario predicts the highest levels of production in the portion of the Bridge-Seton system between La Joie and Terzaghi Dams, but treats this section as if it was independent, and does not consider the requirements other areas of the system outside of these boundaries.

- **Alternative N2**: Highest productivity within Carpenter reservoir and the middle Bridge River, after making trade-offs to accommodate the needs of other parts of the system.
    - This scenario, which is the final choice of the BC Hydro WUP consultative committee, predicts the highest levels of production in the portion of the Bridge-Seton system between La Joie and Terzaghi Dams, given the constraints of both ecosystems and hydroelectric generation in Downton and Seton reservoirs, and in the upper and lower Bridge Rivers.

Because stable isotope signatures of fish in the Carpenter reservoir are most similar to those of reservoir Chironomidae and middle Bridge River drift, and not pelagic zooplankton, it is advisable to choose a scenario that encourages macroinvertebrate production in reservoir littoral areas and the middle Bridge River production. However, no further discrimination between scenarios can be made, because it is impossible to use stable isotope analysis alone to recommend how to make tradeoffs between reservoir and middle Bridge River production. Therefore, based on my data, I can only make very limited recommendations as to which proposed operating scenarios would better promote fish production in the Carpenter reservoir.

When the four scenarios are compared using only the performance measures of littoral riverine and pelagic production, it is impossible to make a recommendation as to which scenario would most benefit fish production (Table 8). While the IRM predicts that scenario N2 will result in the lowest pelagic production levels of all four alternatives, this does not mean that scenario N2

has higher values of littoral and riverine production when compared with the other scenarios. Instead, scenario B is predicted to have the highest level of littoral production, while scenario N2 actually has a low level of littoral production. The model does predict that scenario N2 has the highest river productivity of all four alternatives, but the actual difference is small and likely not biologically significant.

If fish utilized littoral and riverine production equally, then the predicted production levels for each of these sources could be treated as additive, and the scenario with the highest level of production from the middle Bridge River and the reservoir littoral zone would be the best alternative for fish production given these few performance measures. If this assumption were true, then scenario B, the status quo, would be the first choice for managers, followed by scenarios M5, N2, and G, in that order. However, this assumption is very strong, and if fish actually utilize river production and littoral production differently, then scenario B, may not be the ideal alternative for managers wishing to promote fish production in the Carpenter reservoir. For example, if fish are more dependent on river production than littoral production, then scenario N2 may be the best of the four alternatives, because it has the highest level of riverine production. However, as mentioned previously, the difference between the level of river production for scenario N2 and the other scenarios is small, and may not be biologically relevant.

The IRM also predicts annual power generation (GWh/year) and water rent for each scenario (where water rent is the cost of water used by BC Hydro payable to BC Water and Land, as a condition of the water license for the Bridge-Seton system). Scenarios M5, and N2 are predicted to have the same

power generation, and those two scenarios plus scenario B have similar water rent, about 2 600 GWh and $13 million, respectively. Scenario G, with its stable reservoir elevation, is predicted to have the lowest annual power generation (609 GWh) and water rent ($3 million) of the four alternatives. Although biological data cannot be used to recommend a specific operating scenario that would benefit fish production, it can be said that scenario G is the least desirable scenario by which to operate this hydroelectric reservoir given the low annual power generation predicted for this alternative compared to the three other alternatives.

Because Carpenter reservoir is not an independent water body, any operating scenario implemented on the reservoir will affect how other parts of the Bridge-Seton system operate and function. Since other terrestrial and aquatic habitat and wildlife requirements must be considered, and the capacity for hydroelectric generation must meet the demands of BC Hydro customers, the Bridge River WUP will include scenario N2 as its recommended operating strategy for managers.

It should be noted that none of the 4 operating strategies involve any major changes to current reservoir volume. Increasing reservoir habitat through increased volume was found to be favorable to managing for lake trout productivity in Lake Granby, Colorado. A high reservoir volume in this regulated system, coupled with abundant food resources, greatly increased lake trout production (Martinez and Wiltzius 1995). Although similarities exist in life history foraging behavior between lake trout and bull trout (Scott and Crossman 1973), increased lake volume may not be a feasible management option for production of this endangered species within Carpenter reservoir.

Production in Lake Granby is driven by zooplankton carbon sources, and overstocking with kokanee fry there has provided lake trout with an unnatural and abundant prey source, further increasing production of this apex predator. Production in Carpenter reservoir does not appear to be driven by zooplankton carbon, and no stocking occurs at present within the reservoir.

APPLICATION OF STABLE ISOTOPE ANALYSIS TO FUTURE STUDIES ON SIMILAR SYSTEMS

Although stable isotope analysis was an essential tool in describing fish food web dynamics within the Carpenter reservoir hydroelectric system, this method is best used as a complement to information obtained from other ecological studies, as opposed to a stand-alone technique. Limitations of stable isotope studies include low taxonomic resolution of potential prey items, inability to properly reflect complex food webs, potential for non-separation of isotopic signatures of potential energy sources, potential for diet shifts in space and time, and unknown actual metabolic fractionation rates of organisms. However, while pervasive and just cause for concern, these limitations can be addressed through the combined use of different field methods and articulation of objectives to ensure the bounds of the study are clear and that objectives can be achieved with this technique.

While stable isotope analysis was able to address the objectives of the present study, there is much potential for this technique to be even more effective at revealing the nature of food web linkages within regulated systems. Future studies that use this technique for the purpose of diet analysis within rivers and lakes could benefit from the following considerations.

As shown in this study with the similarity in carbon signatures between fish and reservoir Chironomidae, as well as in other studies (e.g. Johnson *et al.* 2002; Vander Zanden and Vadenboncoeur 2002; Hecky and Hesslein 1995), benthic carbon is an important contributor to lacustrine productivity. Food web studies or models would be more realistic with the explicit incorporation of this energy pathway, and so benthos from both the littoral and profundal zones should be sampled, preferably quantitatively. Doing so would provide researchers not only with information regarding the importance of benthic energy to lacustrine and riverine food webs, but also how the strength of contribution of benthic energy to food webs compares to the proportion of total available energy made up by benthic energy present in the system.

However, profundal benthos are difficult to distinguish from pelagic plankton because benthos have $\delta^{13}C$ signatures that reflect those of settling pelagic plankton or some component thereof (Vander Zanden and Rasmussen 1999). Thus, use of stable isotope analysis should be used in conjunction with gut analysis to determine whether signatures found in fish tissues are the result of foraging on benthic or pelagic organisms. Use of complementary diet analyses is also important because stable isotope analysis alone can underestimate the importance of benthic-pelagic coupling in lake ecosystems if researchers mistake $\delta^{13}C$ signatures of fish tissues as being derived from pelagic instead of benthic sources (Vander Zanden and Vadenboncoeur 2002).

Detailed analysis of the pelagic zooplankton community may also be beneficial to further understanding the linkages involved in benthic-pelagic coupling within lacustrine and riverine ecosystems. In the present study, no

attempts were made to differentiate zooplankton by taxa and size. Zooplankton size can affect availability of this prey source to different planktivorous fish species, thus affecting fish tissue signatures (Branstrator *et al.* 2000). Also, different taxonomic compositions of zooplankton may be utilized by benthic macroinvertebrates as compared to pelagic fish. Benthic communities would reflect a $\delta^{13}C$ signature representative of the whole of the zooplankton community (due to settling of all taxa), whereas fish signatures may only reflect a subset of that community, depending on foraging selectivity by size and taxa.

