ECOTOXICOLOGICAL IMPACTS OF RUN-OF-RIVER DAMS ON THE AMERICAN DIPPER (*CINCLUS MEXICANUS*) AND MOUNTAIN STREAM FOOD WEBS

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ABSTRACT

Run-of-river (RoR) hydroelectric dams are an increasingly common alternate energy source on mountain streams. Despite reductions in size and greenhouse gas emissions compared to conventional impoundments, RoR dams may have ecotoxicological impacts through disruption of the natural flow regime. The American Dipper (*Cinclus mexicanus*) is a high trophic-level river bird that occupies mountain streams year-round and is a well-described indicator of stream health; thus, it is an ideal species to study potential impacts of RoR hydropower on river food webs. From August 2014 to November 2015, I conducted seasonal river bird surveys at 14 streams in coastal British Columbia, Canada and sampled food webs at 13 of these streams (7 regulated and 6 unregulated). Regulated streams create stable habitats that consequently supported significantly higher dipper densities (β=0.78, SE=0.36, p=0.030), a higher proportion of after hatch year (AHY) dippers, and consistent occupancy during breeding and non-breeding seasons compared with free-flowing streams.

Analyses of stable isotope ratios in dipper whole blood revealed strong model support for differences in blood isospace between regulated and unregulated stream types, likely driven by the significantly lower invertebrate $\delta^{34}S$ below RoR dams (p=0.010) and ^{34}S-depleted blood at regulated streams (β=-2.42, SE=0.95, p=0.029). Given that the bacteria responsible for ^{34}S-depleted food webs are also the primary methylators of inorganic mercury (Hg) into its toxic and bioavailable form, methylmercury (MeHg), I further investigated Hg levels in American Dippers and their prey. Despite the observation of distinct dipper isospace between stream types, there was no model support for differences in mean dipper blood (417.6 ± 74.1 S.E.) ng/g ww at regulated streams, 340.7 ± 42.7 S.E. ng/g ww at unregulated streams) or feather (1564 .6 ± 367.2 S.E. ng/g dw regulated, 1149.0 ± 152.1 S.E. ng/g dw unregulated) Hg concentrations between stream types.

One recently regulated stream (Douglas Creek, Harrison Watershed), however, supported dippers with MeHg concentrations of toxicity concern (up to 8459.5 ng/g dw in feathers and 1824.6 ng/g ww in whole blood). With a negligible salmon subsidy at these streams and the absence of a known anthropogenic Hg point source, the elevated Hg concentrations recorded in dippers at this regulated stream could be explained by a combination of a) elevated atmospheric deposition of Hg in densely forested, temperate mountain streams, b) Hg-methylation by sulfate-

reducing bacteria under anaerobic headpond conditions, and c) increased availability of high-protein prey.

Slow-flowing, stabilized stream reaches regulated by RoR dams potentially offer an opportunity for dippers to exploit a consistent food resource closer to their high elevation breeding territory, enabling them to take on a year-round “resident strategy” that is more typical of low elevation river habitats. The enhanced microbial activity and MeHg production that can occur in RoR headponds, however, suggests that even small dams with minimal storage can create pond-like habitats that may act as ecological traps for river bird specialists. Although at this point there appear to be no effects of river regulation on body condition, future work is needed to determine if long-term chronic MeHg toxicity can impair productivity or survival of predatory river birds.

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CHAPTER 1:
GENERAL INTRODUCTION: ECOTOXICOLOGICAL CONSEQUENCES OF FLOW DIVERSION FOR STREAM ECOSYSTEMS

1.1 IMPACTS OF REDUCED AND STABILIZED FLOW REGIME ON STREAM ECOSYSTEMS: DOCUMENTED RESPONSES AND KNOWLEDGE GAPS

1.1.1 Rivers and the importance of maintaining natural flow regimes

Rivers are dynamic ecosystems defined by a unique natural flow regime that varies with climate and catchment controls on runoff (Poff *et al.*, 1997; Poff and Zimmerman, 2010). Along with their associated riparian zones, rivers provide numerous ecological services for humans and wildlife that are highly dependent on flowing waters (Naiman *et al.*, 1993; Naiman and Decamps, 1997; Arthington *et al.*, 2010). Streamflow regulates the transport of sediment and woody debris within a channel, which shapes the in-stream and riparian habitat that serves as a template for the biotic community (Poff *et al.*, 1997). Anthropogenic activities that disrupt stream flow, such as hydroelectricity generation, may alter biotic community structure and riverine ecosystem integrity through changes to physical habitat and water quality, impaired longitudinal connectivity (Vannote *et al.*, 1980), and greater invasion success of exotic and introduced species (Poff *et al.*, 1997; Bunn and Arthington, 2002). Ecological impacts of large hydroelectric dams are well studied (Rosenberg *et al.*, 1997; World Commission on Dams, 2000; Bunn and Arthington, 2002; Renofalt *et al.*, 2010), but the ecological consequences of smaller dams remain poorly understood, despite their longer history of human use and recent global re-emergence as renewable energy sources (Abbasi and Abbasi, 2011; Robson *et al.*, 2011; Anderson *et al.*, 2015). Small dams can still modify streamflow and may similarly impact stream-dependent organisms that have evolved under specific flow regimes.

Though small dams offer benefits over conventional hydropower related to reduced greenhouse gas emissions from reservoirs and smaller overall impact footprints, flow abstraction and barrier effects occur independent of stream size and will likely alter smaller stream ecosystems regulated by small dams (Abbasi and Abbasi, 2011). These alterations include: loss of terrestrial habitat due to flooding; altered physical habitat and water quality within the reservoir and downstream of the dam; changes to downstream aquatic ecosystems and biodiversity; a reduction in sediment and nutrient transport due to barrier effects, reduced flow, and reduction of natural peak flows; impeded insect drift and fish migration; MeHg production; and, cumulative effects (World Commission on Dams, 2000; Bunn and Arthington, 2002; Rosenberg *et al.*, 1997).

As the global energy sector attempts to shift away from fossil-fuel dependence, hydropower projects known as run-of-river (RoR) dams are a promising alternate energy source on mountain streams (Robson *et al.*, 2011; Anderson *et al.*, 2015). Like the impacts of other forms of small hydropower, the ecotoxicological consequences of RoR dams remain poorly understood.

1.1.2 Run-of-river hydropower

RoR dams, also known as river diversions or non-storage hydropower, lack a precise definition (Csiki and Rhoads, 2010) and, therefore, regulatory approaches and associated environmental impacts are variable. Csiki and Rhoads (2010) offer a definition of a RoR dam as “a structure that extends across the width of a stream or river channel, has no mechanism inhibiting discharge of water over the dam, and is of a height that generally does not exceed the elevation of the channel banks upstream.” These gravity-fed systems function by diverting a portion of a stream’s flow through an underground conveyance structure (penstock) and turbines before returning the diverted flow to the main stream (Fig. 1.1). Typically, RoR dams differ from conventional hydropower in two major ways: 1) they occur on smaller rivers with smaller barriers; and 2) the impounded water is usually stored for less than 48 hours (forming the headpond), such that the overall anticipated impact is reduced (Community Energy Association, 2008; Anderson *et al.*, 2015). By comparison, in larger reservoirs, the residence time of stored water varies from several days to many years (Baxter *et al.*, 1977). With limited water storage, it is argued that alterations to the natural flow regime are limited to the diversion reach of RoR facilities without substantial alterations to upstream and downstream areas (Lewis *et al.*, 2012).

British Columbia (BC), Canada, like Europe, parts of Asia, and Oceania, is in the midst of a surge in RoR hydropower development, driven by government subsidies, renewable energy legislation, and a growing demand for electricity (Robson *et al.*, 2011; Anderson *et al.*, 2015). British Columbia's mountainous terrain and abundance of glaciers, lakes, and rivers is well suited for RoR electricity generation, which are operated by Independent Power Producers (IPPs) and subsidized by the British Columbia Hydro and Power Authority (BC Hydro) through Electricity Purchase Agreements. It is the responsibility of IPPs to comply with long-term provincial monitoring guidelines (Lewis *et al.*, 2012) and flow requirements (Hatfield *et al.*, 2003) developed for RoR projects in British Columbia, although compliance is not always met (Connors *et al.*, 2014), likely in response to project variability.

RoR projects in BC are typically small (<50MW), but larger facilities (50-200MW) do exist that can store substantial quantities of water (Lewis *et al.*, 2012), which is often referred to as "pondage" (see Fig. 1.1*c*). By comparison, RoR projects in Europe are significantly smaller than in British Columbia, typically mini (<1 MW) and micro (<100 kW) schemes with peak capacities of <10 kW (Anderson *et al.*, 2015). Small-scale hydropower generally refers to dams with a production capacity of < 10MW, as defined by the International Union of Producers and Distributors of Electrical Energy (Larinier, 2008). Relative to RoR projects in other regions and to other forms of small hydropower, RoR dams in BC operate at a fairly large-scale.

Despite reductions in greenhouse gas emissions (methane and nitrous oxide), barrier size, the extent of inundation, and water level fluctuations compared to conventional dams, RoR hydro may have ecological impacts associated with the disruption of natural flow regimes and associated infrastructure (Robson *et al.*, 2011; Anderson *et al.*, 2015). These dams can divert a substantial portion of stream flow from the main channel (Gower *et al.*, 2012), leading to significantly reduced discharge in the diversion reach, which may extend for several kilometers (*e.g.* Innergex's Rutherford Creek diversion reach extends 8.8km, impacting 33% of the total stream length; Table 2.1). Aquatic organisms and terrestrial consumers of aquatic biota residing in or along RoR-regulated streams may be affected by flow abstraction, resulting habitat changes, associated infrastructure, deforestation, and cumulative effects. Abbasi and Abbasi (2011) proposed that the environmental problems associated with small-scale hydropower would be similar to conventional hydropower, if analyzed on an "*impact per kilowatt of power generated"* basis.

Current evidence for the effects of reduced flow related to small dams, especially RoR dams, is variable and limited primarily to studies in Europe and Asia. This poor understanding originates from the diversity of small hydropower projects with respect to barrier-type, extent of reservoir flooding and retention time, proportion of flow diverted, and stability of flow, all of which alter a river's natural flow regime. Thus, stream community responses are also highly variable. A recent review by Anderson *et al.* (2015) summarized potential effects of RoR hydropower on different taxa and entire river ecosystems. They concluded that RoR hydropower does alter habitat characteristics and biotic community structure, but the results are variable and the ecological significance of these effects cannot be effectively analyzed from short-term studies conducted in multiple regions with variable regulatory schemes. Although local impacts to stream physicochemistry, algal and invertebrate communities, and fish have been identified at certain sites, the responses are often highly variable, and the response of entire river ecosystems to RoR dams requires further investigation.

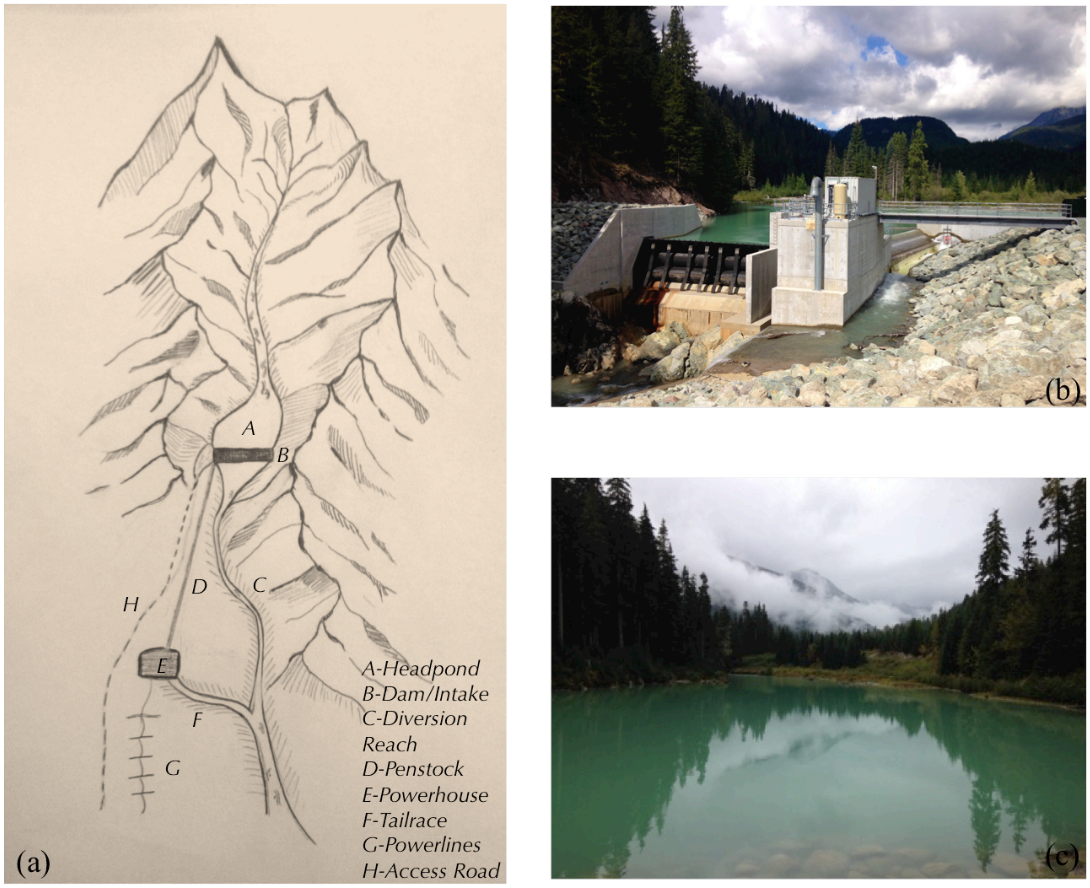

Figure 1.1 Sketch of a typical run-of-river dam (a) and examples from coastal British Columbia, including the Skookum Creek project in the Squamish Valley Watershed (b) and the Rutherford Creek headpond in the Lillooet Watershed (c). Photos and sketch by Veronica Norbury.

1.1.3 Impacts of flow abstraction on in-channel habitat and stream-dependent biota

1.1.3.1 Impacts of flow abstraction on stream physicochemistry

The main hydraulic effects of RoR dams are the formation of a pool upstream of the weir and reduced flow below the intake (Csiki and Rhoads, 2010), which often results in changes to stream physicochemistry. Flow abstraction and barrier effects of RoR dams facilitate the accumulation of fine sediment upstream and downstream of the dam (Csiki and Rhoads, 2010). RoR dams on Rocky Mountain streams in Colorado caused sedimentation, a build-up of fine sediment, and reduced size of channel coarse substrate downstream of diversions and created more slow-flowing habitat compared to upstream reaches (Baker *et al.*, 2011), with the extent of impacts reduced on steeper streams. Since low-flow rivers have higher net heat exchange with the atmosphere and sediment (Meier *et al.*, 2003) due to increased surface area: volume ratios and residence time, the diversion reach and headponds of RoR-regulated streams will likely experience higher summer temperatures and lower winter temperatures compared to natural conditions. Changes to stream physical and chemical features in response to regulation by small dams are typically limited to changes in temperature (Lessard and Hayes, 2003; Dewson *et al.*, 2007) and nutrient retention above the dam (Stanley and Doyle, 2002). Downstream fish and macroinvertebrate abundance and diversity often decline in response to these changes in streamflow and associated changes to stream physicochemistry (Poff and Zimmerman, 2010).

1.1.3.2 Response of algal and benthic macroinvertebrate communities to flow abstraction

Changes to algal and invertebrate communities below small dams occur in response to reduced flow, associated downstream sedimentation, and nutrient retention above the dam (Dewson *et al.*, 2007), with macroinvertebrate abundance and diversity generally declining in response to changes in streamflow and associated habitat changes (Poff and Zimmerman, 2010). Benthic algal species diversity was significantly lower downstream of run-of-river dams in the Xianging watershed of China 2-3 years after river regulation than it was prior to regulation (Wu *et al.*, 2009). Wu *et al.* attributed the decline to a reduction in downstream channel width, water depth, and velocity, resulting from decreased flow. A subsequent study by the same authors, however, found an increase in diatom species richness downstream of 23 cascade RoR dams in the same watershed (Wu *et al.*, 2010). A cascade system refers to several RoR dams on the same river (Wu *et al.*, 2010). Neither study identified significant changes to water quality.

Benthic macroinvertebrate communities are usually less diverse below dams, but responses are variable. Macroinvertebrate density was reduced below river diversions in Maui (McIntosh *et al.*, 2002). Similarly, macroinvertebrate density and biomass were lower downstream of five cascade dams along the Xiangxi river in China, but macroinvertebrate richness and water chemistry were similar upstream and downstream (Fu *et al.*, 2008). Reduced benthic macroinvertebrate species richness and number of EPT (composed of Ephemeroptera (mayfly), Plecoptera (stonefly), and Trichoptera (caddisfly) larvae) taxa were observed below a 1.5m high, 20m wide dam on a tributary of the Xiangi in China (Wang *et al.*, 2013). A decline in limnephilids (a family of shredding caddisfly larvae), in response to leaf litter retention upstream, explained reduced downstream decomposition rates below small surface release dams on mountain streams in central Spain (Gonzalez *et al.*, 2013). Small surface release dams in northern Spain caused a significant decline in downstream benthic macroinvertebrate richness, diversity, and density of functional feeding groups, especially taxa involved in processing leaf litter (Martinez *et al.*, 2013). Shredder and collector diversity was especially reduced in downstream channel habitats presumably through dams preventing passage of coarse material (Martinez *et al.*, 2013). Under experimental flow abstraction in upland Australian streams, McKay and King (2006) did not observe a significant change in total EPT density, but they did record a decline in the diversity of shredders and grazers in diverted reaches. Benthic invertebrate communities within RoR headponds will likely be more representative of pond-like habitats than fast-flowing streams, similar to the shift observed in natural ponds above beaver dams (Naiman *et al.*, 1988).

Research on small dams, including the interaction between flow changes and contaminant exposure, is relatively advanced in France, where it has been estimated that over 60,000 small run-of-river (<15m high) dams exist (Fanny *et al.*, 2013). Benthic macroinvertebrates inhabiting metal-contaminated RoR reservoirs had reduced functional diversity and trait assemblages resembling sedimentary zones of large rivers in lowlands (that require lentic, eutrophic and organic habitats, and experience frequent disturbance). Less contaminated RoR reservoirs had functional benthic macroinvertebrate trait assemblages resembling typical lotic systems (Fanny *et al.*, 2013). This suggests that the combined stressors of altered flow and metal contamination cause significant shifts in invertebrate community structure compared to altered flow regime in the absence of contamination (Fanny *et al.*, 2013).

1.1.3.3 Response of resident and migratory fish to altered flow regime

Highly sensitive to sedimentation and streamflow, resident and migratory fish populations typically exhibit negative responses to altered flow regime, but responses vary on a project-by-project basis (Poff and Zimmerman, 2010). A meta-analysis of potential impacts of RoR hydropower project to fish revealed that RoR dams negatively affect migration and increase mortality through entrainment in turbines, loss of spawning and nursery habitat, and cumulative effects of multiple dams on the same river (Robson *et al.*, 2011). The fluctuating flow regime resulting from a small 700kW dam in Spain caused a 50% decline in the downstream brown trout population within one year due to recruitment failure, while upstream trout densities remained unchanged following regulation (Almodovar and Nicola, 1999). Although the population size structure (mean body size) of fish differed between upstream and downstream reaches of RoR dams (18 dams <10MW in generating capacity) in central and Northern Portugal, species assemblage did not differ significantly between upstream and downstream reaches (Santos *et al.*, 2006). Upstream fish populations had a smaller mean body size at regulated sites with and without suitable fish passage, such as fish ladders (Santos *et al.*, 2006), but these differences in size were not expected to cause genetic divergence among the semi-fragmented populations (Santos *et al.*, 2006), since fish passages or incidental passage over weirs during flood events would facilitate genetic mixing.