Investigation into patterns of fish movement would also be beneficial to studies conducted on large systems. Although the present study sampled fish under the assumption that populations were dispersed randomly over time and space, such distribution is not necessarily correct. Because stable isotopes of energy sources may differ over time and space, these non-random movements may confound attempts to investigate energy pathways in food webs, and should be understood prior to reconstructions of food webs.

Changes in body condition of longer-lived animals, such as fish, over the sampling season may result in changes in stable isotope signatures. Changes in lipid content of muscle tissues may reflect changes in δ13C signature. Future studies should either remove lipids from muscle tissue prior to analysis, or monitor changes in lipid content of tissue with time. Understanding changes in body condition may aid in correctly interpreting seasonal changes in stable isotope signatures of tissues.

CONCLUSION

Despite the coarse resolution of stable isotope analysis in food web studies, this method was appropriate and effective in meeting the objectives of my study. Used in combination with other methods, this approach has the capacity to provide researchers with a depth of understanding of ecological systems that would not otherwise be possible using traditional techniques.

By better understanding how energy sources are utilised by fish food webs in the Carpenter reservoir, appropriate operating strategies may be devised, given the objective of maintaining or increasing fish production in this system. There is great potential for conservation of fish and fish habitat in this system, and promoting energy production in the middle Bridge River and the reservoir would be an essential first step in managing from the perspective that the reservoir is a functioning ecosystem, and not a static, artificial construct within which fish happen to be present.

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FIGURES

Figure 1: Location of the Bridge River, B.C. (BCRP 2002; Land Data B.C. 2003).

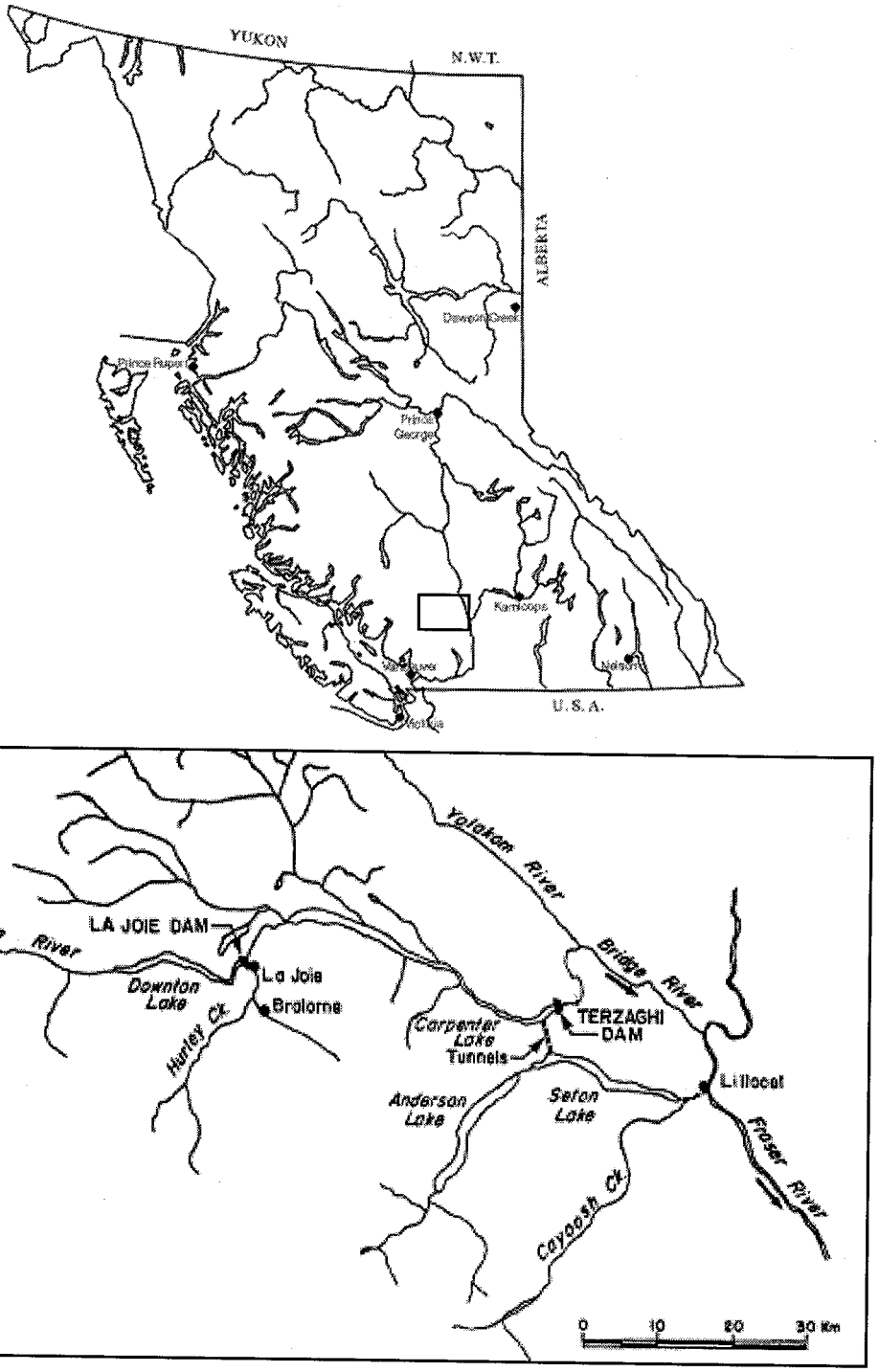


Figure 2: Map of study area showing middle Bridge River, Carpenter reservoir, major tributaries, and location of study sites (open circles).