There is evidence to suggest that small dams on streams *without* fish ladders may alter fish species assemblages. Small surface release dams on cold, wadeable streams in Michigan resulted in significant downstream temperature changes (mean summer temperature ranged from 1°C cooling to warming of over 5°C) and a decline in downstream EPT richness (Lessard and Hayes, 2003). Increased downstream temperature was negatively correlated with the density of several cold-water fish species, including: brown trout (*Salmo trutta*), brook trout (*Salvelinus fontinalis*), and slimy sculpin (*Cottus bairdi*). Overall fish species richness, however, increased downstream of these dams. No significant changes in water quality variables (oxygen, total phosphorous, conductivity), typically seen below deep hypolimnetic release dams, were recorded (Lessard and Hayes, 2003).

Although RoR dams in British Columbia are typically located above natural barriers to salmon migration, direct and indirect impacts to movement and habitats can negatively impact resident fish populations. An independent review on the potential impacts of RoR power on salmonids (salmon, trout, chars, freshwater whitefishes, and graylings), carried out by the Pacific Salmon Foundation and commissioned by Clean Energy BC, found that salmonids were present upstream, in the diversion reach, or downstream of 43/44 operational facilities in British Columbia and that RoR hydroelectric facilities have the potential to negatively impact salmonid populations through mortality due to entrainment, stranding, and habitat changes (Connors *et al.*, 2014). Indirect influences on food availability may also affect resident fish populations, depending on the algal and macroinvertebrate community response to changes in the hydrograph and associated habitat changes.

1.1.4 Impacts of flow abstraction on riparian habitats and terrestrial/ semi-aquatic biota

1.1.4.1 Response of riparian vegetation to altered flow regime

Riparian vegetation communities also exhibit a diverse response to flow regulation and stabilization of the hydrograph (Poff and Zimmerman, 2010) that can be characterized into upstream and downstream changes. Soils inundated by impoundments create an anoxic environment for vegetation, with negative impacts to species that are not adapted to low-oxygen environments, such as conifers (Nilsson and Berggren, 2000). The subsequent decomposition of inundated forests releases the greenhouse gases CO_2 and methane into the atmosphere (St. Louis *et al.,* 2000) and also releases Hg and nutrients (nitrogen and phosphorous) into the water column (Ullrich *et al.*, 2001). In contrast, non-woody vegetation or species adapted to low-oxygen environments, often respond positively to inundation (Poff and Zimmerman, 2010).

Shifts in riparian vegetation resulting from RoR-regulation may not be as extensive or long-lived as observed from storage hydropower, but they do occur, usually resulting in less diverse river margin communities in downstream reaches (Nilsson *et al.*, 1997; Nilsson and Berggren, 2000; Jansson *et al.*, 2000). RoR and storage hydropower in Northern Sweden both created less diverse riparian vegetation communities that were partially attributed to a shift in river margin soil type towards more coarse-grained material (Jansson *et al.*, 2000). This shift occurred in response to increased erosion caused by flow abstraction and increased water level fluctuations compared to free-flowing streams (Jansson *et al.*, 2000). Erosion is likely responsible for the reduced plant cover and species richness along regulated stream margins through direct mortality of colonizing plants or decreased habitat suitability of coarser soils. By acting as sediment traps, reservoirs and impoundments have the potential to erode river margins (Jansson *et al.*, 2000). When clear, lentic water is released from dams, erosion capacity is higher because of the water's ability to increase its load of suspended material (Jansson *et al.*, 2000). Although RoR dams in British Columbia are more likely to cause a build-up of sediment downstream of the dam in response to a loss of seasonal peak flows, recreational release events may cause erosion similar to what was observed in Northern Sweden.

In addition to increased erosion of river margins and sedimentation of in-channel habitats, downstream riparian ecosystems may also experience altered hydrology related to reduced groundwater recharge in the riparian zone. Eventually, reduced groundwater inputs would result in a falling groundwater table and reduction in floodplain extent, with implications for riparian communities (Nilsson and Berggren, 2000). Riparian zones are also naturally vulnerable habitats to invasion by exotic species as a product of frequent disturbances, changes in water availability, and an inherent dispersal mechanism of streamflow (Planty-Tabacchi *et al.*, 1995; Nilsson and Berggren, 2000). Changes to riparian habitats related to altered flow regime may further increase the success of introduced and exotic species. These changes in upstream and downstream riparian plant communities, combined with changes to in-stream habitat, can affect terrestrial consumers of aquatic or riparian food sources.

1.1.4.2 Responses of riparian birds and mammals to altered flow regime

Since Nilsson and Dynesius' (1994) review, impacts of river regulation on birds and mammals have been seldom investigated and the responses of these taxa remain poorly understood (Calvert *et al.*, 2013). The most obvious negative impact of hydropower to terrestrial biota is a loss of habitat following reservoir formation (Baxter, 1977). In mountain streams especially, the restriction of many species to steep valley bottoms results in permanent emigration and extirpation from newly flooded areas (Nilsson and Berggren, 2000). Small nonarboreal mammals that inhabit floodplains experience permanent habitat displacement during predictable flood events (Anderson *et al.*, 2000) and most likely exhibit the same response during unpredictable flooding of reservoirs. Grizzly bears avoid areas undergoing construction for hydroelectric dams and likely respond negatively to improved vehicular access to impacted areas (Smith *et al.*, 1990).

Inundation and the creation of lentic habitats above dams, however, may benefit some species, at least for a short time. The attraction of breeding water birds to reservoirs is well-documented (Lid, 1981, Moksnes, 1981, translated in Nilsson and Dynesius, 1994; Reitan and Sandvik, 1996; Reitan and Thingstad, 1999). For example, Osprey (*Pandion haliaetus*) populations along the Willamette River, Oregon have increased in response to large hydroelectric reservoirs and improved nest-site availability on associated powerlines (Henny *et* *al.*, 1996). Ducks and wading birds often breed at high density along the margin of hydroelectric reservoirs in response to elevated nutrients, abundant prey, and reduced predation pressure (Nilsson and Dynesius, 1994). Vegetation that colonizes the drawdown zones of large hydroelectric reservoirs also provide nesting habitat for several shrub-nesting passerine species (van Oort *et al.*, 2015) with benefits of reduced nest predation in aquatic or inundated habitats (Picman *et al.*, 1993; Roy Nielsen and Gates, 2007). Reservoirs that flood forests and leave snags may also create habitat for breeding woodpeckers (Yeager, 1949), beavers and other mustelids (Nilsson and Dynesius, 1994).

Often, the benefits of hydroelectric reservoirs are confounded by the negative impacts on avian productivity or contaminant exposure. Riparian habitats modified by reservoirs have been proposed as ecological traps for several ground-nesting species (*e.g.* Espie *et al.*, 1998; Anteau *et al.*, 2012). Ecological trap theory describes how a sudden environmental change uncouples the cues that individuals use to assess habitat quality from the true quality of the environment (Dwernychuk and Boag 1972, Gates and Gysel 1978). More recently, Schlaepfer *et al.* (2002) coined the term "evolutionary trap" as a situation where the use of a formerly reliable behavioural cue has become maladaptive because of a sudden anthropogenic habitat alteration. An ecological trap, under the conceptual framework described by Robertson and Hutto (2006), may arise when habitat alteration by anthropogenic activity causes a simultaneous increase in habitat attractiveness and reduction in suitability, leading to reduced fitness for individuals settling in the preferred habitat. For example, many species of ground-nesting water birds are attracted to the lush vegetation of draw-down zones, but they may experience reduced productivity through the unpredictable flooding of nests and drowning of recently fledged chicks (Espie *et al.*, 1998; Anteau *et al.*, 2012; van Oort and Cooper, 2015).

The second pathway by which hydroelectric reservoirs or RoR headponds may act as ecological traps to avian species is through elevated exposure to aquatic contaminants, particularly MeHg (see section 1.2). Elevated MeHg concentrations have been detected in fish (Bodaly *et al.*, 2007), passerines (Gerrard and St. Louis, 2001), aquatic avian predators (Evers *et al.*, 2007) and even bats (Syaripuddin *et al.*, 2014) that forage within reservoirs or on insects emerging from these lentic habitats. This proposed pathway assumes that MeHg levels accumulating within organisms would be sufficient to cause adverse effects to health and reproduction. Since fluctuating water levels are atypical of RoR dams, it is more likely that stream dependent species would be more adversely impacted by MeHg exposure or other habitat modifications than direct mortality through inundation.

The documented responses of birds and mammals to hydroelectricity have focused primarily on reservoir effects. Species that are heavily dependent on streamflow conditions and occupy more permanent niches that extend beyond the reservoir may be further impacted by flow abstraction. Since American Dipper foraging behaviour and success is heavily influenced by streamflow (Taylor and O'Halloran, 2001; D'Amico and Hemery 2007), D'Amico (2011) proposed that if outcomes of dipper diving and foraging behaviour in response to river regulation are non-adaptive (with negative impacts on fitness and population dynamics), then regulated rivers could be ecological traps for dippers. D'Amico (2011) hypothesized that under a flow regime stabilized by RoR dams (compensation flow), the link between streamflow and environmental cues would be lost, with likely changes in dipper diving behaviour. It has yet to be determined how dipper foraging behaviour is influenced by anthropogenic changes to flow regime. A broader understanding of the response of terrestrial and semi-aquatic taxa to reduced flow is needed (beyond reservoir effects), as in-stream and riparian habitat changes may lead to cumulative effects on their fitness.

1.2 MERCURY, METHYLMERCURY BIOMAGNIFICATION, AND HYDROELECTRICITY

1.2.1 Mercury: a global pollutant

Hg is a global pollutant, facilitated by its long atmospheric residence time, long-distance transport, and deposition in remote areas. Hg contamination may occur in regions distant from any point source through atmospheric deposition of anthropogenic sources or natural deposits (Fitzgerald *et al.*, 1998; Schroeder and Munthe, 1998; Boening, 2000; Selin *et al.*, 2009). Major natural sources of Hg include degassing from mineral deposits and evasions from surface soils, water bodies, vegetative surfaces, wild fires, volcanoes, and geothermal sources (Schroeder and Munthe, 1998; Boening, 2000; Wang *et al.*, 2004). Current anthropogenic sources of Hg include the burning of fossil fuels, incineration of solid and sewage sludge waste, and metal smelting, refining and manufacturing (Schroeder and Munthe, 1998; Boening, 2000). Hg emissions from artisanal small-scale gold mining may exceed those from coal-fired plants (Wang *et al.*, 2004).

Historical anthropogenic sources of Hg include chlor-alkali plants in many industrialized countries. The risk that Hg poses to wildlife is largely attributed to the ability of it's methylated form, methylmercury (MeHg), to biomagnify through food webs and exert toxic effects, especially neurotoxic and teratogenic effects, on consumers (Schroeder and Munthe, 1998).

1.2.2 Factors influencing methylmercury production in free-flowing and regulated streams

MeHg production is well-documented in reservoirs of large dams (Rosenberg *et al.*, 1997), experimental reservoirs (Bodaly *et al.*, 2004, 2007), and beaver dams (Roy *et al.*, 2009*a,b,* Painter *et al.,* 2015)*,* but remains uninvestigated in RoR headponds. MeHg is a teratogen and neurotoxin that biomagnifies through aquatic food webs (Watras *et al.*, 1998) and bioaccumulates in high trophic level predators (Hall *et al.*, 2005). It is formed during reservoir flooding through microbial methylation of Hg that occurs naturally in inundated soil and the water column (Ullrich *et al.*, 2001; Hall *et al.*, 2005; Ward *et al.*, 2010). Initial flooding of soil results in an influx of inorganic Hg and organic matter into the water and subsequent decomposition of this organic matter favours bacterial methylation of the recently mobilized and legacy Hg (Bodaly *et al.*, 2004). Sulfate-reducing anaerobic bacteria are dominant in reservoirs and are also the primary methylators of Hg (Compeau and Bartha, 1985). The repeated wetting and drying of sediment associated with water level fluctuations in ephemeral wetlands and hydroelectric reservoirs can prolong MeHg production after initial flooding, though this effect can be mitigated by strategic water management techniques (Willacker *et al.*, 2016). In a review of fish Hg concentrations across western North America, Willacker *et al.* (2016) determined that between-year fluctuations in reservoir levels strongly influenced fish Hg exposure, while within-year fluctuations had no effect.

In addition to water management techniques, MeHg production potential is influenced by regional factors that affect Hg deposition and stream-level features that control methylation rate. Mercury concentrations in aquatic environments increase with increased atmospheric Hg deposition (Evers *et al.*, 2007), which is influenced by climate, forest cover, where trees are a major source of dry deposition (Miller *et al.*, 2005), and aquatic-terrestrial connectivity, where the presence of wetlands (St. Louis *et al.*, 1994) and unproductive surface waters (Chen *et al.*, 2005) facilitate bioavailability of Hg through transport, methylation, and bioconcentration

(Driscoll *et al.*, 2007; Ward *et al.*, 2010). Increased atmospheric deposition of Hg often results in elevated exposure in aquatic organisms (Hammerschmidt *et al.*, 2006), consumers of aquatic organisms (Guigueno *et al.*, 2012), and even riparian wildlife (Rimmer *et al.*, 2005).

Several features of stream physicochemistry have also been identified as factors influencing Hg bioaccumulation, but the relationship is not always straightforward (Ward *et al.*, 2010; Lavoie *et al.*, 2013). High dissolved organic carbon (DOC) waters often experience elevated Hg concentrations, likely through facilitating increased microbial growth rates (Ullrich *et al.*, 2001). Under very high DOC conditions, however, MeHg bioavailability and trophic transfer are reduced and demethylation rates may be enhanced, resulting in lower Hg bioaccumulation rates (Lavoie *et al.*, 2013). Temperature, oxygen, and pH also regulate Hg mobility and microbial activity at the stream level (Ullrich *et al.*, 2001; Lavoie *et al.*, 2013). Anoxic conditions promote release of Hg from sediment, whereas oxic conditions favour sediment uptake of Hg (Ullrich *et al.*, 2001). The release of MeHg from sediments and methylation rates increase with higher temperatures (Ullrich *et al.*, 2001). Low pH also increases baseline concentrations of MeHg in periphyton and ultimately biomagnification in streams (Jardine *et al.*, 2013). Hg methylation, therefore, typically increases under warm, anoxic, acidic (Jardine *et al.*, 2013), and high DOC (Watras *et al.*, 1998) conditions and it often peaks under warm, low flow periods (Ward *et al.*, 2010) that may be encountered in some RoR stream reaches and headponds.

Peak MeHg concentrations in reservoirs are reached within a few years of flooding, but maximum concentrations in predatory fish may be delayed up to 10 years after flooding and take up to 20 years to return to background levels (Bodaly *et al.*, 2007). In beaver dams, maximum MeHg concentrations and methylation efficiency (percent of total Hg in the methylated form) in water occurred in dams <10 years old (Roy *et al.*, 2009a,b*)*. Beaver impoundments with coniferous riparian zones also had higher water MeHg concentrations (Roy *et al.*, 2009b). A recent review on fish Hg concentrations in hydroelectric reservoirs concluded that peak concentrations are reached within three years of initial flooding and rapidly decline after 4-12 years (Willacker *et al.*, 2016).

High elevation mountain streams may naturally experience elevated atmospheric inorganic Hg deposition and RoR dams may increase MeHg production at the stream level by a) forming small reservoirs known as headponds and b) increasing stream temperature in the spring and summer under low flow conditions and increased water-atmospheric exchange. The extent of MeHg production may depend on characteristics of the RoR dam, such as: the extent of headpond flooding, fluctuation in headpond water levels, the extent of nutrient retention, and age.

1.2.3 Mercury exposure and toxicity to avian species

A geographic trend in Hg concentrations in wildlife increases from west to east across North America (Evers *et al.*, 1998; Evers *et al.*, 2007; Depew *et al.*, 2013), but several regions in western North America also support birds with Hg levels of toxicity concern (Eagles-Smith *et al.*, 2009; Ackerman *et al.*, 2016; Jackson *et al.*, 2016). Hg exposure in avian species is significantly influenced by foraging guild, habitat type, and ecoregion (Ackerman *et al.*, 2016). Birds foraging in ocean and salt marsh habitats have the greatest Hg exposure, compared with relatively low concentrations in terrestrial habitats. Piscivorous and carnivorous species experience the highest blood-equivalent Hg concentrations, most likely in response to biomagnification across trophic levels (Ackerman *et al.*, 2016; Jackson *et al.*, 2016). Piscivorous birds foraging in wetlands with fluctuating water levels also experience higher Hg exposure and bioaccumulation than their terrestrial counterparts (Jackson *et al.*, 2016). Elevated Hg concentrations have also been recorded in birds foraging on aquatic (Evers *et al.*, 2007) or emergent (Gerard and St. Louis, 2001) prey associated with reservoirs. Although underrepresented in the literature of avian Hg exposure, birds residing at high elevations may also experience elevated Hg exposure through atmospheric deposition (Guigueno *et al.,* 2012; Miller *et al.*, 2005; Rimmer *et al.*, 2005).

Mercury concentrations in the feathers of nestling Osprey increased with higher modeled atmospheric deposition and reduced lake size, possibly in response to the accumulation of Hg in glacial meltwater (Guigueno *et al.*, 2012). Bicknell’s thrush *Catharus bicknelli*), a migratory songbird inhabiting montane forests dominated by conifers, had elevated blood and feather Hg on mountains with higher leaf litter Hg influx patterns (Rimmer *et al.*, 2005), supporting the observation that MeHg exposure can occur in terrestrial habitats that lack any standing water typical of Hg methylation sites (Miller *et al.*, 2005). Evergreen foliage often has higher Hg concentrations than their deciduous counterparts due to the longer needle lifespan and continuous accumulation of Hg after initial growth (Rasmussen, 1995). The combined features of high elevation, highly productive temperate evergreen-dominated forests with low-flow headponds (that support anaerobic bacteria and retain pine needles, leaf litter, and nutrients) may facilitate significant Hg accumulation and methylation potential within the headponds of RoR dams. The extent of MeHg production will likely vary with stream physicochemistry and regulatory practices that dictate reservoir size and turnover time.

Although the pathway of methylmercury toxicokinetics is not well elucidated, there is evidence in vertebrates to suggest a role in oxidative stress (Hoffman and Heinz, 1998; Glaser *et al.*, 2010; Henry *et al.*, 2014), inhibited mitochondrial energy metabolism (Cambier *et al.*, 2009), and reduced neural cell differentiation (Ceccatelli *et al.*, 2013). MeHg accumulates primarily from the consumption of contaminated food (Watras *et al.,* 1998) and exerts negative effects on reproduction, immune function, growth and development, and behaviour in terrestrial and aquatic birds. Reproduction is the most sensitive endpoint of MeHg toxicity in birds and reproductive impairment from dietary MeHg exposure has been documented in piscivorous birds, such as the Common Loon (*Gavia immer*) (Burgess and Meyer, 2008; Evers *et al.*, 2008) and insectivores, such as the Tree Swallow (*Tachycineta bicolor*) (Brasso and Cristol, 2008). MeHg can be maternally deposited into eggs, potentially causing embryonic death and developmental abnormalities, although species vary in their sensitivity to MeHg (Heinz *et al.*, 2009). Although chicks are protected from MeHg toxicity through depuration into growing feathers (Fournier *et al.*, 2002; Kenow *et al.*, 2003; Condon and Cristol, 2009; Kenow *et al.*, 2010), impaired motor coordination (Kenow *et al.*, 2010) and reduced immune function (Kenow *et al.*, 2003) have been documented in Common Loon chicks fed fish containing MeHg in concentrations similar to known prey levels at the high range of ambient exposure.