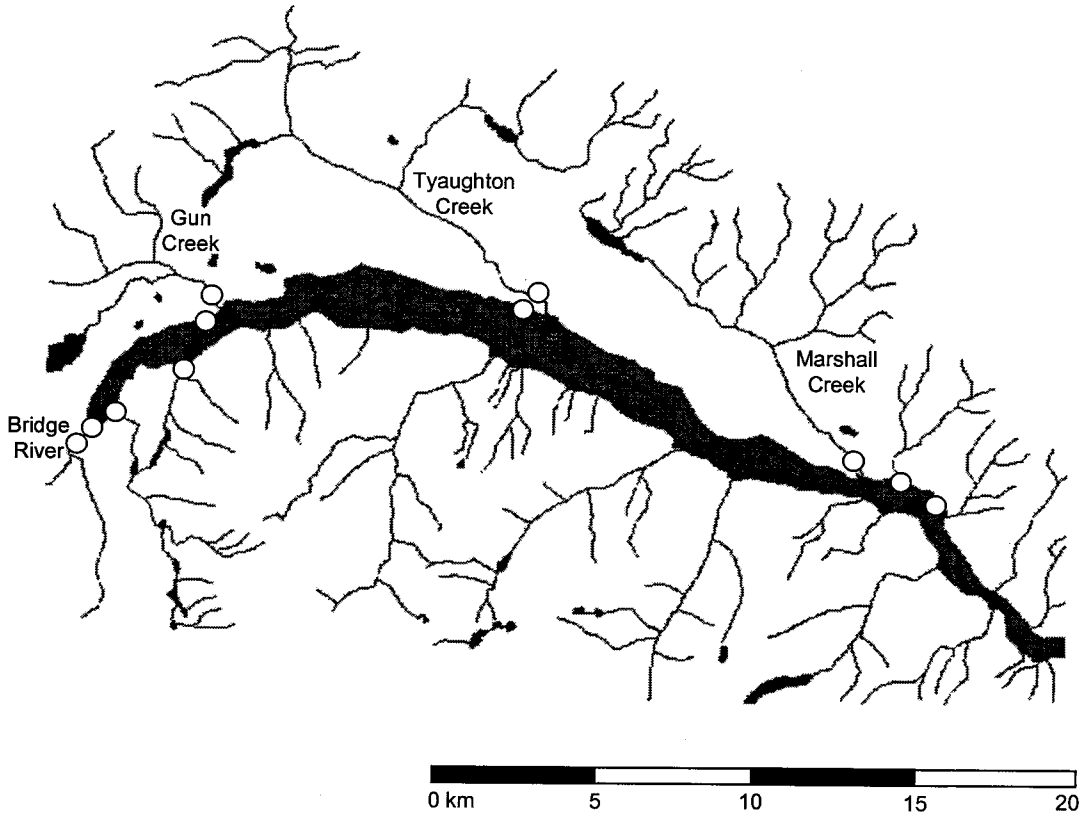


Figure 3: Stable isotope plot of $\delta^{13}C$ and $\delta^{15}N$ signatures (mean ± 2SE) of pooled seasonal signatures for actual zooplankton and kokanee sampled from Carpenter reservoir.

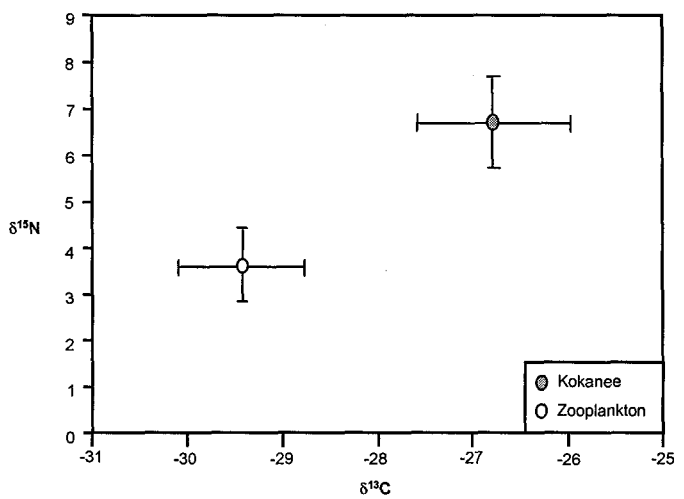


Figure 4: Stable isotope plot of $\delta^{13}C$ and $\delta^{15}N$ signatures (mean ± 2SE) of pooled seasonal signatures for middle Bridge River invertebrate drift, tributary invertebrate drift, Reservoir Chironomidae, actual zooplankton, inferred zooplankton and conditioned terrestrial leaves.

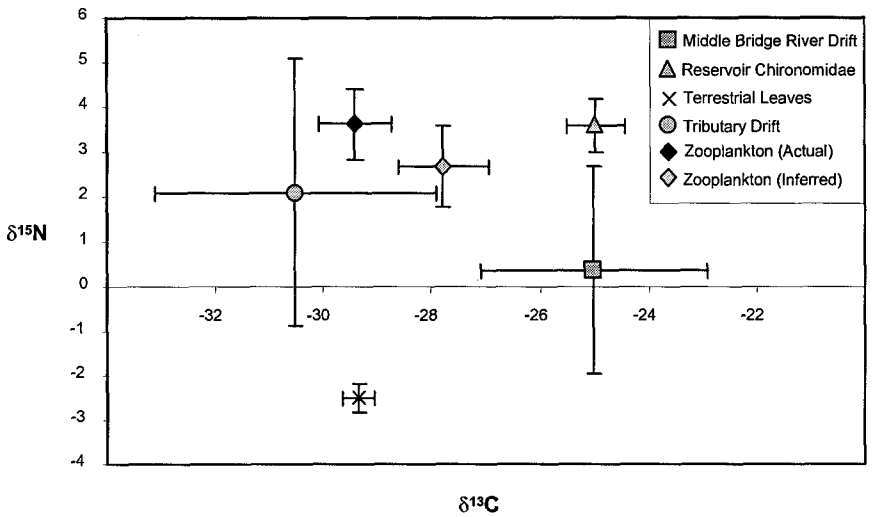


Figure 5: Stable isotope plot of $\delta^{13}C$ and $\delta^{15}N$ signatures (mean ± 2SE) of macroinvertebrate functional groups found in the middle Bridge River and tributary drift, where "MBR" denotes middle Bridge River and "Trib" denotes tributaries.

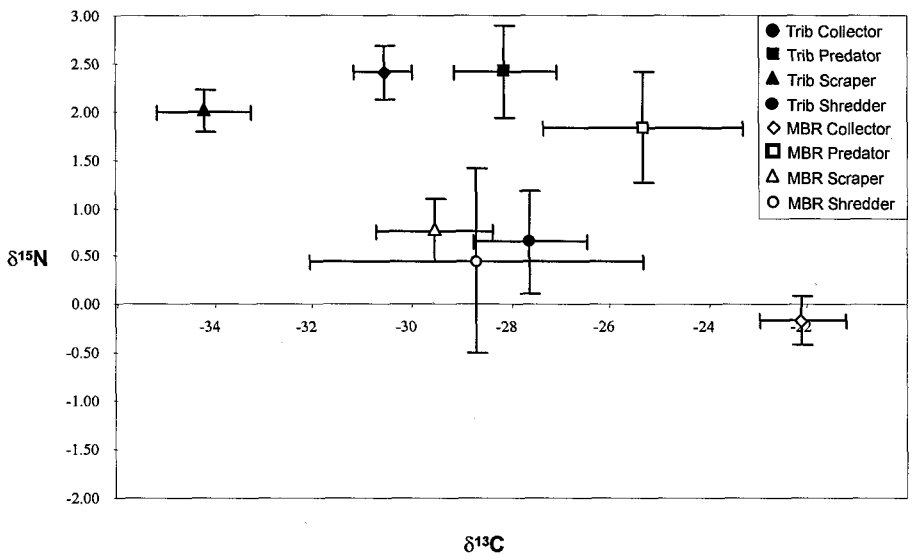


Figure 6: Proportion of numerical abundance of macroinvertebrate functional groups within drift from the middle Bridge River and tributaries (proportion ± 2SE).

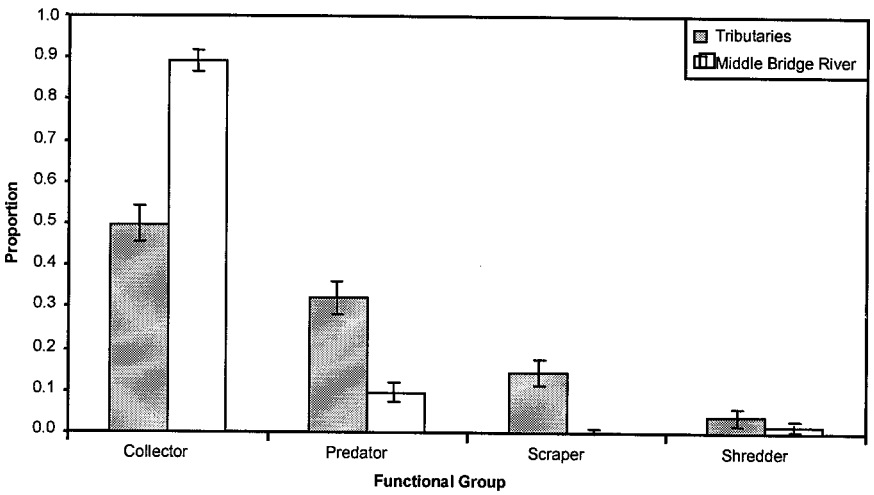


Figure 7: Contribution to biomass (mg/100 m^3) by macroinvertebrate functional groups within drift from the middle Bridge River and tributaries (proportion ± 2SE).