After synthesizing avian Hg exposure data across western North America, Ackerman *et al.* (2016) established blood-equivalent toxicity thresholds, ranging from impaired health, physiology, behaviour and reproduction at 1000 ng/g ww to complete reproductive failure at 4000 ng/g ww. Based on their literature and raw data, they established a lowest observed adverse effect level (LOAL) of 200 ng/g ww, but negative impacts to avian reproduction, health, behaviour, and survival are not likely to occur until prolonged exposure at or near 1000 ng/g ww in whole blood (Ackerman *et al.*, 2016). For example, chronic dosing studies with White Ibis (*Eudocimus albus*) revealed that altered courtship behaviour, including reduced courtship behaviours in males, led to a 13% decline in productive nests when adult blood concentrations reached 780 ng/g ww (Frederick and Jayasena, 2010). Jackson *et al.* (2011) estimated a 30% reduction in the probability of nest success at 1700 ng/g ww in free-living Carolina Wrens (*Thryothorus ludovicianus*) and a 20% reduction in nest success at 1200 ng/g ww.

With variable observed impacts to avian reproduction, behaviour, health, and survival occurring across a wide range of experimental and natural conditions, species-level differences in sensitivity, and dietary exposure varying with habitat and foraging ecology, it is difficult to decide on an MeHg toxicity threshold suitable for dippers. The unique natural history of dippers, with characteristics intermediate between passerines and water birds, further confounds this problem. Therefore, I decided to compare mercury concentrations measured in this study to the blood-equivalent toxicity threshold of 1000 ng/g ww, as synthesized by Ackerman *et al.* (2016). This value represents the most up-to-date synthesis of avian Hg exposure across North America and reflects impacts to behaviour, reproduction, health, and survival in response to dietary MeHg exposure under natural and experimental conditions for terrestrial and aquatic species.

1.3 UNTANGLING FOOD WEBS WITH STABLE ISOTOPE ANALYSIS

Stable isotope analysis is a simple and inexpensive method to characterize food webs and trace contaminant biomagnification through food webs. Stable isotopes are variations of an atom with the same number of protons and electrons, but a unique number of neutrons. Stable isotopes are energetically stable, do not decay, and are not radioactive (Peterson and Fry, 1987). Isotopes fractionate at different rates in different materials, creating a distinct isotopic signature (heavy: light) that can be traced through mass spectrometry. The lighter elements (carbon, nitrogen, oxygen, hydrogen, and sulfur) are commonly used in isotope ecology because: A) they are abundant in biological compounds and B) the percent mass change caused by the addition of a neutron is greatest and most easily detectable (Michener and Lajtha, 2008). Differences in isotopic ratios between materials are small; therefore, isotopic composition is reported relative to a standard and expressed in parts per thousand deviations from the standard (Michener and Lajtha, 2008). International standard references include carbon from Belemnite in PeeDee limestone, nitrogen gas in the atmosphere, and sulfur from the Canyon Diablo meteorite (Peterson and Fry, 1987). Many laboratories have their own working standard materials that are compared to international standards (Michener and Lajtha, 2008). The isotopic ratio of a sample is expressed as either enriched (positive) or depleted (negative) compared to the reference material.

Stable isotopes provide a spatially- and temporally-integrated measure of diet and unlike other measures of diet, are not confounded by omnivory and complex predator-prey interactions (Post, 2002). Stable isotopes of carbon (^{13}C:^{12}C), nitrogen (^{15}N:^{14}N), hydrogen (^{2}H:^{1}H), sulfur (^{34}S:^{32}S), and oxygen (^{18}O:^{16}O) are effectively used in ecological studies to estimate an organism's relative trophic position within a food web (*e.g.* Anderson and Cabana, 2007), determine the relative contribution of different food sources to a consumer's diet (*e.g.* Rasmussen, 2010), study seasonal shifts in diet (*e.g.* Darimont and Reimchen, 2002; Reimchen *et al.*, 2003), and determine local differences in diets related to movement and migration (Hobson, 1999). In ecotoxicology, stable isotopes are used to trace contaminants through food webs (Kidd *et al.*, 1995; Atwell *et al.*, 1998; Jardine *et al.*, 2012) and have been used successfully with American and European dippers (Morrissey *et al.*, 2010a,b, 2014).

Stable isotopes of carbon ($\delta^{13}C$) can be used to assess changes in the energy source of coastal mountain stream ecosystems following flow diversion by run-of-river dams. Several characteristics of $\delta^{13}C$ make it a useful tracer of terrestrial or aquatic-derived carbon in aquatic systems, including: very limited fractionation with trophic transfer, integration of nutrient sources over time, and distinct signatures of primary producers in adjacent habitats (Finlay, 2001). Terrestrial plant detritus has a fairly constant $\delta^{13}C$ at -28‰, but lotic algal signatures range from -47 to -12‰ (Finlay and Kendall, 2007). This variability in isotopic values for algae is related to dissolved inorganic carbon availability, whereupon restricted boundary layer diffusion of CO_2 occurs into algal cells under low streamflow conditions. This results in less discrimination against the heavy isotope in slower-flowing waters. In rivers, autochthonous (algal) carbon sources are ^{13}C-depleted relative to terrestrial sources in fast-flowing upstream reaches, but ^{13}C-enriched relative to terrestrial sources in slower-flowing downstream reaches (Rasmussen, 2010). Since regulated streams surveyed in this study area are high elevation, better characterized as headwater streams dominated by terrestrial inputs, I predicted that headponds would have a ^{13}C-enriched isotopic signature due to restricted boundary layer diffusion occurring at low flows.

Stable isotopes of carbon may also provide information on the diet-mediated exposure pathway of MeHg (Jardine *et al.*, 2012) to high-trophic level stream biota such as dippers. Last, δ^{13}C may also be useful in describing dipper habitat use in relation to RoR dams. By sampling the stream food web along a longitudinal gradient from upstream to downstream, δ^{13}C signatures of dippers can be compared to benthic macroinvertebrate signatures sampled upstream or downstream. In addition, the δ^{13}C isotope is useful in tracing salmon-derived lipids that can make up a significant proportion of dipper diets (Morrissey *et al.*, 2012).

The ratio of ^{15}N: ^{14}N isotopes (δ^{15}N) increases by 2 ‰ to 5 ‰ (on average 3.4 ‰) with each trophic level, as the lighter isotope is preferentially excreted (Peterson and Fry, 1987; Kelly, 2000; Hobson and Bairlein, 2003). Therefore, δ^{15}N has been used extensively to determine the relative trophic position of organisms (Post, 2002; Hobson and Welch, 1992) and to trace MeHg biomagnification through food webs (Atwell *et al.*, 1998; Jardine *et al.*, 2012; Morrissey *et al.*, 2012). The relative contribution of fish to dipper diet will influence their trophic level and MeHg exposure.

Stable isotopes of sulfur are used less often than those of carbon and nitrogen in stable isotope ecology, but they may provide useful information when used in conjunction with these isotopes. The ratio of ^{34}S: ^{32}S is typically conserved through food webs, like ^{13}C:^{12}C, although discrimination factors are higher for consumers with high-protein diets (Peterson and Fry, 1987; McCutchan *et al.*, 2003). Measurement of δ^{34}S is useful for distinguishing between benthic and pelagic food webs (Peterson and Fry, 1987) and discriminating the source of primary production in estuaries (Peterson *et al.*, 1985). Similarly, conditions that stimulate bacterial sulfate reduction lead to increased production of ^{34}S-depleted sulfides (e.g. H_2S), which react with iron and organic matter in sediments, resulting in lower δ^{34}S of the total sulfur in sediments (Peterson and Fry, 1987).

Although research on sulfur isotope fractionation is limited in stream ecosystems, a growing body of research is showing that δ^{34}S is useful as a marker for bacterial sulfate reduction and processes associated with sulfide recycling in lakes, estuaries, and wetlands (Detmers *et al.*, 2001; Herbert and Wassenaar, 2005; Croisetière *et al.*, 2009). Sulfate-reducing bacteria produce sulfides depleted in ^{34}S compared with initial sulfate in pure culture and sediments are commonly depleted in ^{34}S relative to seawater sulfate (Habicht and Canfield, 1997). Within a given lake, benthic macroinvertebrates feeding on sediment (either directly or through predation) had lower δ^{34}S values than those feeding on suspended particles, reflecting ^{34}S-depleted sulfur in sediments (Croisetière *et al.*, 2009). Measuring sulfur values in predatory fish allowed their dietary pathway (benthic or planktonic) to be distinguished (Croisetière *et al.*, 2009). The extent of depletion depends on multiple factors, including the rate of bacterial sulfate reduction (Habicht and Canfield, 1997). This isotope may be useful in quantifying and tracing the extent of sulfate-reducing bacterial activity associated with RoR headponds, as the δ^{34}S isotopic signature is essentially conserved in consumers with little isotopic fractionation. Further, it may act as a marker for MeHg production within reservoirs and headponds, given that sulfate-reducing bacteria are the principal methylators of Hg (Compeau and Bartha, 1985).

1.4 STUDY SPECIES: THE AMERICAN DIPPER

1.4.1 Life history

Five species of dipper (*Cinclus*) inhabit swift upland streams of North and South America, Mexico, Europe, and Asia (Tyler and Ormerod, 1994). The American Dipper is the only truly aquatic songbird in North America and a valuable representative of interface ecology, as they use in-channel and riparian habitats for foraging and breeding (Price and Bock, 1983; Morrissey *et al.*, 2004c, Walton and Wright, 2008). Dippers feed on benthic macroinvertebrates, salmonid eggs, and small fish within the channel of fast-moving mountain streams (Price and Bock, 1983; Morrissey *et al.*, 2004b, Walton and Wright, 2008) by diving and swimming underwater with their wings, or running along the stream bottom (D'Amico, 2011). Dippers may be permanent residents on coastal mountain stream reaches or migrate to higher elevation reaches during the breeding season, from late March to August (Morrissey *et al.*, 2004a).

These river birds have been used extensively as indicators of stream health (Ormerod and Tyler, 1994; Morrissey *et al.*, 2005) and explored as indicators of the impacts of altered flow regime (D'Amico *et al.*, 2000; D'Amico, 2011) and Hg contamination (Henny *et al.*, 2005), but not under these stressors simultaneously. Highly sensitive to changes in streamflow (D'Amico and Hemery, 2007) and able to bioaccumulate contaminants to high levels relative to other stream consumers (Ormerod and Tyler, 1994), this species provides the opportunity to study synergistic interactions between contaminants, abiotic and biotic stressors—an approach that is often lacking in ecotoxicological studies (Relyea and Hoverman, 2006). Current monitoring protocols for RoR dams in British Columbia focus on the protection of fish and fish habitat; however, dippers may be better sentinels of stream health with ecological factors readily and effectively monitored.

1.4.2 Dippers as sentinels of stream health

Several characteristics of dipper biology support the use of this species as an indicator of stream ecosystem integrity. First, dippers are year-round residents on mountain streams, where they do not stray far from the stream channel, and do not undergo extensive migration to other latitudes (Price and Bock, 1983; Morrissey *et al.*, 2004a). Dipper habitat overlaps with the ideal placement of run-of-river dams and their limited altitudinal migration makes them indicators of regional stressors, such as contaminants or changes in the stream hydrograph.

Second, dippers are conspicuous and easily distinguished from other passerines and river birds. Monitoring dipper productivity and survival (Morrissey *et al.*, 2004b, Gillis *et al.*, 2008), foraging behaviour (D'Amico and Hémery, 2007), and contaminant exposure (Ormerod and Tyler, 1994; Henny *et al.*, 2005; Morrissey *et al.*, 2005), in response to different variables has been effectively accomplished in past studies. Dippers often build nests under bridges, which are easily accessible to collect eggs for measuring contaminant levels (Henny *et al.*, 2005). Further, dipper eggs have been effectively used to represent contaminant levels in streams (Ormerod and Tyler, 1994; Henny *et al.*, 2005; Morrissey *et al.*, 2005) and Hg toxicity values for avian embryos are available (Heinz *et al.*, 2009), facilitating interpretation of observed egg contaminant levels and inference of population-level impacts. Dipper blood and feathers can also be analyzed for contaminants, representing short-term or long-term dietary exposure.

Third, dippers are relatively high trophic-level predators that bioaccumulate contaminants from the water and their diet, reflecting local contaminant levels. Consumption of aquatic prey is the main pathway of Hg exposure for dippers (Henny *et al.*, 2005). Dippers feed on benthic macroinvertebrates and salmonid eggs and fry, which are sensitive to contaminants and siltation (Price and Bock, 1983; Feck and Hall, 2004; Ormerod and Tyler, 1991). Contaminant bioaccumulation in dipper eggs, feathers, and blood has been documented and they are established bioindicators of stream quality (Ormerod and Tyler, 1994; Morrissey *et al.*, 2005).

Resident dippers feeding at higher trophic level (more salmon) bioaccumulate higher concentrations of contaminants than migrants (Morrissey *et al.*, 2012), as do females that feed preferentially on salmon during egg-laying (Morrissey *et al.*, 2010a). The high elevation, densely forested stream habitat used by dippers may experience high levels of atmospheric deposition of Hg, similar to Bicknell's Thrush inhabiting montane riparian areas (Rimmer *et al.*, 2005) and Osprey foraging in alpine lakes (Guigueno *et al.*, 2012). The potential methylation of Hg within RoR headponds may faciliate high levels of dietary uptake of MeHg by dippers foraging in this novel, high-elevation aquatic habitat.

MeHg potentially produced in reservoirs of regulated streams will be detectable in dipper blood, feathers, and eggs. Though there are no published MeHg turnover values for passerine tissues, half-lives have been published for the whole blood of Great Skua (*Catharacta skua*; Bearhop *et al.*, 2000) at 31.5-63 days, ~74 days for Mallard (Heinz and Hoffman, 2004), and 44–65 days for Cory's Shearwater (*Calonectris diomedea*; Monteiro and Furness 2001). The MeHg half-life for dipper whole blood is likely less than these published values for waterbirds, as passerines have a higher metabolic rate. Dippers, however, have a lower metabolic rate than other passerines as an adaptation for life in cold waters (Murrish, 1970). Therefore, I estimated MeHg half-life in dipper whole blood as ~30 days, which was used a conservative turnover estimate for Bicknell's Thrush (Rimmer *et al.*, 2010). MeHg measured in feathers indicate the amount deposited during active feather growth (Wolfe *et al.*, 1998). Feathers collected in the early fall will indicate MeHg exposure during feather growth (Hobson and Clark, 1992; Bearhop *et al.*, 2002), which occurs after the late summer/early autum moult in dippers. Body feathers provide the most representative tissue for estimating whole bird Hg content (Furness *et al.*, 1986).

The most informative stable isotope analyses will study organisms that have established diet-tissue fractionation factors (the factor by which the ratio of two isotopes changes during the energy transfer between the diet and specific tissue of the consumer), measure isotopic ratios in multiple tissues to measure temporal diet shifts, adequately characterize baseline isotopic ratios, and integrate life history of the study organisms (Jardine *et al.*, 2006). The present study fits the above criteria: isotopic turnover and fractionation values are well established in avian whole blood (Bearhop *et al.*, 2002; Hobson and Clark, 1992; Hobson and Bairlein, 2003; Evans Ogden *et al.*, 2004), isotopic ratios will be measured in whole blood and feathers, baseline isotopic ratios will be characterized in benthic macroinvertebrates, and the life history of dippers is well understood. Here, I measured stable isotopes of C, N, and S through river food webs in order to characterize changes to dipper diet and Hg exposure related to flow changes by RoR dams.

Turnover rates of δ^{13}C and δ^{15}N in avian blood are fairly rapid, indicating recent dietary conditions. Whole blood of the Greater Skua (*Catharacta skua*) had a half-life of 14.4 days for δ^{15}N and 15.7 days for δ^{13}C (Bearhop *et al.*, 2002). Similarly, the δ^{13}C half-life in captive Japanese Quail (*Coturnix japonica*) was 11.4 days (Hobson and Clark, 1992). The Garden Warbler (*Sylvia borin*) had a half-life of 11 ± 0.8 days for δ^{15}N and 5.0 ± 0.7 to 5.7 ± 0.8 for δ^{13}C (Hobson and Bairlein, 2003). Dunlin (*Calidris alpina pacifica*) have reported half-lives of 11.2 ± 0.8 days for δ^{13}C and 10.0 ± 0.6 days for δ^{15}N (Evans Ogden *et al.*, 2004). Dippers have a lower metabolic rate than non-aquatic passerines of the same size (Murrish, 1970), so turnover values are likely intermediate between those of the Garden Warbler and Greater Skua; however, birds in the above experiments were studied in captivity and likely have lower metabolic rates than their wild counterparts. Although turnover values are affected by metabolic rate and nutritional stress (Hobson *et al.*, 1993), whole blood isotopic values represent fairly recent dietary information, likely <20 days for both δ^{15}N and δ^{13}C. The turnover rate of δ^{34}S is assumed to be similar to carbon and nitrogen (Vander Zanden *et al.*, 2015). Measuring multiple stable isotopes in dipper blood provides accurate information on their recently assimilated diet.

1.5 STUDY AREA

The 14 mountain streams (7 regulated and 7 unregulated) surveyed during this study span three watersheds in the Coast Mountain range of British Columbia’s Fraser Basin: the Squamish (49°54'4.22"N 123°17'21.09"W), Lillooet (50°18'14.38"N 122°42'11.75"W), and Harrison River (49°44'32.45"N 122° 8'2.81"W) watersheds (Fig. 2). The majority of creeks and rivers surveyed are steep, third-order streams within the Coastal Western Hemlock, Mountain Hemlock, and Engelmann Spruce Subalpine fir biogeoclimatic zones. As hybrid streams (Eaton and Moore, 2010), these creeks and rivers experience peak runoff during the winter (November-January) in response to heavy rainfall and a secondary peak runoff event, known as the spring freshet (April or May) in response to snowmelt (Coulthard *et al.*, 2016). Minimum flows occur in the summer, or often in the early fall, when snowmelt has ceased and temperatures are highest (Eaton and

Moore, 2010). In the case of RoR-regulated streams, however, the hydrograph is stabilized (due to flow diversion) and the magnitude of peak flooding events are reduced.

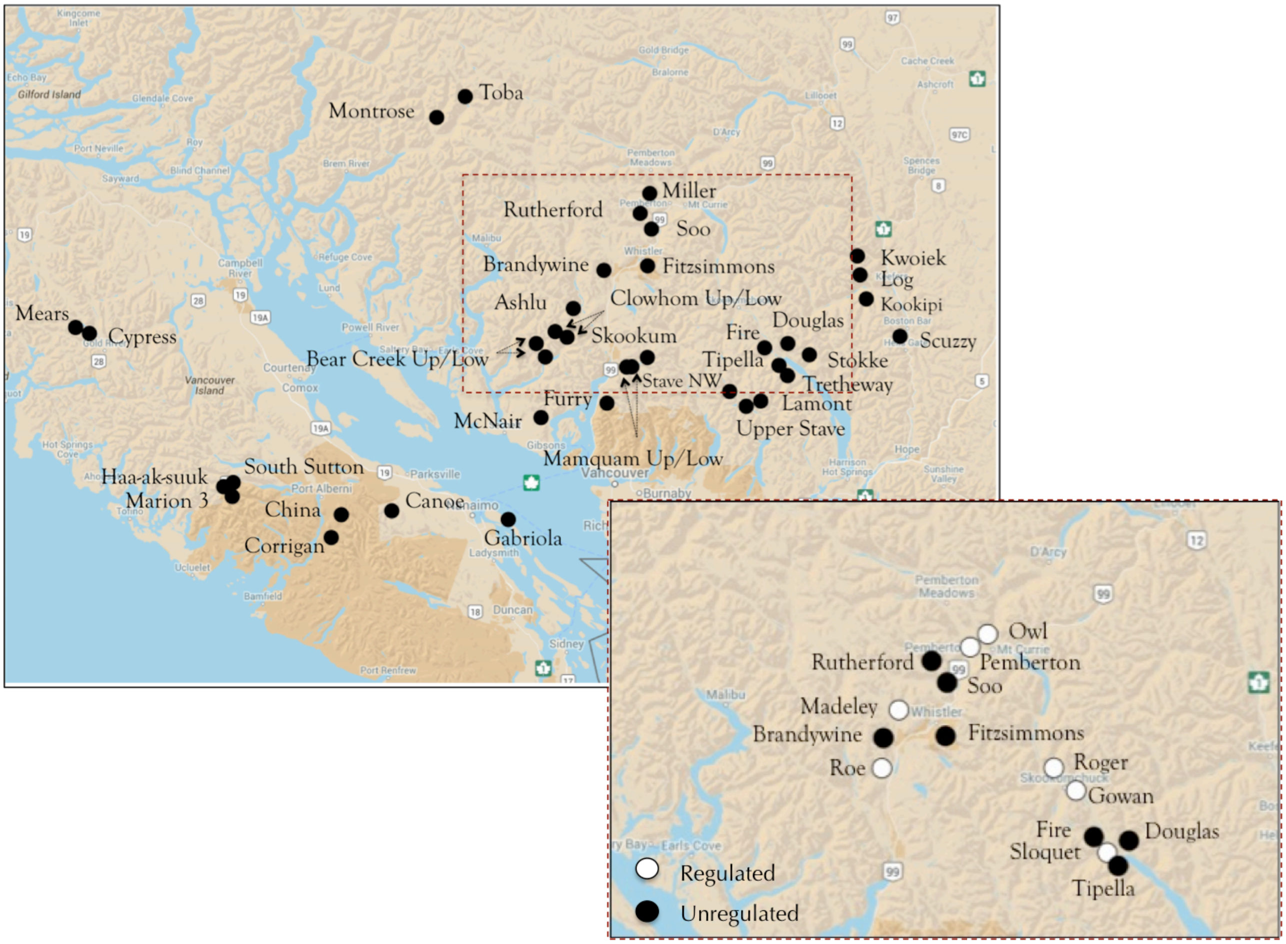

Figure 1.2 Operational run-of-river projects in southwestern British Columbia as of January 2016 (upper left) and location of 14 study streams (7 regulated and 7 unregulated) surveyed in this study (lower right), spanning the Squamish, Lillooet, and Harrison watersheds in the Coast Mountain range of the Fraser River Basin.

1.6 THESIS OBJECTIVES AND MAJOR HYPOTHESES

Although local responses of certain taxa, particularly fish, to RoR developments have been identified, there are knowledge gaps on the ecosystem-level response to RoR regulation. To address this, I studied the response of mountain stream food webs to regulation by RoR dams across three adjacent watersheds in coastal British Columbia using stable isotope analysis. I also addressed potential MeHg exposure in RoR-reservoirs, which has not been assessed in any studies or reviews on the known and predicted impacts of RoR dams. I examined headponds and other habitats experiencing flow changes through RoR-regulation from the perspective of ecological traps, as I expected stream-dependent biota to encounter both benefits and costs related to flow regime stabilization.

The main objectives of this study were to 1) explore potential impacts of RoR dams on dipper occupancy, demographics, and body condition and 2) characterize dipper diet and MeHg exposure in relation to flow diversion by RoR dams. To accomplish this, I combined a study of American Dipper and other river bird habitat use with stable isotope and Hg analysis of dippers and their prey to measure changes to the stream food web and contaminant exposure. There was uncertainty over whether RoR dams would impair or enhance American Dipper habitat and components of fitness, but in sampling multiple streams, I expected that one or more responses might be related to the longitudinal changes associated with the RoR headponds and flow diversion.

I hypothesized that Hg concentrations would be higher in dipper tissues at regulated streams, reflecting the higher rates of Hg-methylation described in large hydroelectric reservoirs and beaver dams. I also hypothesized that the mechanism of MeHg production within RoR headponds would be through the activity of sulfate-reducing bacteria. I predicted dippers to have the highest blood and feather Hg concentrations if they were foraging at the most-recently inundated headponds with the highest amount of leaf litter and largest flooded area, which are known to increase MeHg production. I also hypothesized that headponds, dominated by slow-flowing waters and lower oxygen conditions, would have distinct isotopic profiles compared with upstream and downstream reaches. Specifically, I predicted that invertebrates sampled within the headponds and dippers foraging within the headponds would reflect this distinct isotopic signature of ^{13}C-enrichment and ^{34}S-depletion, indicating limited boundary layer diffusion at low flow and the activity of anaerobic bacteria.

Beyond exploring the ecotoxicological effects of RoR regulation on mountain streams, my study provides new information about the extent of MeHg contamination in locations of western North America free from known Hg point sources. In addition, it broadens our knowledge about Hg biomagnification in natural-flowing and regulated streams, which are less understood than lentic ecosystems.

CHAPTER 2:

ABUNDANCE-OCCUPANCY PATTERNS OF RIVER BIRDS IN RESPONSE TO THE MODIFIED UPSTREAM AND DOWNSTREAM HABITAT CREATED BY RUN-OF-RIVER DAMS

2.1 INTRODUCTION

With nearly two-thirds of the world's large rivers already fragmented by dams (World Commission on Dams, 2000; Nilsson *et al.*, 2005), run-of-river (RoR) dams on smaller streams are emerging as an alternate approach to harnessing hydroelectric energy across the globe. Also known as river diversions or non-storage hydropower, RoR dams differ from conventional dams in two main ways: 1) they operate on smaller rivers with smaller barriers (a small weir) and have a reduced impact area; and 2) impounded water is usually stored for less than 48 hours without an extensive reservoir (Community Energy Association, 2008; Anderson *et al.*, 2015), compared to a residence time of several days to years for stored water in larger impoundments (Baxter *et al.*, 1977). RoR projects function by diverting a portion of a stream's flow from the dam through underground pipes (known as the penstock) before returning it downstream; thus, they rely on a steep elevation-gradient, and consequently, minimal storage. Further, it is argued that because altered magnitude and timing of stream flow is limited to the diversion reach (portion of the stream with abstracted flow), there is no substantial impact to the upstream and downstream flow regime (Lewis *et al.*, 2013).

RoR dams are often regarded as clean or environmentally-benign energy sources because of their smaller overall size and reduced greenhouse gas emissions compared to conventional hydropower (Paish, 2002). There is, however, increasing evidence to suggest that RoR dams have appreciable impacts on stream biota (Robson *et al.*, 2011; Anderson *et al.*, 2015). American Dippers, the only truly aquatic songbird in North America, share the specificity for high-elevation, fast-flowing mountain stream habitat suitable for RoR projects. Dippers are year-round residents on mountain streams and do not undertake extensive latitudinal migration; however, migration to higher elevation reaches during the breeding season (late March to August) is common in many Pacific Northwest populations (Price and Bock, 1983; Morrissey *et* *al.*, 2004b, Walton and Wright, 2008). Formerly known as the Water Ouzel, these songbirds do not stray far from the stream channel where they breed and overwinter, feeding on benthic macroinvertebrates, small fish, and fish eggs by diving and swimming underwater with their wings, or running along the stream bottom (D'Amico, 2011). Dippers have been used extensively as indicators of stream health (Ormerod and Tyler, 1994; Henny *et al.*, 2005; Morrissey *et al.*, 2005). With several biotic and abiotic factors known to influence dipper fitness, it is possible that RoR-associated habitat modifications may alter year-round habitat use.

Dippers are sensitive to variation in river flow regime (D'Amico and Hemery, 2007; D'Amico, 2011; Royan *et al.*, 2014) and it is possible that they will respond to changes in the stream foodweb related to flow diversion by run-of-river dams. Flow regulation by RoR dams may directly or indirectly impact dipper fitness through changes to the flow regime that affect prey availability, stream physicochemistry, and in-channel and riparian habitat. White-throated dipper (*Cinclus cinclus*) time-activity budgets are highly tied to streamflow (D'Amico and Hemery, 2007) and dippers may exhibit non-adaptive foraging in response to stabilized flow and/or unpredictable recreational release events. In both situations, changes in flow are not associated with seasonal environmental cues (rainfall or drought) and dippers may be forced to alter their foraging strategies, with possible consequences for their survival (D'Amico, 2011). In contrast, habitats modified by the stabilized flow regime may serve as a refuge for dippers as our climate changes and catastrophic flood events become more common (Royan *et al.*, 2014), or simply by reducing the energetic demands of foraging in fast-flowing waters (D'Amico *et al.*, 2000).

A recent review on the responses of river bird specialists to sudden and extreme flow events concluded that White-throated Dippers are the most vulnerable species to shifts in river flow and flooding events (Royan *et al.*, 2014). The headpond may serve as a pool habitat that supports a larger diversity of invertebrate prey more typical of lentic habitats (*e.g.* limnephilidae). With the combination of higher spring and summer temperature, lower flows, and nutrient retention, headponds may provide a novel habitat with benefits of improved dipper foraging efficiency compared to habitats experiencing high and more variable flows. Taylor and O'Halloran (2001) documented an immediate shift in White-throated Dipper diet following a sudden flood event in Ireland and predicted that preferred prey become less available/less energetically profitable during high water levels, which could affect chick growth and survival.

Brown Dippers (*Cinclus pallasii*) in Taiwan also experienced declines in productivity in response to severe floods caused by typhoons, which decreased invertebrate abundance (Hong *et al.*, 2016). Late season floods and longer recovery periods for the invertebrate community were especially stressful to dipper reproductive output (Hong *et al.*, 2016). Although Eurasian Dippers in the Pyrénées of France exhibited maximal foraging efficiency during spring snowmelt, large amounts of time were spent resting (D'Amico and Hemery, 2007). This indicates that foraging at high flow has high energetic demands, while regulated flows may reduce the energy requirements of foraging in addition to providing more or higher quality prey within the headpond.

Changes to streamflow may also indirectly impact dipper fitness through changes to stream physicochemistry, in-channel and riparian habitat, and associated biotic community structure. Winter is a time of high energetic stress for dippers, indicated by high rates of adult mortality (Price and Bock, 1983) and time-activity budgets dominated by foraging with little time spent resting (D'Amico and Hemery, 2007). Flow abstraction by RoR impoundments can alter stream temperatures, producing warmer than average summer waters and cooler winter waters. Elevated summer temperature may indirectly impact dippers through earlier emergence or mortality to the invertebrate prey community; however, elevated temperature may increase overall stream productivity and therefore benefit dippers through indirect effects on food availability. Colder temperatures and shallow waters in the diversion reach in winter may lead to stream freezing and subsequent reductions in open water habitats. By comparison, headponds may serve as year-round ice-free habitat for dippers.

Changes in natural flow within the diversion reach of run-of-river dams may alter the prey base to which dippers have adapted. Reduced abundance and diversity of benthic algal (Wu *et al.*, 2009) and invertebrate communities (Gonzalez *et al.*, 2013; Fanny *et al.*, 2013), and reduced macroinvertebrate density (McIntosh *et al.*, 2002) have been observed below small dams. In resident fish, researchers have observed variable effects downstream of small dams ranging from no change in species assemblage (Santos *et al.*, 2006), to reduced density of some species but overall increases in species richness (Lessard and Hayes, 2003), to 50 % declines in populations (Almodovar and Nicola, 1999). These responses are often attributed to flow changes and associated changes to in-stream habitat, such as increased sedimentation and siltation. No previous studies have looked at dippers or other river birds in association with RoR developments, however, dippers are known to exhibit similar negative responses to reduced availability of benthic macroinvertebrates (Ormerod and Tyler, 1991; Feck and Hall, 2004) and salmon prey (Obermeyer *et al.*, 2006; Morrissey *et al.*, 2012), loss of riffle habitat (Loegering and Anthony, 1999; Vaughn *et al.*, 2007), and siltation (Price and Bock, 1983). Changes to riparian vegetation associated with flow abstraction and associated erosion (Nilsson *et al.*, 1997; Nilsson and Berggren, 2000; Jansson *et al.*, 2000), combined with pre-existing or new forest fragmentation for access roads, may also reduce dipper nest site availability, which is a limiting factor for breeding success (Price and Bock, 1983; Mazeika *et al.*, 2012).

To date, research on ecological responses to RoR impoundments has focused primarily on migratory fish. Variation in run-of-river projects with respect to barrier-type, extent of reservoir flooding and retention time, proportion of flow diverted, stability of flow, site geography, and the presence of resident salmonids makes monitoring the response of transient fish and fish habitat to this energy source difficult. By comparison, American Dippers occupy an important and more permanent niche at the interface between the stream channel and riparian zone. Dipper presence and abundance are likely highly suitable bioindicators of altered flow regime related to run-of-river dams. Therefore, my specific objectives were to compare regulated and unregulated streams in terms of dipper 1) seasonal stream occupancy and year-round residency and 2) demographics and body condition in coastal British Columbia, Canada. I could not explicitly predict whether RoR dams would impair or enhance local American Dipper populations, but I hypothesized that dipper responses would vary in relation to inherent site characteristics of habitat quality and regulation practices.

2.2 METHODS

2.2.1 Study Site Selection

The 7 regulated streams surveyed in this study included: Brandywine Creek (BRANDY), Fitzimmons Creek (FITZ), Rutherford Creek (RUTH), Douglas Creek (DOUG), Fire Creek (FIRE), Tipella Creek (TIP), and the Soo River (SOO). The 6 free-flowing, unregulated streams included: Roe Creek (ROE), Madeley (MAD), Pemberton Creek (PEM), Owl Creek (OWL), Gowan Creek (GOW), and Sloquet Creek (SLO) (Table 2.1). Elevations of regulated streams ranged from 302 m-1000 m, while those of unregulated streams ranged from 55-881 m. Most

RoR dams on the regulated streams were low-flow, high-head schemes, where head is the difference in elevation of water at the intake and elevation of the turbine inlet in the powerhouse (Anderson *et al.*, 2015). Anadromous salmon (*Oncorhynchus spp.*) were absent upstream of the powerhouse on regulated streams, but five of the lower elevation unregulated reference streams may have supported at least one species of anadromous salmon. Resident rainbow trout *(Oncorhynchus mykiss)* inhabited all surveyed streams, with the exception of the highest elevation regulated stream, Fitzsimmons Creek (Table 2.1).

Prior to establishing survey transects in the fall of 2014, operational regulated streams were screened by the following selection criteria: a) suitable dipper habitat and b) accessibility for wading or walking in or along the stream channel and setting mist-nets across a sufficient portion of the stream to catch birds. Regulated streams in this study varied in their regulatory techniques (water retention time above the dam, % water diverted, megawatt capacity), stream morphology, and operational date (Table 2.1), but all were high elevation mountain streams providing potential year-round habitat for dippers. Unregulated streams were selected based on the former criteria in addition to a third criterion of similar stream geomorphology and close proximity to neighbouring regulated streams.

At each regulated stream, a 1km linear survey transect was established from 500 m upstream to 500 m downstream of the point of diversion. At unregulated streams, 1 km transects were established from 500 m upstream to 500 m downstream from a mid-point based on accessibility and elevation. In total, 14 linear stream kilometers (7 km regulated, 7 km unregulated) were surveyed in this study during breeding and non-breeding seasons.

Table 2.1 Site characteristics and regulatory information for the regulated and unregulated streams surveyed in coastal British Columbia.

Stream	Type	Watershed	Stream Order	Mid-point/ Intake Elevation (m)	Anad. Salmon in Transect	Resident Trout in Transect	Commission Year	Capacity (MW)	Headpond Perimeter (m)	Length of Diversion Reach (km)	Stream Length (km)	% Stream Length Impacted by Flow Abstraction
Brandywine	Reg	Squamish	3	828	No	Yes	2005	7.6	150	4.4	14.5	30.3
Madeley	Unreg	Squamish	3	851	No	Yes					9.5	
Fitzsimmons	Reg	Lillooet	3	995	No	No	2010	7.9	200	3.4	18	18.9
Roe	Unreg	Squamish	3	708	No	Yes					12.2	
Rutherford	Reg	Lillooet	3	742	No	Yes	2004	49.9	500	8.8	26.7	33
Pemberton	Unreg	Lillooet	2	262	Yes	Yes					15.2	
Soo	Reg	Lillooet	4	589	No	Yes	1994	13	2200	1.6	45.8	3.5
Owl	Unreg	Lillooet	3	366	Yes	Yes					20.5	
Douglas	Reg	Harrison	3	370	No	Yes	2009	27	500	3.1	22	14.1
Gowan	Unreg	Lillooet	3	140	Yes	Yes					18.2	
Fire	Reg	Lillooet	3	384	No	Yes	2009	23	300	4.3	13.8	31.2
Sloquet	Unreg	Lillooet	4	55	Yes	Yes					30.8	
Tipella	Reg	Harrison	3	338	No	Yes	2009	18	180	2.5	14	17.9
Roger	Unreg	Lillooet	3	170	Yes	Yes					30.3	

2.2.2 Trapping and density surveys

All banding and re-sight methods were approved by the University of Saskatchewan Animal Care Committee and Environment Canada (permit no. 10268 M). From September to November of 2014 and 2015, 99 adult dippers (n=48 in 2014 and n=51 in 2015, plus 3 recaptures from 2014) were banded at 13 (7 regulated, 6 unregulated) of the 14 surveyed streams (7 regulated, 7 unregulated). Dippers were captured using 6, 9 or 12 m mist-nets set across shallow reaches of each stream and banded with a unique combination of a USGS numbered metal band and three colour bands. Mist-nets were typically set below the dam or near the mid-point of reference streams within the 1km survey transect at each site. All trapping occurred during autumn, when dippers are less territorial and found at higher densities (Price and Bock, 1983; Morrissey, 2004; Whitehorne*,* 2010) and stream levels are low enough to set mist nests across the channel.

For each individual dipper, tarsus and bill length were measured with dial calipers to the nearest 0.1mm, maximum wing chord and tail length were recorded with wing rules to the nearest 0.5mm, and mass was recorded to the nearest gram. In 2015, I was able to reliably age individuals based on eye colour and condition of primary coverts; after hatch year (AHY) adults have dark, chestnut-coloured eyes with rounded primary converts, while hatch-year (HY) birds have olive-coloured eyes with pointed and often white-tipped primary coverts (Pyle, 1997). In 2015, I attempted to sex AHY birds by size, as male dippers have slightly larger measurements than females; however, some birds fell in the range of overlap, so I included a category of "unknown sex".

I captured and banded adult dippers for 2-3 consecutive days at 6 regulated and 5 unregulated streams during the autumn of 2014 and conducted re-sighting surveys 1-2 days after the last banding attempt to satisfy the assumption of population closure during the primary fall periods. The same streams were surveyed during the spring of 2015 on two occasions: pre-freshet (mid-late April) and post-freshet (early-mid June); during these breeding season surveys, one additional regulated and two unregulated sites were added to the study, for a total of 7 regulated and 7 unregulated streams. During the fall of 2015, I followed the trapping and re-sight survey methodology from 2014 and added an additional re-sight survey at the end of October. With at least two encounter occasions within each primary sampling interval (fall 2014, spring

2015, and fall 2015), I was able to run a robust-design occupancy analysis. The robust design occupancy analysis allows "missing" data to be omitted for streams that were not initially visited until spring, 2015. Despite numerous attempts and a few dipper sightings during the fall and spring, I was unable to capture dippers at one of the unregulated streams, Roger Creek.

Density surveys followed the unreconciled independent double-observer approach (Riddle *et al.*, 2010), whereby each observer keeps a separate tally of all observations to facilitate an estimation of detection probability. Within each 1 km transect, a pair of observers walked in an upstream or downstream direction along the stream bank and in wadeable channels and recorded the location and activity of all dippers and other river birds seen and heard on a stream transect map. To reduce communication and maximize survey integrity, observers walked along opposite stream banks whenever possible or staggered their survey start times by a distance that would not result in the first observer flushing birds ahead of the second observer. Unique colour combinations were easily identified from a distance of 30 m with 10x40 binoculars. If a band code combination was not initially distinguishable, observers tracked down the bird and ensured the correct code was recorded. Survey duration was typically 1-1.5 hours, depending on the terrain.