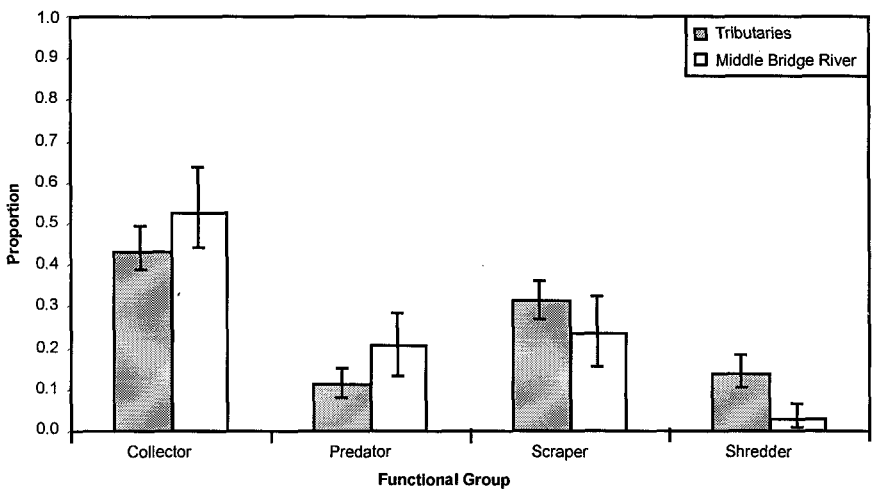


Figure 8: Size and area effects on $\delta^{13}C$ and $\delta^{15}N$ signatures (mean ± 2SE) of fish tissues from fish caught throughout the Carpenter system.

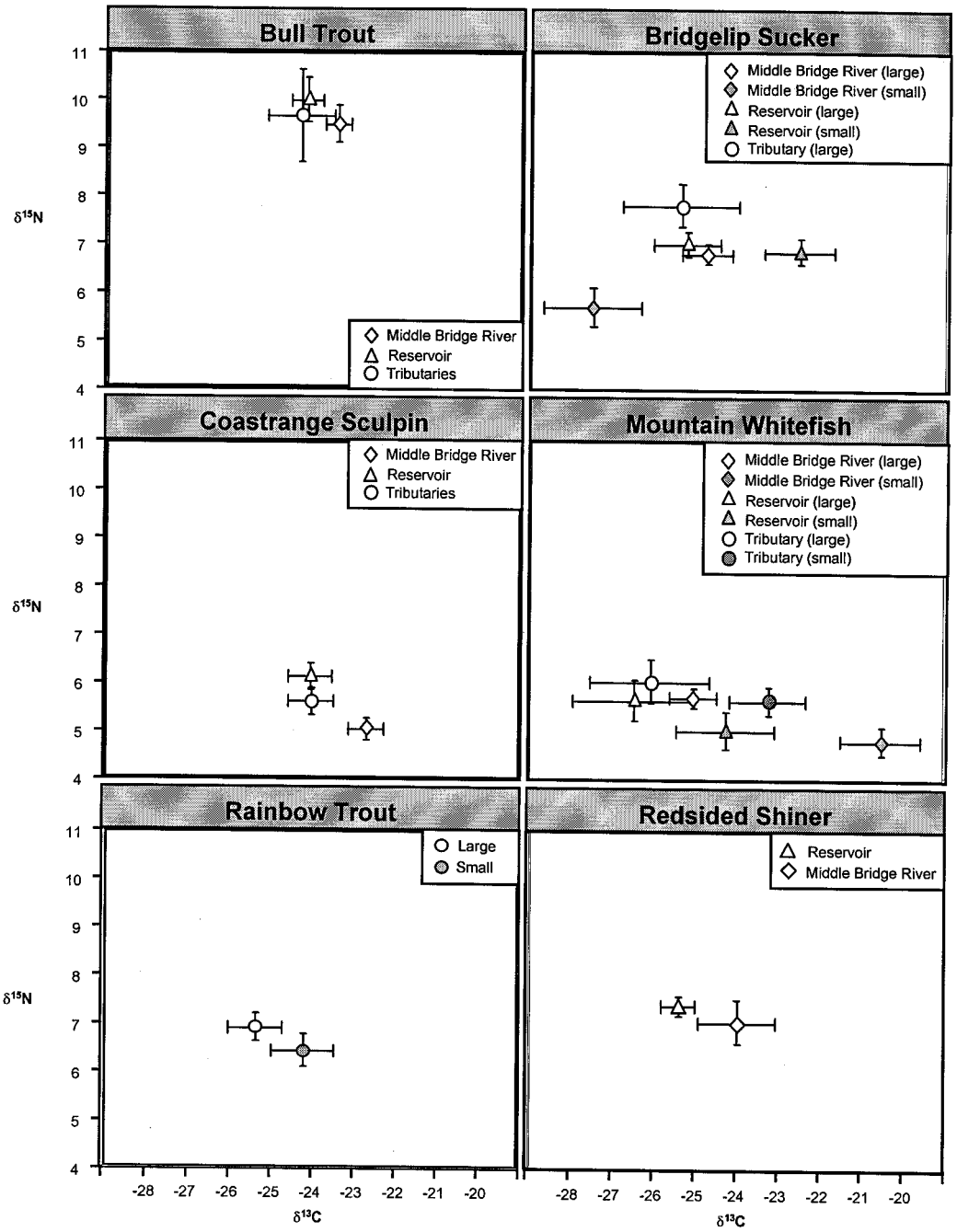


Figure 9: Stable isotope plot of $\delta^{13}C$ and $\delta^{15}N$ signatures (mean ± 2SE) of fish and potential energy sources in the whole of the Carpenter system where fish species are pooled by size and area.