2.2.3 Statistical analyses

2.2.3.1 Seasonal density and occupancy

Seasonal density estimates (number of dippers observed per linear stream kilometer) were calculated from un-reconciled independent double observer counts (Riddle *et al.*, 2010) during each re-sight survey (fall 2014, pre-freshet 2015, post-freshet 2015, fall2015a, fall2015b). Detection probabilities for each season were estimated using the Royle-N-Mixture Model for repeated counts (Royle, 2004) in program PRESENCE 11.2 (Hines, 2006). These models are parameterized using independent counts from each observer during the survey and treating each observer's count as a separate "visit"; therefore, repeated counts at the same stream are used to estimate detection probability (Riddle *et al.*, 2010). Since both visits occur simultaneously using this approach, detection probability is estimated here as the probability that an individual bird is detected given that it is present and available in the study area (Riddle *et al.*, 2010).

As suspected from few discrepancies in counts between observers, detection probabilities were high with little variation between seasons: pre-freshet (0.93 ± 0.05); post-freshet (0.86 ± 0.09); fall 2015A (0.97 ± 0.03); and, fall 2015B (0.85 ± 0.12). During the fall of 2014, I was the only observer conducting counts, so I assumed detection probability was the same as the first survey during the fall of 2015, since it was conducted at the same time of year. Counts from seasonal surveys were adjusted by seasonal detection probabilities and density was calculated as the number of dippers observed divided by the detection probability. Since detection probabilities were always high, adjusted densities were often identical to original counts.

To compare seasonal densities between regulated and unregulated streams, I ran a zero-inflated generalized linear mixed effects model with a poisson family and log-link function in the package *glmmADMB* (Skaug *et al.*, 2016; Fournier *et al.*, 2012) in R version 3.2.3 (R Core Team, 2015). This model accounted for over-dispersion in the data due to an excess of zeroes from instances when no birds were detected. To account for repeated measures across the same streams over the seasons, stream was included as a random effect. Watershed was also included as a random effect to account for potential regional factors influencing dipper distribution and density. The following factors were included as fixed effects: stream type (regulated/unregulated), season, the presence of anadromous salmon, and intake (or midpoint, in the case of free-flowing streams) elevation, as these are known or hypothesized to affect dipper densities.

Regulated streams were counted as salmon-bearing if salmon were known to be present upstream of the powerhouse, using information provided by Innergex, the British Columbia Fisheries Inventories Data Queries (FIDQ), and personal observation. The status of salmon presence at unregulated streams was also obtained from the FIDQ and personal observation. The interactions between stream type*season and stream type*elevation were also tested, but I was unable to test the interaction between salmon*stream type, as none of the regulated streams supported anadromous salmon within the survey transect or upstream of the tailrace. I tested for partial autocorrelation of the model residuals using the pacf function in R and did not find evidence of temporal autocorrelation; therefore, it was not necessary to include an autocorrelation function in these models.

Seasonal dipper occupancy rates were compared between regulated and unregulated streams using the robust design stream occupancy analysis in program MARK (White and

Burnham, 1999), with streams grouped by type (regulated/unregulated). The robust design included 3 primary intervals (fall 2014, spring 2015, and fall 2015) and 2-3 secondary occasions within each primary interval (Fig. 2.1). Due to sample size limitations (11 streams surveyed in 2014 and 14 streams in 2015), I was unable to include in-stream and riparian covariates in the occupancy models.

To compare the stream occupancy rate of marked and unmarked dippers between regulated and unregulated streams, I ran a multi-state occupancy model in MARK (White and Burnham, 1999) on the re-sight surveys. Under this model, I used two levels of detection: banded (coded as 2) and unbanded (coded as 1). This model allows estimation of the following parameters: Ψ1, probability that a site is occupied regardless of band state; Ψ2: probability that a site is occupied by a banded bird; ρ1, probability that occupancy was detected given true state=1(unbanded); ρ2, probability that occupancy was detected given true state=2 (banded); and, δ, probability that banded birds were observed, given detection of occupancy. With a limited number of streams, it was not possible to parameterize a multi-state occupancy model under the robust design, so equal time intervals were assigned between all re-sight survey periods. For the purpose of comparing occupancy between regulated and unregulated streams and not across seasons, this multi-state approach was the most appropriate option.

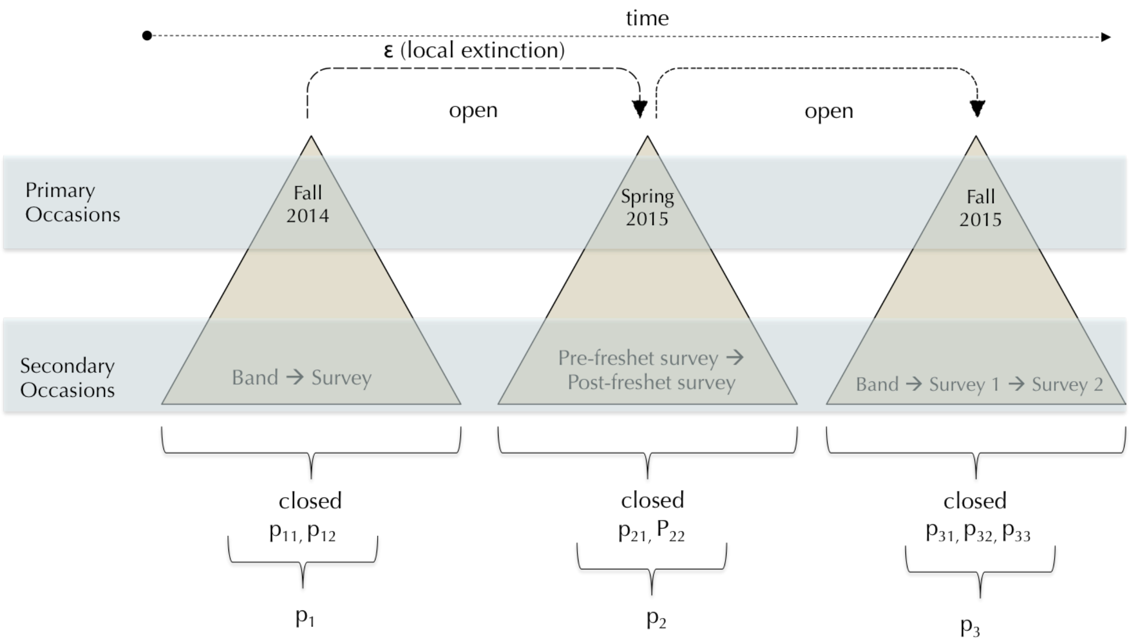

Figure 2.1 Schematic of the robust design for estimating American Dipper occupancy rates of regulated and unregulated streams, adapted from the robust design (Pollock *et al.*, 1990) and the robust occupancy models of MacKenzie *et al.* (2003). This model allows estimating of the following parameters: **Ψ** (proportion of sites occupied at each time period); **ε** (probability of an occupied site becoming unoccupied), and **ρ** (detection probability on a visit to the site) between primary and secondary surveys (occasions). The model assumed a closed population during the survey interval (fall 2014, spring 2015 and fall 2015) with an open population among survey periods.

2.2.3.2. Philopatry and year-round residency

To compare year-round residency of dippers between regulated and unregulated streams, I surveyed each stream twice during the breeding season (before and after the spring freshet). If a bird was detected on the same stream during the breeding season as where it was banded the previous fall, it was classified as a year-round resident. The proportion of confirmed year-round residents was compared between the two stream types. To assess the degree of philopatry of dippers at regulated and unregulated streams, I also compared the proportion of individuals banded in 2014 and re-sighted at the same stream in 2015.

2.2.3.3. Dipper age, sex, and body condition

I calculated the proportion of AHY dippers captured at each stream and tested for a difference between regulated and unregulated streams using a generalized linear model (glm, package *stats*, R version 3.2.3) with a binomial family and logit link function. To account for differences in sample size at each stream and therefore unequal variance between stream types, age proportions were weighted by the total number of dippers banded at each stream. Stream type, elevation, salmon, and the interaction between elevation and type were included as fixed effects. Watershed was excluded as a random effect, since it did not explain a sufficient amount of variation in age proportion to warrant inclusion (standard deviation <0.001).

The proportion of female AHY dippers captured at each stream was also compared between regulated and unregulated streams using a generalized linear model (glm, package *stats*, R version 3.2.3) with a binomial family and logit link function with no random effects, as watershed accounted for negligible variation (standard deviation <0.001). Proportions were weighted by the total number of AHY dippers captured at each stream and I tested for effects of stream type, elevation, salmon, and the interaction between elevation and type. Only 22 AHY dippers were captured at 11 streams in 2015; therefore, the sex proportion data are limited by low sample size.

A scaled mass index was calculated using the *smatr* package in R (Warton *et al.*, 2012) as a measure of body condition. Mass was scaled by wing chord length, as wing length had the strongest correlation with dipper mass on a log-log scale relative to other body morphometrics ($r=0.67$, $p<0.0001$). Prior to developing the scaled mass index, I checked for a significant interaction (differences in slopes) between age and sex using 2015 demographic data. Using package *smatr* in R, I tested the single major axis regression with an interaction between wing and age and wing and sex. Neither age ($\chi^2=0.085$, df=1, p=0.77) nor sex ($\chi^2=0.27$, df=2, p=0.88) had a significant interaction with wing length as predictors of mass and therefore it was not necessary to calculate separate scaling equations for different ages or sexes or include age or sex as factors in the linear mixed effects models.

The scaled mass index corrects body mass for body size based on a single major axis regression, rather than linear combinations computed by PCA, using the following equation adapted from Peig and Green (2009), following the methodology of Tonra *et al.* (2016) in a recent American Dipper study:

Scaled Mass Index = $M_i\ [L_0/L_i]^{b_{SMA}}$ .... (Equation 2.1)

M_i= mass of bird i;
L_0= mean (or other arbitrary value) wing length (or other linear morphometric) of all individuals in the population;
L_i= wing length (or other linear morphometric) of individual i;
b_{SMA}= slope of the log-log regression between mass and wing length (or other linear morphometric)

Linear mixed effects model were run with package *lme4* (Bates *et al.*, 2015, R version 3.2.3) to test for differences in body condition of dippers at regulated and unregulated streams. Stream type, elevation, and the presence of anadromous salmon were included as fixed effects. I also tested the interactions between stream type*year and stream type*elevation. Stream was included as a random effect to account for non-independence of dippers banded at the same stream. Watershed and sampling year were excluded as random effects because they did not explain a significant amount of variation in body condition index (standard deviation < 0. 001). A general linear model (glm, package *stats*, R version 3.2.3) and *post-hoc* Tukey HSD test were also run to test for differences in dipper body condition between individual streams.

2.2.3.4. Model selection

All models were selected based on the information-theoretic approach using Akaike's Information Criterion adjusted for small sample sizes (AIC_c, Burnham and Anderson, 2004). Model selection tables were generated using the package *MuMIn* (Barton, 2016) in R. Models were run using maximum likelihood (ML) estimation and parameter estimates from the best-fitting models were calculated using restricted maximum likelihood estimation (REML). If a random effect did not explain substantial variation in the response variable (standard deviation <0.001), it was excluded from the model. When multiple models were competitive ($\Delta AIC_c \leq 2$), conditional model-averaged parameter estimates were calculated using the package *MuMIn*

(Barton, 2016), whereby parameters are only averaged across models when there is sufficient support for their inclusion as factors. Elevation was included as a continuous variable in all models and stream type refers to the categories “regulated” or “unregulated”.

2.3 RESULTS

2.3.1 Stream occupancy and seasonal density estimates

2.3.1.1 Seasonal count data

Variation in dipper density was higher at regulated streams compared to unregulated streams (Appendix 1). Dipper density at regulated streams ranged from a low of zero at some streams during all seasons, except fall 2014, to a maximum of 14 adult dippers/km at Brandywine Creek during the fall of 2014. Densities at unregulated streams ranged from a low of zero in all seasons to a maximum of 5 birds/km at Roe Creek during fall 2014 (Table 2.2). Average dipper density during the fall of 2014 was 5.9 ± 1.9 (S.E.) birds/km at regulated streams and 2.3 ± 1.1 birds/km at unregulated streams. Pre-freshet survey density dropped to a mean of 1.4 ± 0.3 birds/km at regulated streams and 1.2 ± 0.4 (S.E.) birds/km at unregulated streams, but increased to 2.4 ± 1.3 birds/km at regulated streams during the post-freshet survey. Post-freshet densities remained low at unregulated streams (1.3 ± 0.3 birds/km). Early fall 2015 densities were low at regulated and unregulated streams compared with the previous autumn (Mean_{reg}=1.6 ± 0.8 birds/km, $\text{Mean}_{\text{unreg}}$=0.9 ± 0.5 birds/km), and dropped later on in the fall (Mean_{reg}=1.2 ± 0.6 birds/km, $\text{Mean}_{\text{unreg}}$=0.3 ± 0.2 birds/km), with dippers becoming quite scarce at unregulated streams in late October (Fig. 2.2).

The top two models supported differences in dipper densities between seasons and stream type, but not the interaction between season and stream type (Table 2.3). Model-averaged estimates for the top two models supported significantly higher dipper denisty at regulated streams compared to unregulated streams across seasons (β=0.78, SE=0.36, p=0.030). Aside from significantly higher fall 2014 densities ($p \leq 0.005$), dipper densities were not significantly different among seasons, as indicated by *post-hoc* Tukey HSD tests (Appendix 2). Elevation and the presence of anadromous salmon within the survey transect did not appear to influence dipper density (Table 2.3).

Over the 2 years, 74 dippers were sighted at regulated streams during surveys. Of these, 54% of the birds were initially sighted in the headponds of the regulated streams, usually foraging along the headpond edge or diving in the pool (Fig. 2.3). As the density of dippers at regulated streams decreased over time, proportionately more were first sighted within headponds (Fig. 2.4). Dippers were also commonly sighted directly below the dam, often foraging in the cascade created by the weir.

Table 2.2 Comparison of American Dipper densities (Mean ± S.E. birds/km) at regulated and unregulated streams during breeding and non-breeding seasons in streams of southwestern British Columbia (BC) during this study and those of other published studies in the Pacific Northwest.

Location	Year	Survey Linear Distance (km)	Spring density (April)	Summer density (June)	Early fall density (Sept/Oct)	Late fall density (Nov)	Winter density (Dec-Feb)	Source
Regulated coastal BC	2014	6	__	__	5.86 ± 1.88 (2.07-14.48)		__	This study
Unregulated coastal BC	2014	5	__	__	2.27 ± 1.05 (0-5.17)		__	This study
Regulated coastal BC	2015	7	1.38 ± 0.31 (0-2.15)	2.16 ± 1.03 (0-8.15)	1.62 ± 0.78 (0-4.14)	1.18 ± 0.57 (0-3.53)	__	This study
Unregulated coastal BC	2015	7	1.23 ± 0.36 (0-2.15)	1.33 ± 0.30 (0-2.33)	0.89 ± 0.47 (0-3.10)	0.34 ± 0.22 (0-1.18)	__	This study
Seton River, Lillooet, BC	2000-2002	10.6	__	up to 0.5	__	__	up to 10.8	Walton & Wright, 2008
Chilliwack River, BC	2000-2004	16	3.5 ± 0.4 (May) 7.0 ± 0.8 (March)	2.1 ± 0.3	__	9.8 ± 1.4 (7.2-11.6)	8.0 ± 0.8	Morrissey *et al.* (2004a)
Boulder Creek, Colorado	1971-1973	__	(0.5-1.4)[1]	(0-1.4)[2]	(0-2.2)[3]	(1.9-2.2)[4]	(1.0-1.8)[5] (2.0-2.8)[6]	Price and Bock (1983)
South Boulder Creek, Colorado	1971-1973	__	(1.2-1.4)[1]	(0-2.2)[2]	(0-4.7)[3]	(3.7-4.7)[4]	(1.5-3.8)[5] (2.2-5.8)[6]	Price and Bock (1983)

[1]Density of breeding adults in April and May extracted from Price and Bock (1983) Figs.12,13, [2]Density in June and July extracted from Price and Bock (1983), Figs.12,13, [3]Density in September and October extracted from Price and Bock (1983), Figs.12,13, [4]Density in November extracted from Price and Bock (1983), Figs.12,13, [5]Density in December-February extracted from Price and Bock (1983), Figs.12,13, [6]Density in ice-free winter habitats (December-February) extracted from Price and Bock (1983), Figs.12,13

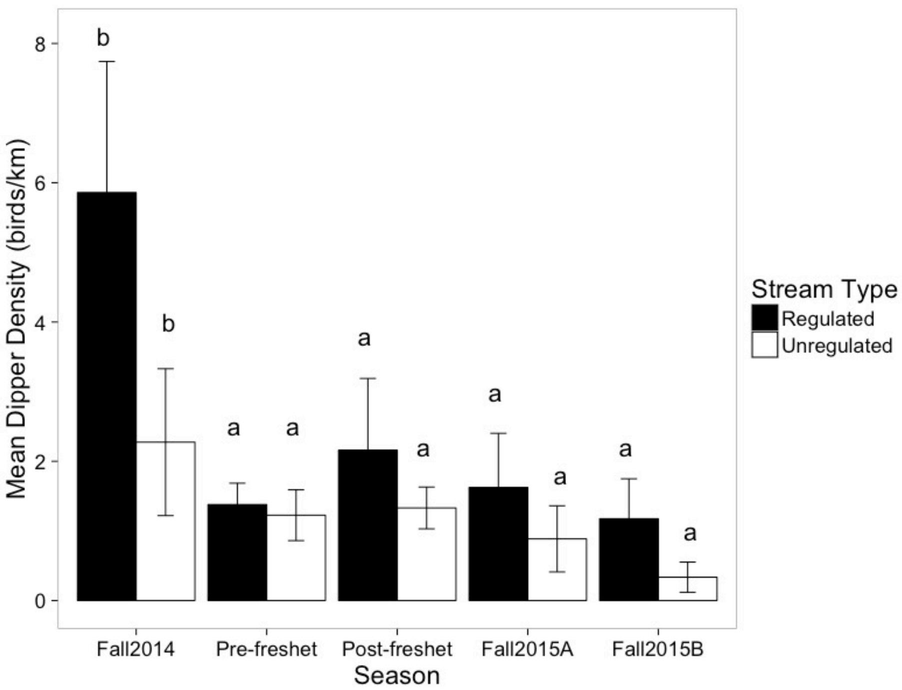

Figure 2.2 Comparison of seasonal American Dipper density (Mean ± S.E.) between regulated and unregulated streams in southwestern British Columbia during 5 survey periods. Across seasons, dipper density was significantly higher at regulated streams ($\beta=0.78$, SE=0.36, $p=0.030$). Groups sharing the same letter are not significantly different ($p>0.05$), as indicated by a *post-hoc* Tukey HSD test. Fall 2014 densities were significantly higher than all other seasons ($p\leq0.005$), but there was no significant interaction between stream type and season and no model support for elevational effects or presence of salmon.

Table 2.3 Model selection results testing for differences in seasonal dipper densities between regulated and unregulated streams. A zero-inflated poisson GLMM was run using the package *glmmADMB* in R. Season, stream type, elevation, salmon, and interactions between type*elevation and season*type were included as fixed effects. Stream and watershed were included as a random effects. Models with AICc weight>0 and the null model (intercept-only) are presented for comparison.