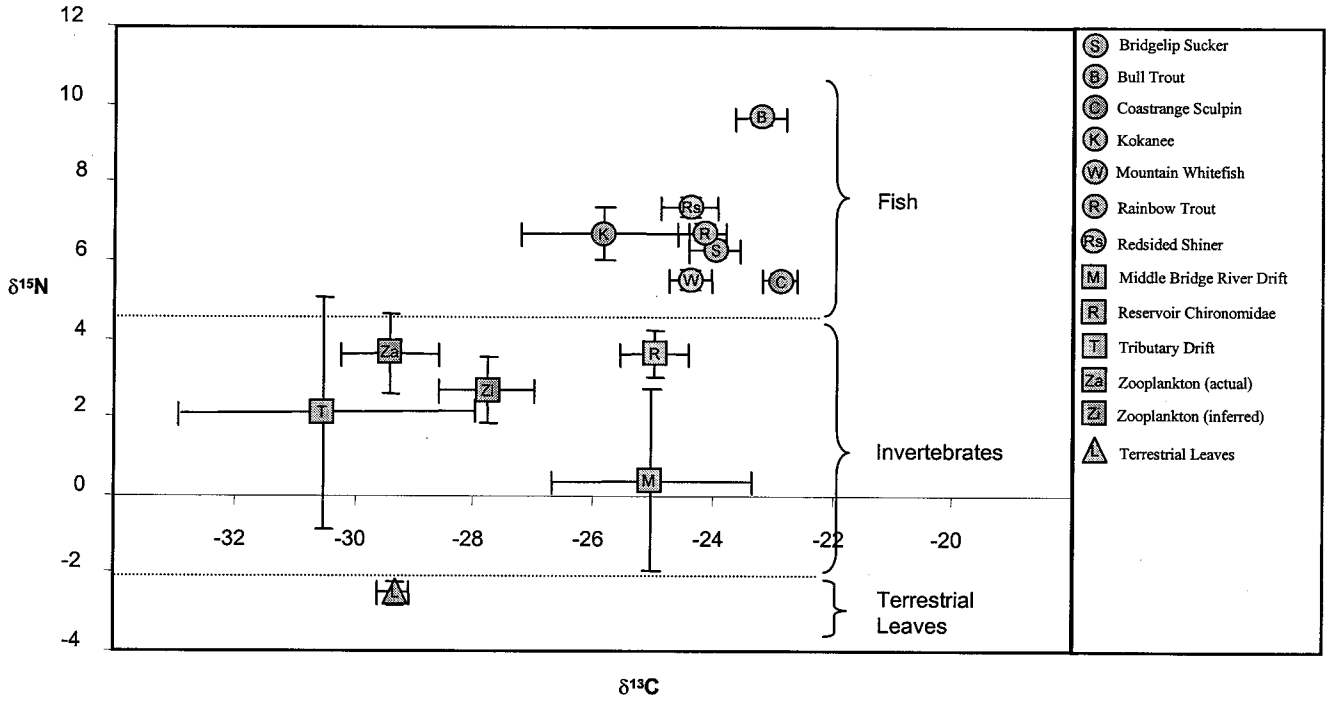


Figure 10: Stable isotope plot of $\delta^{13}C$ and $\delta^{15}N$ signatures (mean ± 2SE) of fish and potential energy sources in the whole of the Carpenter system where fish species are pooled by size and area, and middle Bridge River (MBR) drift is expanded to show functional groups.

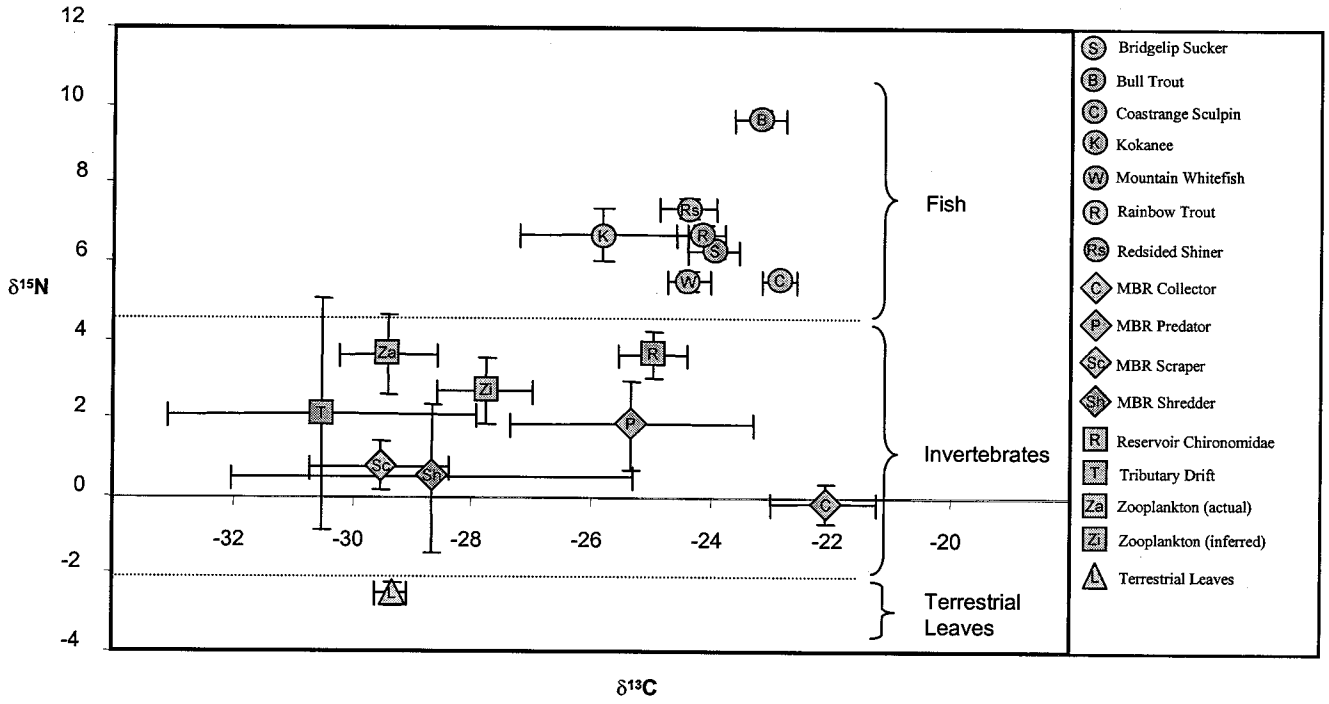


Figure 11: Stable isotope plot of $\delta^{13}C$ and $\delta^{15}N$ signatures (mean ± 2SE) of fish tissues caught from the middle Bridge River compared to $\delta^{13}C$ and $\delta^{15}N$ signatures (mean ± 2SE) of potential energy sources, with middle Bridge River (MBR) drift expanded to show macroinvertebrate functional groups.

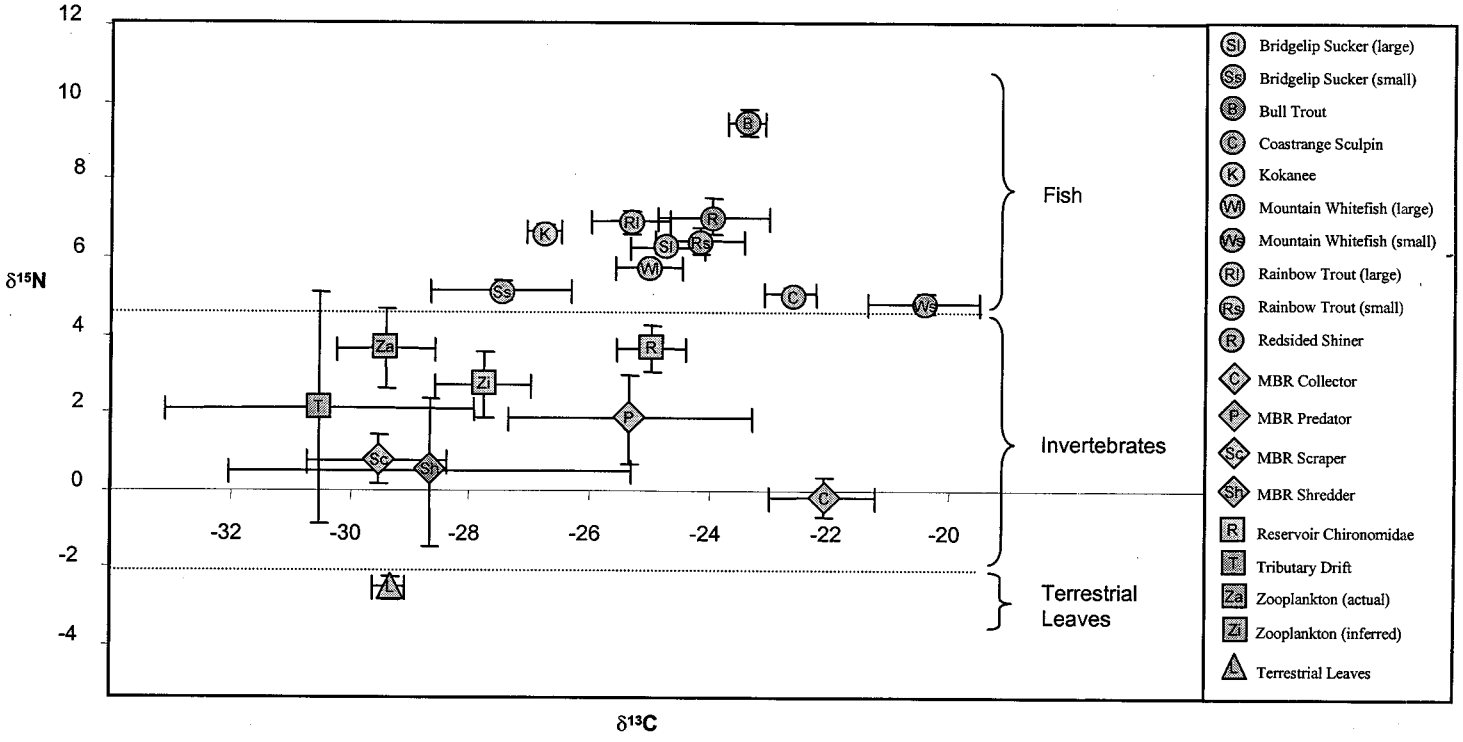


Figure 12: Stable isotope plot of $\delta^{13}C$ and $\delta^{15}N$ signatures (mean ± 2SE) of fish tissues caught from the reservoir compared to $\delta^{13}C$ and $\delta^{15}N$ signatures (mean ± 2SE) of potential energy sources, with middle Bridge River (MBR) drift expanded to show macroinvertebrate functional groups.

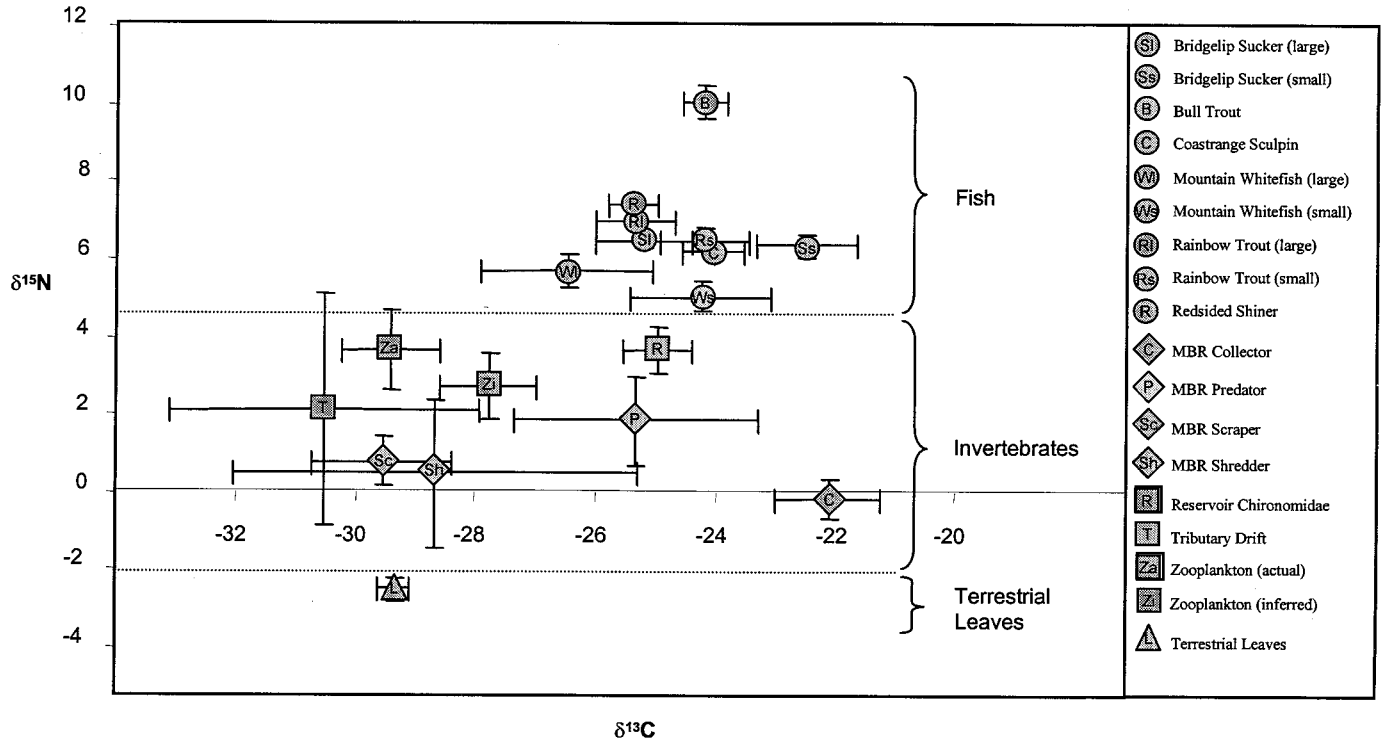
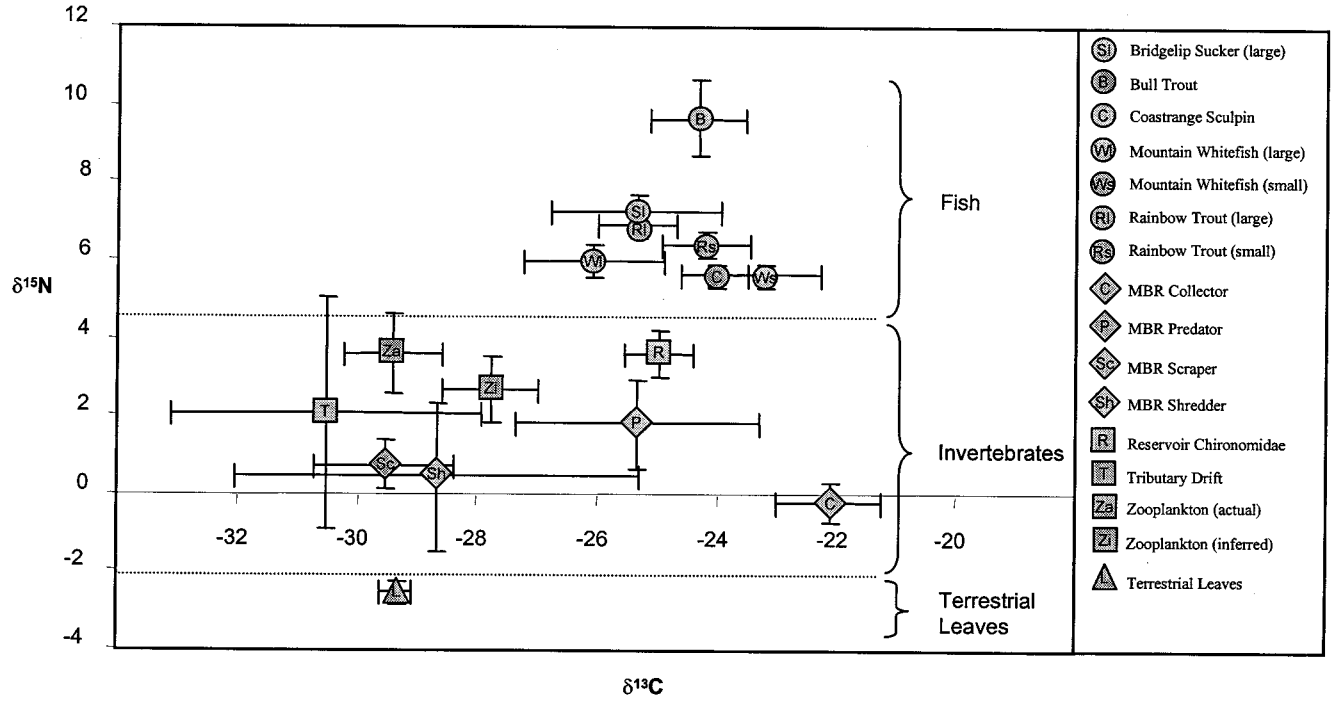