Response	**Model Structure**	**AICc**[1]	**Δ AICc**	**Deviance**[2]	**Model Weight**	**df**
Count (# dippers/ stream km)	**Type+Season**	**221.0**	**0.00**	**199.86**	**0.72**	**9**
	Type+Season+Salmon	223.4	2.39	199.48	0.22	10
	Type+Season+Salmon+ Elevation	226.2	5.19	199.41	0.053	11
	Type*Elevation+Season +Salmon	228.9	7.90	199.14	0.014	12
	null	246.7	25.71	238.08	0	4

[1] Akaike's Information Criterion, corrected for small sample sizes

[2] -2 (Log Likelihood)

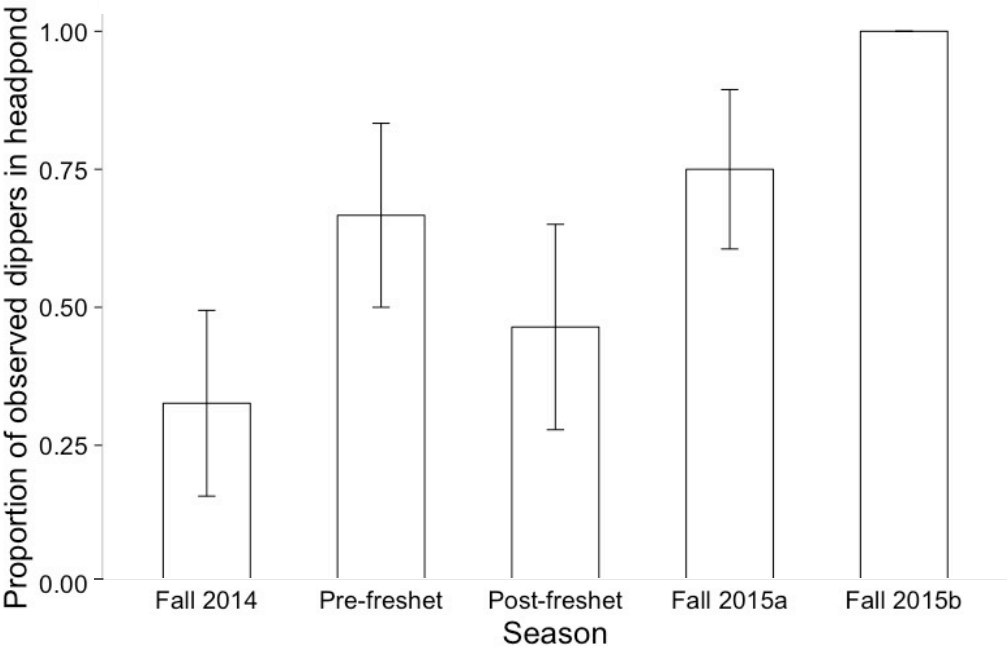

Figure 2.3 Proportion of observed dippers (Mean ± S.E.) sighted in the headpond at regulated streams. During double observer surveys, the initial location of each individual bird was recorded on a map of each stream.

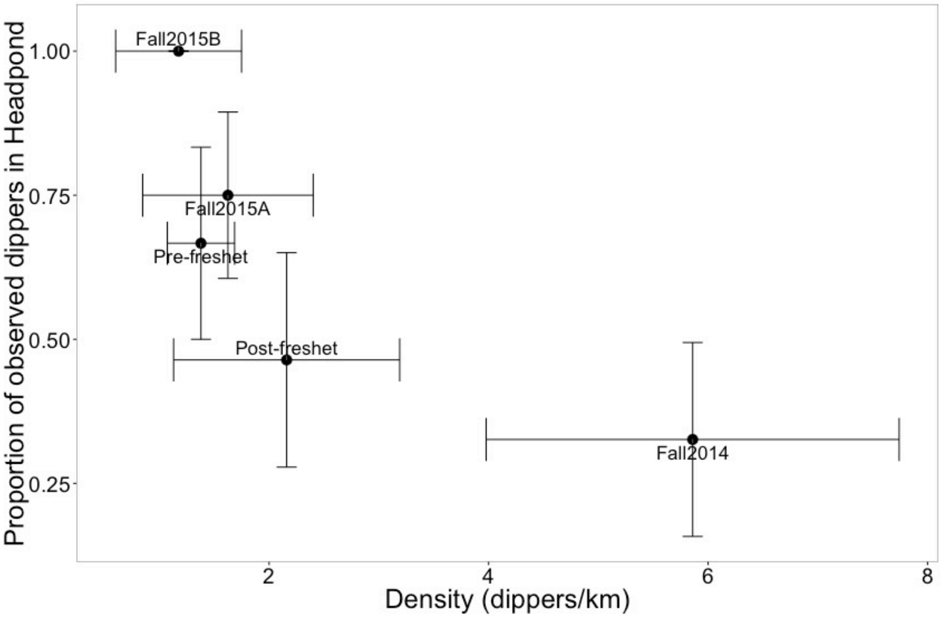

Figure 2.4 Relationship between the proportion of observed American Dippers (mean ± S.E.) sighted in the headponds of regulated streams and seasonal density (mean ± S.E., birds/km). At low dipper densities, a higher proportion (up to 100%) of birds were observed in the headpond.

2.3.1.2 Robust design occupancy models

The best-approximating occupancy model under the robust design was the null model (Table 2.4). Under this model, occupancy was estimated as constant at 100 % (Ψ =1, SE=0) over time (seasons) and type (regulated/unregulated), with zero probability of streams becoming unoccupied (ε=0, SE=0). Detection probabilities (ρ) were estimated at regulated and unregulated streams for each season, averaging 0.91 ± 0.06 for fall 2014, 0.82 ± 0.07 for spring 2015, and 0.57 ± 0.08 for fall 2015. There was some model support for effects of season (t) on occupancy rates, but parameter estimates for the model supporting stream type (g) differences in occupancy were identical to the null model. The model including seasonal differences in occupancy rate (t) estimated 100 % occupancy during fall 2014 and spring 2015, but reduced occupancy during fall 2015 (Ψ =0.45, SE=0), which is consistent with our observation of lower densities during this time. Under this model, estimates of detection probabilities and the probability of a site becoming unoccupied (ε) were the same as the null model.

Table 2.4 Robust design occupancy model selection results comparing dipper occupancy between regulated and unregulated streams. Models with AICc weights >0 and the null model are presented for comparison.

Model	AICc[1]	Delta AICc	AICc Weights	Model Likelihood	k[2]	Deviance[3]
{Ψ (.)ε (.) ρ 1(.) ρ 2(.) ρ 3(.)}[4]	**108.86**	**0**	**0.63**	**1**	**5**	**54.97**
{Ψ (t) ε (.) ρ 1(.) ρ 2(.) ρ 3(.)}	111.67	2.81	0.15	0.25	6	54.97
{Ψ (g) ε (.) ρ 1(.) ρ 2(.) ρ 3(.)}	111.67	2.81	0.15	0.25	6	54.97
{Ψ (.),ε (.), p(.)}	114.32	5.46	0.041	0.065	3	65.56

[1] Akaike's Information Criterion, corrected for small sample size

[2] Number of parameters

[3] -2 (Log Likelihood)

[4] This model allows estimating of the following parameters: Ψ (proportion of sites occupied at each time period); ε (probability of an occupied site becoming unoccupied), and ρ (detection probability on a visit to the site). Effects of stream type (g), time period (t), and the interaction between stream type and time (g*t) are indicated for each parameter, while (.) indicates no effect of stream type or time.

2.3.1.3 Multi-state occupancy models

The multistate occupancy model suggested no difference in the occupancy rate of *unbanded* dippers ($\Psi 1=1$, SE=0) between stream types. The multi-state occupancy model that included group differences in the occupancy rate of *banded* birds between regulated ($\Psi 2=1$, SE=0) and unregulated ($\Psi 2=0.50$, SE= 0.22) streams was competitive with the null model (Table 2.5), which differed in AIC_c by only 1.67 points. Although the null model had a lower AIC_c value, a maximum likelihood test for the effect of group differences in occupancy rate of banded birds ($\Psi 2$) indicated a significant effect of stream type ($\chi^2=4.827$, df=1, p=0.028), with overall higher occupancy of banded birds on regulated streams. This result suggests that there is an effect of stream type on the occupancy rate of banded dippers, with regulated streams supporting higher occupancy of banded birds. The probability that banded birds were detected was constant for regulated and unregulated streams ($\delta=0.50$, SE=0.086) and did not vary across seasons. Although detection probabilities were constant across stream type and all re-sight surveys, the estimated detection probability for banded birds was higher than unbanded birds ($\rho 1=0.44 \pm 0.12$ for unbanded dippers, $\rho 2=0.70 \pm 0.066$ for banded dippers).

Omitting Roger Creek (the unregulated stream where I was unable to capture and band dippers, despite numerous attempts) from the multi-state occupancy analysis produced similar results, with model support for a higher occupancy rate of banded dippers at regulated streams (Appendix 3), and similar parameter estimates (Appendix 5). Even with the most conservative approach (assuming the dipper sighted at Roger Creek was banded), there was model support for higher occupancy rates of banded dippers at regulated streams (Appendix 4), although the difference was not statistically significant (Appendix 5).

Table 2.5 Multi-state occupancy model selection results comparing occupancy of banded and unbanded dippers between regulated and unregulated streams.

Model	AIC_c[1]	ΔAIC_c	AIC_c Weights	Model Likelihood	k[2]	Deviance[3]
Ψ1(.)Ψ2(.)ρ1(.)ρ2(.)δ(.)[4]	162.92	0	0.70	1	5	93.71
Ψ1(.)Ψ2(g) ρ1(.)ρ2(.)δ(.)	164.59	1.67	0.30	0.43	6	88.88

[1] Akaike's Information Criterion, corrected for small sample sizes
[2] Number of parameters
[3] -2 (Log Likelihood)
[4] This model allows estimation of the following parameters: Ψ1, probability that a site is occupied regardless of band state; Ψ2: probability that a site is occupied by a banded bird; φ1, probability that occupancy was detected given true state=1(unbanded); φ2, probability that occupancy was detected given true state=2 (banded); and, δ, probability that banded birds were observed, given detection of occupancy. Effects of stream type (g) are indicated for each parameter, while (.) indicates no effect of stream type.

The multistate model including group (stream type) differences in Ψ2 (occupancy rate of banded birds) is further supported by seasonal differences in the proportion of banded and unbanded dippers observed at regulated and unregulated streams (Appendix 6). No banded dippers were observed during the spring surveys at unregulated streams and the proportion of banded birds sighted at regulated streams was higher during all seasons, except early fall 2015 (Fig. 2.5).

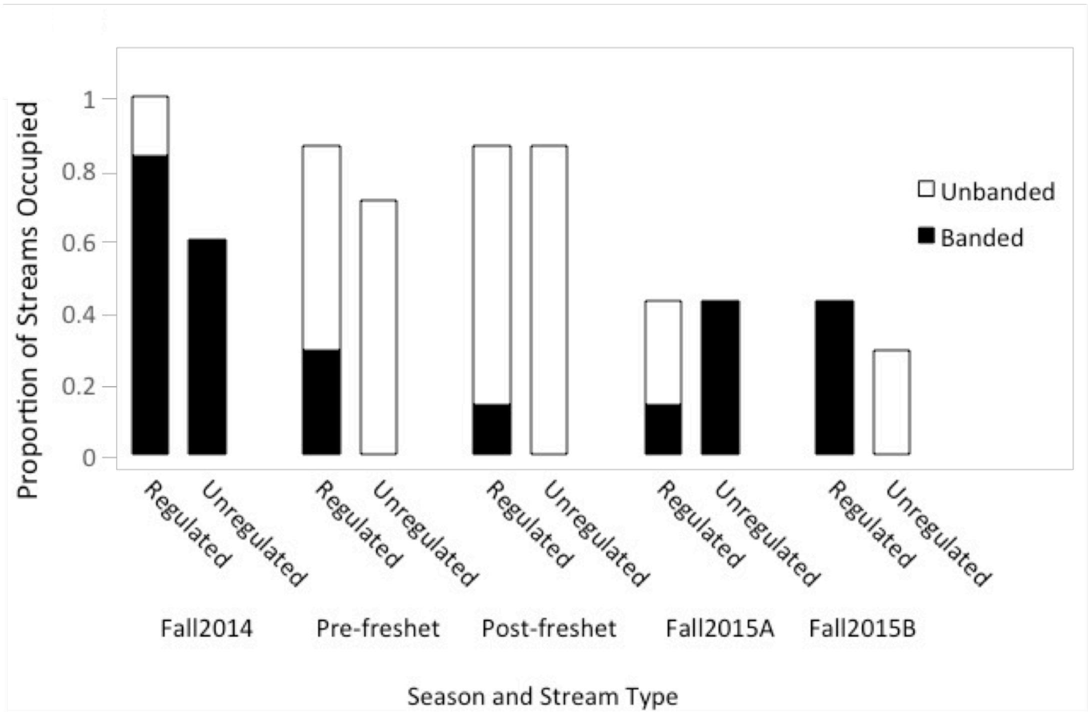

Figure 2.5. Proportion of regulated and unregulated streams occupied by adult banded (black bars) and unbanded (white bars) dippers during seasonal surveys (2014-2015) in southwestern British Columbia.

2.3.2 Philopatry and year-round residency

The proportion of adult dippers banded during the fall of 2014 and re-sighted during the spring 2015 surveys was 3/30 (10 %) for regulated streams and 0/18 (0 %) for unregulated streams. The number of dippers re-sighted during the fall of 2015 that were banded in 2014 was 3/30 (10 %) for regulated streams and 3/18 (16.7 %) for unregulated streams (Table 2.6). One dipper banded at an unregulated stream during fall 2014 was re-sighted at a regulated stream during fall 2015. All other re-sightings were at the same stream as initial capture. Due to low sample size and limited survey repetition, I was unable to estimate apparent survival of dippers banded in fall 2014 and re-sighted in fall 2015.

Table 2.6 Proportion of confirmed resident dippers (sighted during breeding and non-breeding seasons on the same stream) and second year re-sights (banded fall 2014 and re-sighted fall 2015 on same stream) at regulated and unregulated streams (n=48 dippers banded during fall 2014).

Stream Type	**% of confirmed resident dippers**	**% of birds re-sighted at the same stream of capture**
Regulated	10 % (3/30)	10 % (3/30)
Unregulated	0 % (0/18)	16.7 % (3/18)

2.3.3 Age, sex, and body condition

2.3.3.1 Age and sex differences between regulated and unregulated streams

The best approximating model for the proportion of adult AHY dippers captured at each stream included stream type as the only explanatory variable and stream as a random effect (Table 2.7). There was no model support for the effect of elevation, the interaction between elevation and type, nor the presence of anadromous salmon. Regulated streams tended to have a higher proportion of AHY dippers compared to unregulated streams (β=1.15, Adj. SE=0.65, p=0.077). The mean proportion of AHY dippers banded at regulated streams was 0.60 ± 0.073 compared to 0.22 ± 0.074 at unregulated streams (Fig. 2.6, Appendix 7). The proportion of AHY captured at unregulated streams ranged from 0-0.43, while the proportion of AHY dippers captured at regulated streams ranged from 0.43-1.0 (Fig 2.6). The fact that the null model is within 2 AIC_c units of the top model is likely related to a small sample size, since only dippers captured in 2015 were confidently aged and therefore included in the models.

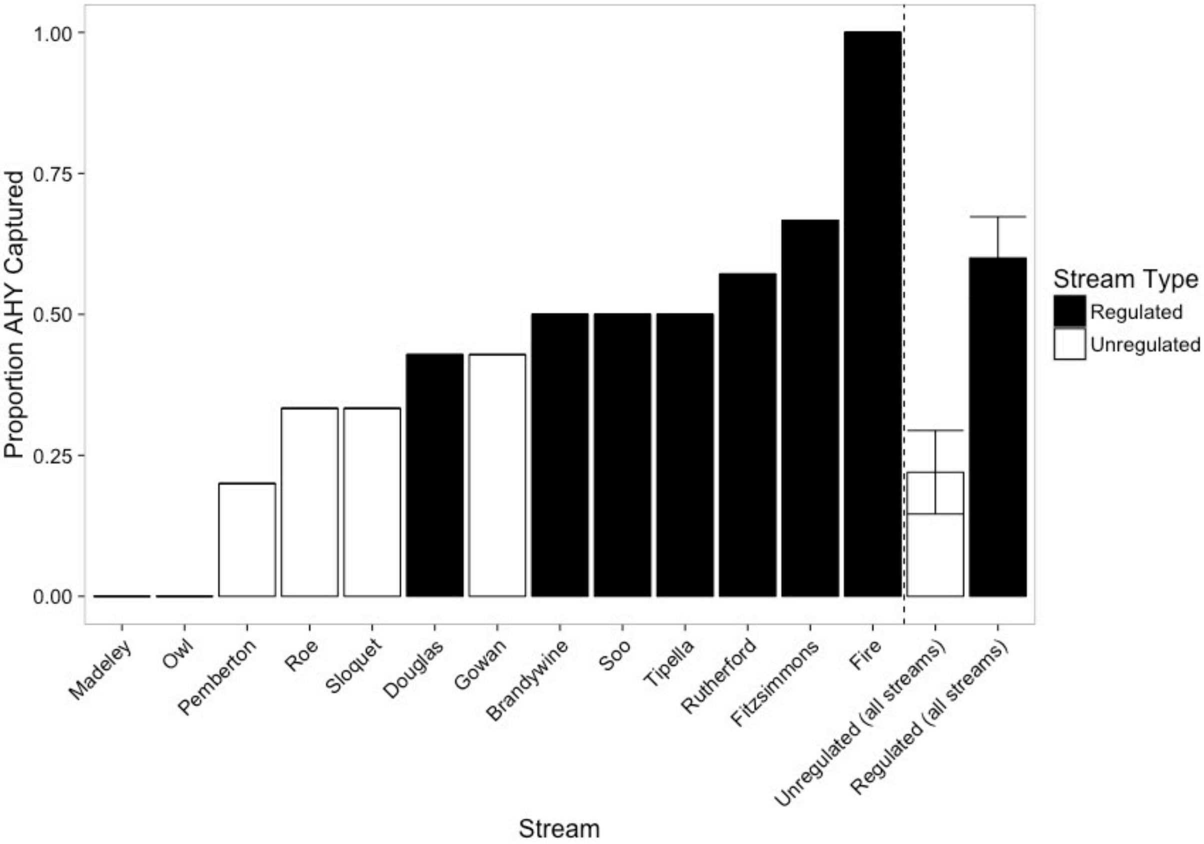

Figure 2.6 Proportion of AHY dippers captured at regulated and unregulated streams in southwestern British Columbia during fall 2015 (n=54 dippers captured in 2015 with 29 from regulated and 25 from unregulated streams). Regulated streams tended to support a higher proportion of AHY dippers than unregulated streams (β=1.15, Adj. S.E.=0.65, p=0.077).

Table 2.7 Model selection results testing the effect of stream type, salmon, and elevation on the proportion of AHY dippers captured at regulated and unregulated streams during fall 2015 (n=54). Models were run using glm in R, with a binomial family and logit link function. Proportions were weighted by the total number of AHY dippers banded at each stream.

Response	Model Structure	df	AICc[1]	Δ AICc	Model Weight	Deviance[2]
Proportion of AHY dippers captured	**Stream Type**	**2**	**31.6**	**0**	**0.57**	**26.41**
	null	1	32.9	1.29	0.30	30.54
	Stream Type+Elevation	3	34.9	3.25	0.11	26.37
	Stream Type*Elevation	4	38.5	6.91	0.018	25.52
	Stream Type*Elevation+ Salmon	5	43.0	11.44	0.0020	24.48

[1] Akaike's Information Criterion, corrected for small sample sizes

[2] -2 (Log Likelihood)

The best-approximating model testing for differences in the proportion of adult female dippers banded at regulated and unregulated streams was the null model (Table 2.8, Appendix 8), indicating no effect of stream type, elevation, or anadromous salmon on dipper sex ratios.

Table 2.8 Model selection results testing the effect of stream type, salmon, and elevation on the proportion of adult (AHY) female dippers captured at regulated and unregulated streams during fall 2015. Weights were applied to the proportions to account for variation in the total number of dippers captured at each stream (n=23 AHY dippers captured in 2015). Models were run with glm using a "binomial" family, logit link function, and weights equal to total number of AHY dippers banded at each stream. Models with weight>0 and null are included for comparison.