Figure 13: Stable isotope plot of $\delta^{13}C$ and $\delta^{15}N$ signatures (mean ± 2SE) of fish tissues caught from tributaries compared to $\delta^{13}C$ and $\delta^{15}N$ signatures (mean ± 2SE) of potential energy sources, with middle Bridge River (MBR) drift expanded to show macroinvertebrate functional groups



TABLES

Table 1: Size class lengths (mm) for fish by species.

Species	Size	Length (mm)
Bridgelip Sucker	Large	150 +
	Small	0 - 150
Bull Trout	Large	150 +
	Small	0 - 150
Coastrange Sculpin	Large	50 +
	Small	0 - 50
Mountain Whitefish	Large	150 +
	Small	0 - 150
Kokanee	Large	150 +
	Small	0 - 150
Rainbow Trout	Large	150 +
	Small	0 - 150
Redsided Shiner	Large	50 +
	Small	0 - 50

Table 2: Regressions of mean isotope signatures on sampling date, with $\delta^{13}C$ and $\delta^{15}N$ signatures of fish tissues grouped by significant size and area effects (MBR – middle Bridge River, Reservoir – Carpenter reservoir, Tributaries – Gun, Marshall, and Tyaughton Creeks, System – where no area effects, data has been pooled over space).

			$\delta^{13}C$			$\delta^{15}N$		
Species	**Age Class**	**Region**	**r**	**p**	**n**	**r**	**p**	**n**
Bridgelip Sucker	Large	MBR	0.63	<0.01	26	-0.10	0.61	26
		Reservoir	0.68	<0.01	15	0.31	0.27	15
	Small	Reservoir	0.24	0.41	14	-0.33	0.24	14
Bull Trout		MBR	0.13	0.45	34			
		Reservoir	0.04	0.85	23			
		System				-0.03	0.81	62
Coastrange Sculpin		MBR	0.29	0.02	65	-0.10	0.42	65
		Reservoir	0.68	<0.01	45	-0.50	<0.01	45
		Tributaries	0.33	0.04	40	-0.51	<0.01	40
Mountain Whitefish	Large	MBR	-0.07	0.58	60	0.02	0.91	60
		Reservoir	-0.10	0.52	46	0.23	0.12	46
		Tributaries	0.21	0.65	7	0.59	0.17	7
	Small	MBR	0.53	0.04	16	-0.17	0.54	16
		Reservoir	-0.15	0.67	10	-0.50	0.14	10
		Tributaries	0.50	0.05	16	-0.53	0.03	16
Rainbow Trout	Large	System	0.49	<0.01	41	0.08	0.64	41
	Small	System	0.54	<0.01	30	-0.43	<0.01	30
Redsided Shiner		MBR	0.39	0.34	8			
		Reservoir	0.33	0.03	43			
		System				-0.12	0.40	52

Table 3: Relations between $\delta^{13}C$ and $\delta^{15}N$ signatures of fish tissues and body length grouped by significant area effects (MBR – middle Bridge River, Reservoir – Carpenter reservoir, Tributaries – Gun, Marshall, and Tyaughton Creeks, System – where no area effects, data has been pooled over space) .

		$\delta^{13}C$			$\delta^{15}N$		
Species	**Region**	**r**	**p**	**n**	**r**	**p**	**n**
Bridgelip Sucker	MBR	-0.30	0.09	33	-0.33	0.06	33
	Reservoir	-0.12	0.53	29	0.01	0.95	29
	Tributaries	-0.08	0.90	5	-0.42	0.48	5
Bull Trout	MBR	0.07	0.69	34			
	Reservoir	0.15	0.50	23			
	Tributaries	0.14	0.82	5			
	System				<0.01	0.99	63
Coastrange Sculpin	MBR	-0.11	0.40	65	-0.13	0.30	65
	Reservoir	-0.13	0.41	45	-0.01	0.97	45
	Tributaries	-0.23	0.15	40	0.27	0.09	40
Mountain Whitefish	MBR	-0.19	0.14	62	0.17	0.18	62
	Reservoir	0.39	0.12	17	-0.06	0.82	17
	Tributaries	-0.04	0.85	23	0.37	0.08	23
Rainbow Trout	System	0.14	0.24	71	0.01	0.94	71
Redsided Shiner	MBR	-0.18	0.67	8			
	Reservoir	0.30	0.05	43			
	System				0.16	0.25	52

Table 4: Seasonal $\delta^{13}C$ and $\delta^{15}N$ signatures of potential energy sources (mean ± 2 SE) and their seasonal trends.

Taxon	n	Isotope	Mean ± 2SE	Seasonal Trend
Terrestrial Leaves	49	$\delta^{13}C$	-29.34 ± 0.30	r = 0.33; p = 0.02
	49	$\delta^{15}N$	-2.50 ± 0.32	r = 0.40; p < 0.01
Zooplankton (actual)	9	$\delta^{13}C$	-27.28 ± 0.82	r = -0.80; p = 0.01
	9	$\delta^{15}N$	2.69 ± 0.54	r = 0.63; p = 0.07
Middle Bridge River Drift	52	$\delta^{13}C$	-25.02 ± 2.09	r = 0.57; p < 0.01
	52	$\delta^{15}N$	0.36 ± 2.33	r = 0.35; p = 0.81
Tributary Drift	143	$\delta^{13}C$	-30.18 ± 1.49	r = 0.04; p = 0.65
	143	$\delta^{15}N$	2.00 ± 1.66	r = 0.16; p = 0.16
Reservoir Chironomidae	14	$\delta^{13}C$	-24.98 ± 0.54	n/a
	14	$\delta^{15}N$	3.60 ± 0.60	n/a

Table 5: DIC $\delta^{13}C$ seasonal values (mean ± 2 SE) and seasonal trends for the middle Bridge River, the reservoir, and tributaries. Entries with the same superscript letter were not significantly different.

Area	n	$\delta^{13}C$ mean ± 2 SE	Seasonal Trend
Middle Bridge River	26	-5.14 ± 0.44[a]	r = -0.41; p = 0.04
Reservoir	22	-4.81 ± 0.40[a, b]	r = 0.25; p = 0.27
Tributaries	32	-4.35 ± 0.48[b]	r = 0.14; p = 0.43

Table 6: $\delta^{13}C$ and $\delta^{15}N$ signatures of fish species grouped by significant area and size effects (mean ± 2 SE). Entries with the same superscript letter were not significantly different.

Species	Region	Size Class	n	$\delta^{13}C$	$\delta^{15}N$
Bridgelip Sucker	MBR	Large	26	-24.73 ± 0.62^{a}	6.24 ± 0.18^{a}
		Small	7	-27.49 ± 1.18^{d}	5.13 ± 0.36^{b}
	Reservoir	Large	15	-25.22 ± 0.80^{a}	6.45 ± 0.24^{a}
		Small	7	-22.50 ± 0.84^{b}	6.29 ± 0.26^{a}
	Tributaries	Large	14	$-25.36 \pm 1.40^{a, d}$	7.25 ± 0.44^{c}
Bull Trout	MBR	n/a	34	-23.44 ± 0.30^{a}	9.48 ± 0.36^{a}
	Reservoir		23	$-24.19 \pm 0.38^{a,b}$	9.98 ± 0.44^{a}
	Tributaries		5	-24.32 ± 0.80^{b}	9.66 ± 0.96^{a}
Coastrange Sculpin	MBR	n/a	65	-22.69 ± 0.44^{a}	5.03 ± 0.22^{a}
	Reservoir		45	-24.05 ± 0.52^{b}	6.12 ± 0.26^{b}
	Tributaries		40	-24.03 ± 0.56^{b}	5.61 ± 0.28^{c}
Mountain Whitefish	MBR	Large	46	$-25.03 \pm 0.56^{a, b}$	5.70 ± 0.16^{a}
		Small	7	-20.48 ± 0.94^{d}	4.79 ± 0.28^{c}
	Reservoir	Large	7	$-26.47 \pm 1.42^{a, b}$	$5.63 \pm 0.42^{a, b}$
		Small	16	$-24.25 \pm 1.18^{b, c}$	$4.00 \pm 0.36^{b, c}$
	Tributaries	Large	10	$-26.07 \pm 1.42^{a, b}$	6.02 ± 0.42^{a}
		Small	16	-23.22 ± 0.94^{e}	$5.63 \pm 0.28^{a, b}$
Rainbow Trout	n/a	Large	17	-25.35 ± 0.64^{a}	6.89 ± 0.27^{a}
		Small	29	-24.19 ± 0.74^{b}	6.41 ± 0.32^{b}
Redsided Shiner	MBR	n/a	8	-23.97 ± 0.92^{a}	7.04 ± 0.44^{a}
	Reservoir		43	-25.39 ± 0.40^{b}	7.38 ± 0.18^{a}
Kokanee	MBR	n/a	5	-26.78 ± 0.28	6.69 ± 0.17

Table 7: Effect of body size and area on fish tissue $\delta^{13}C$ and $\delta^{15}N$ signatures (1-way and 2-way ANOVAs)

Species	Area	2-way ANOVA (area) $\delta^{13}C$	2-way ANOVA (area) $\delta^{15}N$	Size	2-way ANOVA (size) $\delta^{13}C$	2-way ANOVA (size) $\delta^{15}N$		2-way ANOVA (size within area) $\delta^{13}C$	2-way ANOVA (size within area) $\delta^{15}N$	1-way ANOVA (area) $\delta^{13}C$	1-way ANOVA (area) $\delta^{15}N$	1-way ANOVA (size) $\delta^{13}C$	1-way ANOVA (size) $\delta^{15}N$
Bridgelip Sucker	MBR/ Trib	$t_{1, 67}$ = -5.38, $p < 0.01$	$t_{1, 67}$ = -6.47, $p < 0.01$	Large/ small	$F_{1, 67}$ = -4.66, $p < 0.01$	$F_{1, 67}$ = 0.90, $p = 0.37$	MBR Large/ small	$t_{1, 67}$ = 6.18, $p < 0.01$	$t_{1,67}$ = 3.43, $p < 0.01$				
	Res/ Trib	$t_{1, 67}$ = -0.30, $p = 0.76$	$t_{1, 67}$ = -1.69, $p = 0.10$				Res Large/ small	$F_{1, 67}$ = 7.40, $p = 0.07$	$F_{1,67}$ = -21.99, $p < 0.01$				
	MBR/ Res	$F_{1, 67}$ = 25.82, $p < 0.01$	$F_{1, 67}$ = 25.12, $p < 0.01$				Trib Large/ small						
Bull Trout										$F_{2, 61}$ = 5.94, $p < 0.01$	$F_{2, 61}$ = 1.49, $p = 0.23$		
Coastrange Sculpin										$F_{2, 150}$ = 11.23, $p < 0.01$	$F_{2, 150}$ = 20.86, $p = 0.23$		
Mountain Whitefish	MBR/ Trib	$t_{1, 102}$ = 5.40, $p < 0.01$	$t_{1, 102}$ = -2.62, $p = 0.01$	Large/ small	$F_{1, 102}$ = 49.14, $p < 0.01$	$F_{1, 102}$ = 22.37, $p < 0.01$	MBR Large/ small	$t_{1,102}$ = -2.43, $p = 0.02$	$t_{1,102}$ = 1.58, $p = 0.12$				
	Res/ Trib	$t_{1, 102}$ = -3.15, $p < 0.01$	$t_{1, 102}$ = -1.40, $p = 0.16$				Res Large/ small	$t_{1,102}$ = 1.40, $p = 0.17$	$t_{1,102}$ = -0.03, $p = 0.97$				
	MBR/ Res	$F_{1, 102}$ = 23.52, $p < 0.01$	$F_{1, 102}$ = 0.19, p = 0.66				Trib Large/ small	$t_{1,102}$ = 11.12, $p < 0.01$	$t_{1,102}$ = 2.35, $p < 0.13$				
Rainbow Trout												$F_{62, 64}$ = -2.33, P = 0.02	$F_{62, 64}$ = 2.33, P = 0.03
Redsided Shiner										$t_{1, 51}$ = 2.84, $p < 0.01$	$t_{1, 51}$ = -1.46, $p = 0.15$		

Table 8: B.C. Hydro Integrated Response Model results for littoral production index, pelagic production index, river production, water rent, and annual power generation for alternative operating scenarios B, G, M5 and N2.

Performance Measure	Alternative B	Alternative G	Alternative M5	Alternative N2
Littoral Production Index (P/B m^{-2})	8.5 ± 0.38	4.4 ± 0.17	6.6 ± 0.32	4.6 ± 0.24
River Productivity (P/B m^{-3})	0.5 ± 0.03	0.4 ± 0.03	0.4 ± 0.02	0.5 ± 0.02
Pelagic Production Index (P/B m^{-3})	1073 ± 86.79	991.50 ± 18.23	1047.30 ± 13.53	889.90 ± 18.25
Annual Water Rent ('000 000 $)	12.91 ± 0.56	2.94 ± 0.01	12.81 ± 0.46	12.89 ± 0.48
Annual Power Generation (GWh)	3600*	608.58 ± 22.28	2646.42 ± 94.88	2662.75 ± 98.70

* Value obtained from B.C. Hydro (2003a), because not provided with IRM data.