Response	**Model Structure**	**df**	**AICc**[1]	**Δ AICc**	**Model Weight**	**Deviance**[2]
Proportion of adult female dippers captured	**null**	**1**	**21.3**	**0**	**0.96**	**18.89**
	Stream Type*Elevation	4	27.7	6.33	0.040	13.00
	Stream Type+Elevation	5	35.0	13.66	0.001	13.00

[1] Akaike's Information Criterion, corrected for small sample size

[2] -2 (Log Likelihood)

2.3.3.2 Body condition and morphometrics

Model selection results supported inclusion of effects of stream type on body condition, but there was no model support for effects of salmon, elevation, or the interaction between type and elevation (Table 2.9). Although there was a trend of higher body condition at regulated streams, model-averaged estimates across the top two models (**Δ**AICc<2) indicated no significant difference between regulated and unregulated streams (β=0.65, adj. S.E.=1.33, p=0.62). Body condition, represented by a scaled mass index (SMI) was fairly consistent across all streams, with the exception of relatively low SMI of dippers captured at Owl Creek, an unregulated stream (Fig. 2.7).

Table 2.9 Model selection results comparing American Dipper body condition (mass scaled by mean wing length) between stream types. Stream type, elevation, salmon, and the stream type*elevation interaction were included as fixed effects. Stream was included as a random effect. Models were run as linear mixed effects models with package *lme4* in R. Models with weight>0 and null are included for comparison.

Response	**Model Structure**	**df**	**AICc**[1]	**Δ AICc**	**Model Weight**	**Deviance**[2]
Body Condition Index	**Stream Type**	**4**	**581.5**	**0**	**0.55**	**573.04**
	null	**3**	**581.9**	**0.44**	**0.44**	**575.64**
	Type+Elevation+Salmon	6	591.7	10.24	0.003	578.81
	Type+Elevation	5	593.7	12.28	0.001	583.10

[1] Akaike's Information Criterion, corrected for small sample sizes

[2] -2 (Log Likelihood)

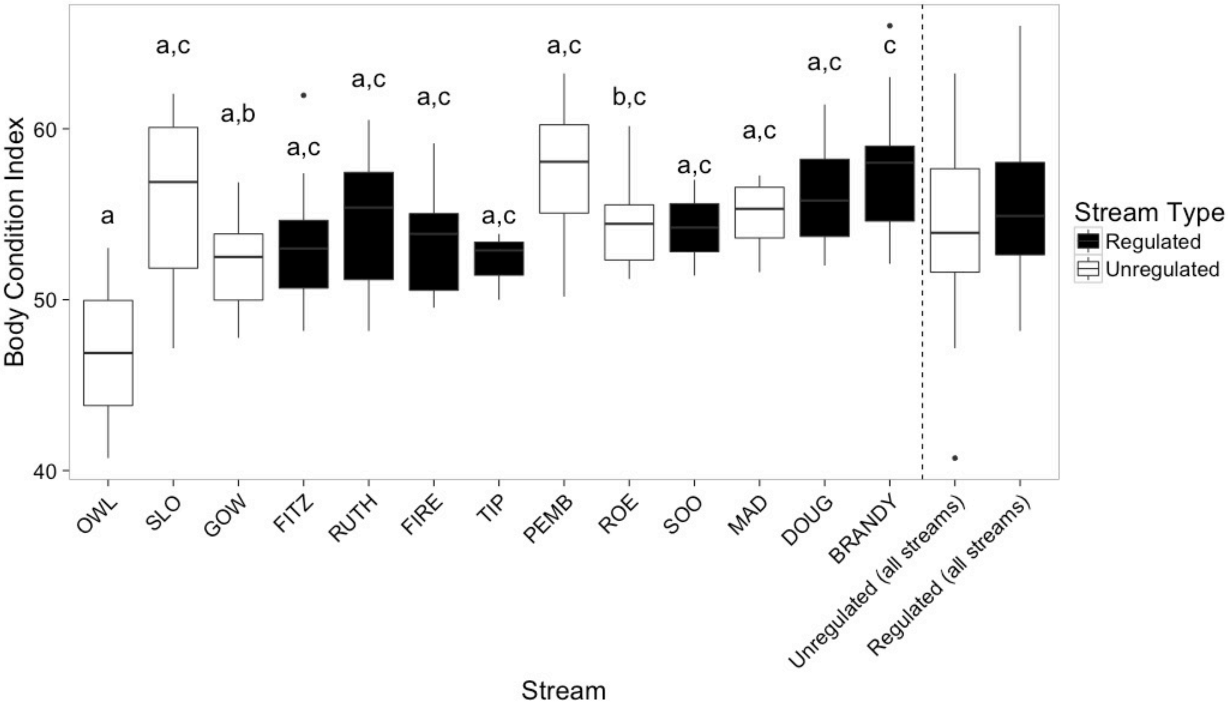

Figure 2.7 Dipper body condition (represented by a scaled mass index) among all individual regulated and unregulated streams (n=99 dippers) sampled in southwestern British Columbia, 2014-2015.

2.3.4. Habitat changes related to flow diversion by RoR dams

At each stream, I typically observed a shift from rapid and cascade-dominated channels to channels dominated by riffle and runs in response to flow abstraction (Fig. 2.8). Reduced flow was also associated with an increase in channel-cover by small boulders, reductions in channel-cover by large woody debris and size of the dominant streambed material, and increased sedimentation and siltation below the dam. Within the diversion reach at most regulated streams, I noticed an increase in the amount of periphyton (mixture of algae, bacteria, fungi, microinvertebrates, and detritus) and a reduction in the extent of moss covering the large boulders, likely in response to reduced flow and increased sunlight on the channel resulting from deforestation along the access roads.

(a)

(b)

Figure 2.8 Examples of in-stream habitat changes downstream of run-of-river dams in coastal British Columbia. (a) Stream channel upstream (left) and downstream (right) of the Brandywine Creek run-of-river dam in the Squamish watershed. (b) Stream channel upstream (left) and downstream (right) of the Fire Creek run-of-river dam in the Lillooet watershed. Photos were taken simultaneously at each stream during the fall of 2015. Photos by: V. Norbury.

The major habitat change observed at regulated streams was the creation of a novel, pond-like habitat directly upstream of the dam. Within this study, headpond habitat varied from slightly increased depth and reduced water velocity (Brandywine Creek), to a large 2km perimeter flooded area above the Soo River dam (Fig. 2.9).

Figure 2.9 Examples of the variation in headpond formation above run-of-river dams in coastal British Columbia, including Douglas Creek (top left), Brandywine Creek (top right), and Soo River (bottom). Photos by: V. Norbury.

2.3.5. Occupancy of regulated and unregulated streams by other river bird species

Common Merganser (*Mergus merganser,* COME) and Belted Kingfisher (*Megaceryle alcyon*, BEKI) were often observed at regulated and unregulated streams during the autumn (Fig. 2.10), but BEKI were observed at a higher proportion of regulated streams (Fig. 2.11). Regulated streams also supported a higher diversity of waterfowl during the spring breeding season, including Harlequin Duck (*Histrionicus histrionicus*; HARL), Barrow's Goldeneye (*Bucephala islandica,* BAGO), Mallard (*Anas platyrhynchos*, MALL), Bufflehead (*Bucephala albeola, BUFF),* and Canada Goose (*Branta Canadensis,* CANG*)*. These waterfowl were almost exclusively observed foraging within the headponds. Harlequin ducks were the most common duck, observed foraging within the headponds of Fitzsimmons Creek during the early fall (likely before migration to the ocean) and the headponds of Brandywine, Fitzsimmons, and Rutherford Creeks during the breeding season. Harlequin Ducks were likely breeding in or near the headponds at these higher elevation regulated streams, as part of their life cycle is to nest adjacent to fast-moving mountain streams. Juvenile Harlequins were observed foraging within the diversion reach of Rutherford Creek in June 2015. I did not observe Harlequin Ducks at any of the unregulated streams. Townsend's Solitaire (*Myadestes townsendi*), an insectivorous passerine that breeds at high elevation and feeds primarily by flycatching, was also observed foraging directly below the weir of some regulated streams.

The Soo River headpond (2km perimeter) supported the highest diversity of waterfowl during the breeding season, including Barrow's Goldeneye, Mallards, Buffleheads, and Canada Geese. In addition to waterfowl, over 20 passerine species were observed in and around this headpond and Pileated Woodpeckers (*Dryocopus pileatus)* and Northern Flickers (*Colaptes auratus*) were observed nesting in the large snags created by flooding. Headponds appear to create pond-like habitat for waterfowl that would not otherwise occur on these high elevation mountain streams in spring.

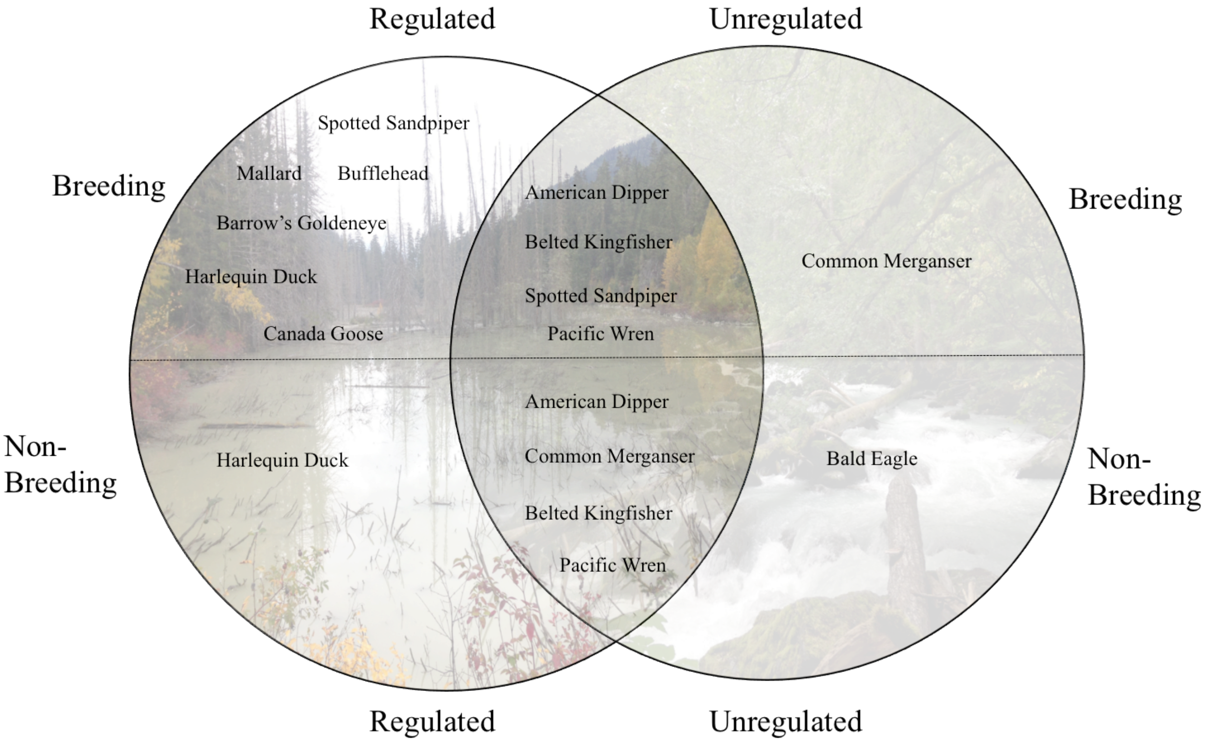

Figure 2.10 River birds, waterfowl, and riparian passerines observed at regulated and unregulated mountain streams in coastal British Columbia during breeding and non-breeding seasons, 2014-2015.

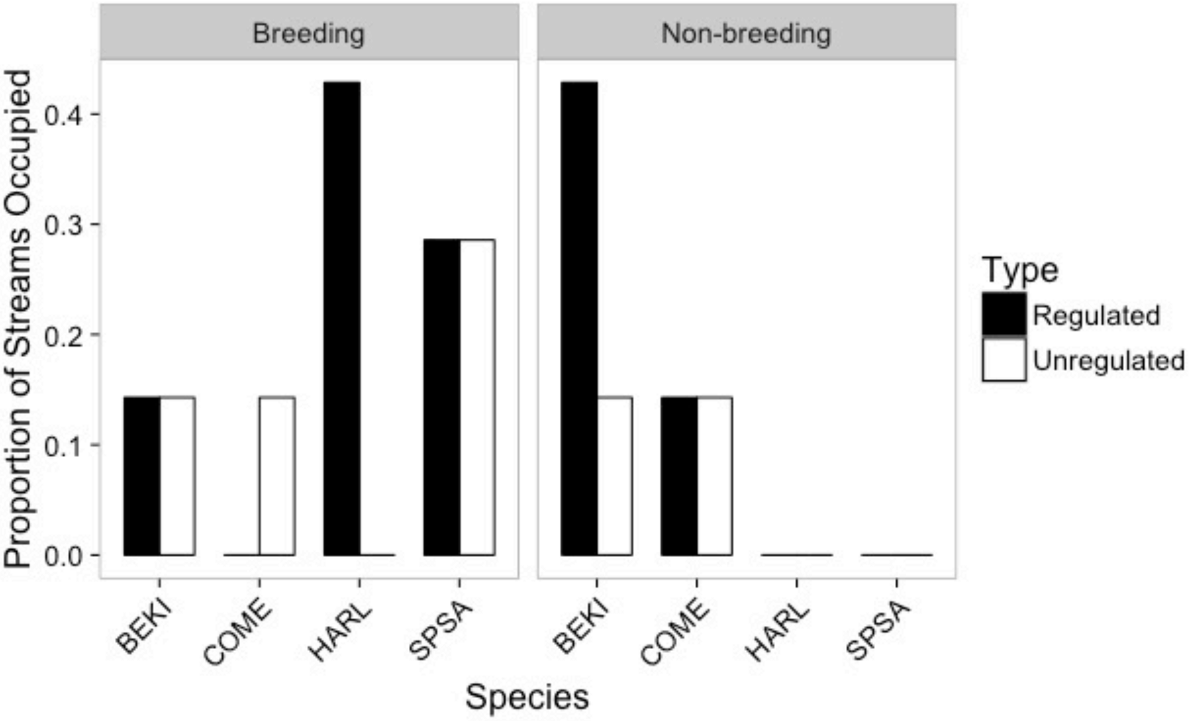

Figure 2.11 Proportion of regulated and unregulated mountain streams occupied by the most commonly sighted water birds during the breeding and non-breeding seasons, 2014-2015, British Columbia. Only birds observed during point count surveys are included in these proportions.

2.4 DISCUSSION

2.4.1 Habitat use of mountain streams by American Dippers in response to reduced and stabilized flow created by run-of-river dams

Although both the regulated and unregulated streams in this study supported breeding and overwintering American Dippers, the regulated streams appeared to be selected for across seasons. At the regulated streams, the novel headpond habitats and diversion reach were frequently used for foraging. The combined evidence of high dipper densities in the low-flow habitats, greater occupancy rate of banded dippers at regulated streams, a higher rate of confirmed year-round residents, and a greater proportion of AHY adults captured at regulated streams, suggests that high elevation, regulated streams provide stable year-round habitat for American Dippers. This is interesting, given that previous annual life cycles described for dippers in the Pacific Northwest include either year-round residency on larger, lower elevation rivers, or altitudinal migration to high-elevation breeding territories and a return to lower-elevation, salmon-bearing streams during autumn (Price and Bock, 1983; Morrissey *et al.*, 2004).

Average fall densities recorded at the regulated and unregulated streams in this study are comparable to those documented in other dipper populations of the Pacific Northwest, where densities averaged 9.8 ± 1.4 dippers/km on the Chilliwack River, British Columbia in November (Morrissey *et al.*, 2004a) and up to 10.8 dippers/km on the Seton River, British Columbia (Walton & Wright, 2008). Peak fall densities of 14 dippers/km recorded at the Brandywine Creek RoR dam, however, surpasses the highest reliable estimate of dipper density of 7.2-11.6 dippers/km recorded in early November on the Chilliwack River in British Columbia (Morrissey *et al.*, 2004a)—a significantly larger river than Brandywine Creek that supports high densities of anadromous salmon. This is consistent with observations of non-territoriality in wintering American Dippers (Price and Bock, 1983; Willson and Hocker, 2008). October densities in Boulder, Colorado ranged from 1.9-4.7 birds/km (Price and Bock, 1983), with dippers occupying stream reaches kept ice-free by hydroelectric plants (Price and Bock, 1983). The relatively high number of dippers observed at some regulated streams is further supported by observations of American Dippers overwintering at high densities (up to 10.8 birds/km) at regulated streams in the Seton river area of the Lillooet watershed, with maximum densities observed on a reach regulated by a run-of-river dam (Walton and Wright, 2008).

Not surprisingly, 2015 autumn densities in this study were significantly lower at both stream types than those reported in 2014. This is likely in response to a severe drought year in summer 2015, which resulted in historically low water levels documented in other watersheds across southern B.C. (Coulthard *et al.*, 2016). Drought conditions are expected to impair dipper productivity and survival through changes in water quality and macroinvertebrate community composition (Finn *et al.*, 2009; Whitehead *et al.,* 2009). Higher autumn densities would be expected in normal precipitation years.

Breeding densities at both stream types in this study were higher than those documented in the Seton River area of Lillooet, British Columbia (up to 0.5 dippers/km; Walton and Wright, 2008) and high elevation streams in Boulder, Colorado, United States (1.2-1.4 dippers/km during spring and 0-2.2 dippers/km during summer; Price and Bock, 1983), but lower than the Chilliwack River, British Columbia (2.4-3 birds/km; Morrissey *et al.*, 2004c). The regulated streams in this study supported more breeding dippers than unregulated streams after the spring-freshet, which were comparable to those observed in summer on the Chilliwack River in the summer. Brandywine Creek was a hotspot for year-round dipper activity, and also supported an unusually high summer density of 7 adult dippers/km following the spring freshet (mid-June).

My observation of higher seasonal densities at regulated streams is complimented by a higher occupancy rate of banded birds and a higher proportion of AHY dippers captured at regulated streams. The higher proportion of AHY dippers and resident sightings at regulated streams suggests higher site fidelity at these streams, although these analyses and observations were limited by low sample size. Overall, it appears that regulated streams support more year-round residents and serve as more suitable year-round habitat compared to unregulated streams that are primarily occupied by hatch-years and transient adults. At unregulated streams, the proportion of banded dippers re-sighted in the early fall was comparable to the number of re-sightings at regulated streams, but the absence of re-sights of banded dippers during the breeding season and late fall of 2015 suggests that these unregulated mountain stream habitats are being used more transiently. Higher site fidelity at regulated streams is likely driven by a stable, reliable food source during breeding and overwintering that requires less foraging effort. This is consistent with the observation that White-throated dipper populations are known to be more sedentary under stable habitat conditions (Galbraith & Tyler, 1982).

2.4.2 Factors influencing dipper natural history strategies, productivity, and survival

Two features of dipper natural history, potentially impacted by hydropower, are known to influence their productivity: altitudinal migration (Morrissey *et al.*, 2004b, Gillis *et al.*, 2008) and the availability of salmonids to their diet (Tonra *et al.*, 2016). Altitudinal migration between winter sites on low elevation rivers and breeding sites on high elevation streams is common in dippers of the Pacific Northwest (Morrissey *et al.*, 2004a, Price and Bock, 1983). This behaviour is most likely driven by seasonal changes in the stream hydrograph, riparian and in-stream habitat features, and salmon availability (Morrissey *et al.*, 2004a) or ice formation at very high elevation streams (Price and Bock, 1983). Breeding at high elevations is advantageous to dippers because of the greater availability of suitable nest sites such as cliff ledges, overhangs and boulders found more commonly on smaller, steep high elevation streams and tributaries. The return to larger, lower elevation salmon-bearing streams in autumn is thought to be driven by the presence of open water (ice-free) habitat and a high-energy salmon subsidy (Morrissey *et al.*, 2004b).

There is evidence to suggest a fitness trade-off between migration and year-round residency strategies, where river residents have been reported to have higher annual and lifetime reproductive success whereas migrants have slightly higher annual survival (Gillis *et al.*, 2008). Several studies have determined that earlier laying date is associated with higher productivity in dippers, through benefits of increased clutch size and fledgling survival (Price and Bock, 1983; Morrissey *et al.*, 2004b, Hong *et al.*, 2016). Delayed nesting in migratory American dippers leads to higher nest failure resulting from flooding (during the spring freshet) and increased nest failure through predation (Morrissey *et al.*, 2004*b*). Although migratory strategy does not directly influence overall productivity, resident dippers are able to obtain mates and initiate nesting earlier, avoid nest failure by flooding and predation, and have more opportunity to initiate second clutches (Morrissey *et al.*, 2004b). Resident dippers also spend more time resting and less time foraging than migrants, without any differences in energetic intake, foraging success, or physiological state (Whitehorne, 2010). Since migrants do not have a fitness benefit from moving to higher elevation breeding grounds, competition for limited resources at lower elevations is believed to likely be a driving force of altitudinal migration (Gillis *et al.*, 2008). This argument is also supported by Price and Bock (1983), who observed that nest site availability is often a limiting factor for the success of breeding dippers.

A recent study demonstrated that dippers foraging below dams (with access to salmon and marine derived nutrients) had higher annual survival compared to upstream dippers. In addition, downstream females were in higher body condition and were more likely to attempt multiple broods and produce larger female offspring than upstream dippers (Tonra *et al.*, 2016). American dippers breeding on reaches with salmon near Juneau, Alaska produced heavier fledglings and had less brood reduction than did dippers breeding on reaches without salmon (Orbermeyer *et al.*, 2006). Although anadromous salmon are absent from most RoR-regulated streams in BC, nutrient retention within headponds may increase invertebrate productivity within this habitat, compared to upstream and downstream channel reaches that are otherwise fairly oligotrophic. The combined benefits of stable year-round habitat, improved foraging, and reduced competition with conspecifics at high elevation streams may outweigh the benefits of altitudinal migration and the lost salmon subsidy. Therefore, RoR reaches modified by flow abstraction potentially offer an opportunity for dippers to exploit a consistent food resource closer to their high elevation breeding territory, enabling them to take on a “resident strategy” that is more typical of low elevation river habitats. Of course, a more robust and longer-term dataset is necessary to address this proposition.

2.4.3 RoR headponds: valuable habitat or ecological traps?

Overall, my data suggest that RoR headponds provide valuable year-round habitat for American Dippers and, in some cases, seasonal breeding habitat for riparian species and waterfowl, complimenting observations of avian use of larger hydroelectric reservoirs. Breeding water birds have been documented nesting and foraging in and around hydroelectric reservoirs, but their response depends on time since inundation and water regulation techniques, and any positive impacts are often short-lived. Temporary habitats for woodpeckers are created when forests are inundated and trees are left standing (Yeager, 1949), as observed in the Soo River and Rutherford Creek headponds. Ducks and wading birds are known to breed at higher density in and around recently inundated reservoirs in response to elevated nutrients (Lid, 1981; Moksnes, 1981, translated in Nilsson, 1994) and the resulting emergence of chironomids, which are more typical of lentic habitats (Reitan and Sandvik, 1996). Regulated streams may create better breeding habitat for dippers especially, as fledging typically coincides with high-flows of the spring freshet (Morrissey *et al.*, 2004a), and reduced flows on these regulated streams may improve foraging efficiency of adults during this critical time and allow them to better provision their young. Infrastructure associated with RoR dams may also create nesting habitat inaccessible to predators, with the same benefits to productivity often observed in dippers nesting in bridges over creeks (Loegering and Anthony, 2006). Alternatively, RoR dams may be ecological traps for river bird specialists through potential negative effects on foraging behaviour, nest success, and exposure to elevated methylmercury in headponds.

An ecological trap may arise when habitat alteration by anthropogenic activity causes a simultaneous increase in habitat attractiveness and reduction in suitability, leading to reduced fitness for individuals settling in the preferred habitat (Robsertson and Hutto, 2006). In the case of ground-nesting waterbirds in hydroelectric reservoirs, what appears as suitable breeding and foraging habitat is at high-risk to unpredictable flooding, with negative impacts on productivity

(Markham, 1982; Espie *et al.*, 1998; Anteau *et al.*, 2012; van Oort and Cooper, 2015). By comparison, Quinlan *et al.* (2012) concluded that hydroelectric reservoirs do not function as ecological traps for the shrub-nesting songbird, Yellow Warbler (*Setophage petechia*) and van Oort *et al.* (2015) concluded the same for shrub-nesting Willow Flycatchers (*Empidonax traillii*) or Yellow Warblers. The response of resident river birds, including dippers, to hydropower is relatively uninvestigated, even though these river specialists occupy a more permanent niche along potentially impacted rivers than migratory water birds and riparian passerines. Therefore, I have outlined three mechanisms by which RoR dams could be perceived as ecological traps to American dippers and suggest that these questions are best addressed through a long-term study across regulated and free-flowing streams, with emphasis on comparisons of reproduction and survival.

The first mechanism by which RoR regulation may create ecological traps for dippers, conceptualized by D'Amico *et al.* (2011) is through non-adaptive foraging behaviour under a stabilized flow regime. Studies of White-throated dipper diving behaviour under natural flow regimes have demonstrated that annual patterns in foraging and resting behaviour match the annual pattern of the natural flow regime, while changes in diving behaviour are more complex (D'Amico and Hemery, 2007). Based on the relationships observed by D'Amico and Hemery (2007), D'Amico (2011) argues that under a stabilized flow regime, dippers cannot rely on environmental cues (rain events) as signals for changes in water level, and therefore must rely on immediate responses to rising water level and turbidity to adjust their foraging techniques. Therefore, along regulated rivers, the outcome of their foraging behaviour may be non-adaptive, because the link between environmental cues and actual flow is disrupted (D'Amico, 2011).

The second proposed mechanism by which RoR dams could act as ecological traps to dippers is through increased nest failure, resulting from either delayed nesting at high elevation (Morrissey *et al.*, 2004b), or attraction of predators to headponds. Predators of White-throated dippers (*Cinclus cinclus*) are well described, including mink and other mustelids, rats, owls, hawks, and large trout (Tyler and Ormerod, 1994). American dippers likely have similar predators, but the response of these animals to river regulation is largely unknown. Beavers and other mustelids may respond positively to stabilized reservoirs, which in essence serve as beaver dams (Nilsson and Dyenesius, 1994), and could indirectly lead to higher nest predation. The open habitat created by headponds may also lead to increased predation by avian predators on foraging adult and juvenile dippers. The third mechanism is through elevated exposure to neurotoxic contaminants such as MeHg. Elevated MeHg has been documented in reservoirs of beaver dams (Roy *et al.*, 2009a,b; Painter *et al.*, 2015) and conventional impoundments (Rosenberg *et al.*, 1997)— a topic which I explore in depth in the next chapter.

2.4.4 Conclusions

The data presented in this chapter suggest that low flow habitats create a stable year-round environment for dippers that would otherwise migrate to lower elevation in fall, with no apparent compromise to body condition. This is likely because dipper foraging and productivity is more limited by high flows and available nest sites than a salmon subsidy. Additionally, lentic invertebrates are likely colonizing these headponds (at least initially, with the flood of nutrients), supported by observed foraging on limnephiliid caddisflies and their empty cases scattered along the headpond perimeter and infrastructure below the dam. Further, under a stabilized flow regime, the cost of increased nest failure by flooding that is associated with altitudinal migration and delayed nesting might be removed. With more frequent extreme hydrological events predicted with climate change, river birds are increasingly vulnerable to flow changes (Royan *et al.*, 2014). Stabilized flow regime associated with RoR dams may act as a refuge from unpredictable flows in the short term. More thorough investigation of this species' short and long-term productivity and survival are needed, however, to determine whether RoR dams act as ecological traps by different mechanisms than those described for waterfowl in fluctuating reservoirs.

CHAPTER 3:

CHANGES IN AMERICAN DIPPER DIET AND MERCURY EXPOSURE IN RELATION TO FLOW DIVERSION BY RUN-OF-RIVER DAMS

3.1 INTRODUCTION

Run-of-river dams have the potential to alter mountain stream food webs through changes to stream physicochemistry that are related to a reduced and stabilized flow regime and barrier effects (Anderson *et al.*, 2015). Flow abstraction and barrier effects of RoR dams create modified, low-flow habitats upstream and downstream of the intake and facilitate the accumulation of fine sediment upstream and downstream of the dam (Csiki and Rhoads, 2010). Barriers also disrupt longitudinal connectivity (Vannote *et al.*, 1980), thereby fragmenting the river and disrupting in-channel (Poff *et al.*, 1997) and riparian habitats (Nilsson *et al.*, 1997; Jansson *et al.*, 2000). The cumulative stressors of barriers and flow abstraction have consequences for stream-dependent organisms that have evolved under specific flow regimes and associated habitats (Bunn and Arthington, 2002). While the responses of certain taxa to flow abstraction by RoR dams have been studied, the ecosystem-level impacts of reduced and stabilized flow regime remain poorly understood and the extent of MeHg production and cycling remain uninvestigated.

Variable impacts to riparian vegetation (Nilsson *et al.*, 1997; Nilsson and Berggren, 2000; Jansson *et al.*, 2000), algal (Wu *et al.*, 2009), invertebrate (Gonzalez *et al.*, 2013; Fanny *et al.*, 2013), and fish communities (Almodovar and Nicola, 1999; Lessard and Hayes, 2003; Santos *et al.*, 2006) have been observed across the globe in response to reduced flow. Typically, in-channel communities exhibit a negative response to changes in stream temperature and siltation resulting from flow abstraction and stabilization of the hydrograph (Poff and Zimmerman, 2010). The ecotoxicological response of mammalian and avian communities to flow-abstraction is spatiotemporally variable, with some species benefiting from inundated habitat (e.g. Yeager, 1949; Nilsson and Dynesius, 1994; Henny *et al.*, 1996; Quinlan *et al.*, 2012) while others experience a more dynamic relationship (*e.g.* Smith *et al.*, 1990; Picman *et al.*, 1993; Anderson *et al.*, 2000; Van Oort *et al.*, 2015). Ducks and wading birds, for example, often breed at higher density in the vicinity of inundated reservoirs in response to the nutrient influx, changes in vegetation community, and increased prey availability (Lid, 1981; Moksnes, 1981, translated in Nilsson, 1994). Alongside these benefits, however, is the potential for elevated MeHg availability to stream-dependent biota selecting these habitats.

Methylmercury production has been documented in reservoirs of large dams (Rosenberg *et al.*, 1997), beaver dams (Roy *et al.*, 2009), and experimentally flooded reservoirs (Gerrard and St. Louis, 2001), but is unexplored at run-of-river impoundments. MeHg is formed during reservoir flooding through microbial methylation of Hg present in soil and water (Ullrich *et al.*, 2001; Hall *et al.*, 2005; Ward *et al.*, 2011). Initial flooding of forest soils results in an influx of inorganic Hg and organic matter into the water column and subsequent decomposition of this organic matter favours bacterial methylation of the recently mobilized and legacy Hg (Bodaly *et al.*, 2004). Unlike inorganic mercury, MeHg can biomagnify two to five fold across trophic levels (Ward *et al.*, 2011) and bioaccumulate in high trophic level predators, where it acts as a vertebrate neurotoxin and teratogen (Wolfe *et al.*, 1998). Ackerman *et al.* (2016) reviewed avian Hg exposure across western North America and observed that reservoirs and natural ephemeral wetlands are hotspots for MeHg exposure, which is reflected in the tissues of birds selecting these habitats.

A recent review on avian Hg exposure and toxicity across western North America concluded that birds may experience oxidative stress at blood-equivalent Hg concentrations as low as 200 ng/g ww, but impaired health, physiology, behaviour and reproduction tend to occur at concentrations of 1000 ng/g ww, with more severe impairments to health and reproduction above 3000 ng/g ww in blood (Ackerman *et al.*, 2016). For example, White Ibis experienced impaired courtship behaviour at 730 ng/g ww in whole blood (Frederick and Jayasena, 2010) and free-living Tree Swallow baseline circulating corticosterone was negatively correlated with blood Hg below 1000 ng/g ww in whole blood (Franceschini *et al.*, 2009). At 1700 ng/g ww in whole blood, Carolina Wren experienced a 30% reduction in probability of nest success (Jackson *et al.*, 2011). Common Loon maximum productivity declined by 50% at adult blood concentrations of 4300 ng/g ww (Burgess and Meyer, 2008).

There are two major mechanisms by which changes to stream physicochemistry associated with RoR dams may increase MeHg production at the stream level. The first is the formation of small reservoirs, known as headponds, above the dam or weir and the second is increased stream temperatures in the spring and summer under reduced flow conditions. Several stream-level and regional factors influence MeHg biogeochemical cycling, including: water management techniques and the extent of initial and repeated flooding (Ullrich *et al.*, 2001); the extent of wet- and dry-deposition of inorganic Hg (St. Louis *et al.*, 1994; Miller *et al.*, 2005; Hammerschmidt *et al.*, 2006; Driscoll *et al.*, 2007); and features of stream physicochemistry, such as temperature, oxygen, pH, and the amount of dissolved organic carbon (Ullrich *et al.*, 2001; Lavoie *et al.*, 2013).

Hg methylation typically increases under warm, anoxic, acidic (Jardine *et al.*, 2013), and high dissolved organic carbon (Watras *et al.*, 1998) conditions; thus, it often peaks under warm, low flow periods (Ward *et al.*, 2010). In beaver dams, methylation efficiency decreased with dam age and was highest in impoundments less than 10 years old (Roy *et al.*, 2009). MeHg exposure increased in nestling tree swallows along experimentally flooded reservoirs during the first year of flooding and remained elevated for 6 years (Gerrard and St. Louis, 2001), although there were no apparent toxicological effects. The extent of MeHg production will depend on characteristics of the RoR project and stream physicochemistry, such as: the extent of headpond flooding, frequency of changes in headpond depth, age since regulation, and levels of naturally-deposited inorganic Hg. With impacts of run-of-river dams varying with respect to regulation practices, stream physicochemistry, and watershed geochemistry, it is important to conduct local ecotoxicological assessments focused on a single hydropower design (Anderson *et al.*, 2015).

In the present study, I used American Dippers as bioindicators of the ecotoxicological impacts of high-head run-of-river dams on mountain stream food webs in three adjacent watersheds in southwestern British Columbia. The American Dipper, a river bird inhabiting fast-flowing mountain streams, is a suitable bioindicator for studying the simultaneous impacts of a) decreased and stabilized flow and b) MeHg exposure. Dippers are year-round residents on fast-flowing coastal mountain streams suitable for RoR dams, although some populations exhibit seasonal altitudinal migration within a watershed (Price and Bock, 1983; Morrissey *et al.*, 2004b). In addition to their absence of long-distance migration, dippers are high-trophic level predators that feed on benthic macroinvertebrates and salmonid eggs and fry (Price and Bock, 1983; Morrissey *et al.*, 2004b). As apex predators on mountain streams, American Dippers may experience changes in prey availability and a high risk of elevated dietary MeHg exposure, accumulation, and toxicity (Scheuhammer *et al.*, 2007). Dippers have been successfully used as indicators of stream quality and contaminant exposure (Ormerod and Tyler, 1991; Henny *et al.,* 2004; Morrissey *et al.*, 2010a,b) and their foraging behaviour is strongly tied to variation in streamflow (D'Amico and Hemery, 2007). The simultaneous stressors of flow changes and potential contaminant exposure may negatively impact stream food webs, which will likely be reflected by dipper habitat use and productivity.

Stable isotope analysis is a simple and relatively inexpensive method to characterize food webs and trace bioaccumulation of contaminants from the diet. Stable isotopes provide a spatially- and temporally-integrated measure of diet and unlike other measures of diet, are not confounded by omnivory and complex predator-prey interactions (Post, 2002). With predictable enrichment of 2‰ to 5‰ per trophic level (Peterson and Fry, 1987; Kelly, 2000; Hobson and Bairlein, 2003), δ^{15}N is used to determine the relative trophic position of an organism (Post, 2002; Anderson and Cabana, 2007) and trace MeHg biomagnification through food webs (Atwell *et al.*, 1998; Jardine *et al.*, 2012; Morrissey *et al.*, 2012). In contrast, the limited trophic enrichment and high site specificity of ^{13}C and ^{34}S facilitates tracing the energy source of a consumer's diet (Finlay, 2001; Rasmussen, 2010; Jardine *et al.*, 2012). This is especially useful in streams, where consumer diets vary with respect to the amount of allochthonous (terrestrial) and autochthonous (aquatic) inputs into the stream. Sulfur is also used as a marker for bacterial sulfate reduction and processes associated with sulfide recycling (Detmers *et al.*, 2001), making this isotope useful in predicting the extent of MeHg production in reservoirs, as sulfate-reducing bacteria are the principal methylators of Hg (Compeau and Bartha, 1985).

With decreased flows in the headpond and diversion reach created by run-of-river dams, I hypothesize that these habitats may have distinct isotopic signatures, which would be reflected in American Dipper tissues and their aquatic prey. Specifically, I predicted that headponds would have a ^{34}S-depleted signature in response to activity of sulfate-reducing bacteria in the low oxygen environment. Autochthonous carbon sources will have a ^{13}C-depleted signature relative to terrestrial sources in these high-gradient, fast-flowing streams (Finlay, 2001; Rasmussen, 2010). I predicted headponds to have a ^{13}C-enriched isotopic signature due to limited CO_2 uptake at the boundary layer of algal cells at low flows (Hecky and Hesslein, 1995; Finlay *et al.*, 1999). I also predicted that dippers foraging at regulated streams would have higher blood Hg concentrations in response to elevated MeHg production in the headpond environment and with increases in trophic position (measured from δ^{15}N isotopes).

This study was designed to test the effects of regulation by RoR dams on mountain stream food webs and investigate MeHg production associated with run-of-river headponds. Here, I evaluated the utility of stable isotope tracers, particularly sulfur, as a novel biomonitoring technique for monitoring foodweb changes in response to streamflow changes by small-scale impoundments. As the global energy sector attempts to shift from fossil fuel dependence to renewable energy sources, it is important to understand the full ecotoxicological consequences of independent power projects, which are typically regarded as clean or environmentally-benign (Paish, 2002) energy technologies.

3.2 METHODS

3.2.1 River bird and stream sampling

During the autumn (end of August-end of October) of 2014 and 2015, 99 adult dippers and 3 recaptures from 2014 were captured, banded and measured at 13 streams in coastal British Columbia (Permit no. 10268 M; see methods section 2.2.1). The 7 regulated streams were: Brandywine Creek (BRANDY), Fitzimmons Creek (FITZ), Rutherford Creek (RUTH), Douglas Creek (DOUG), Fire Creek (FIRE), Tipella Creek (TIP), and the Soo River (SOO). The 6 free-flowing, unregulated streams included: Roe Creek (ROE), Madeley (MAD), Pemberton Creek (PEM), Owl Creek (OWL), Gowan Creek (GOW), and Sloquet Creek (SLO) (Table 2.1). I collected 10-15 breast feathers from each individual dipper and ~200 µl of blood from the brachial vein of the wing. This volume is below the recommended volume of blood that can be collected from passerines without causing any harm (1 % of body weight) (Owen, 2011), as dipper mass ranged from 42-66 g across these streams.

At regulated streams, invertebrates and periphyton were sampled at the following four locations in relation to the dam and point of diversion: a) 500 m upstream, b) within the headpond, c) below the dam, and d) 500 m downstream of the intake. At unregulated streams, a mid-point was sampled based on elevation and stream characteristics that were comparable to the regulated streams, then 500 m upstream, and 500 m downstream. Benthic invertebrates were collected during the fall of 2014 and 2015 by kick sampling across various channel habitats (riffles and pools) and turning rocks to mimic dipper foraging (Morrissey *et al.*, 2004b) until a sufficient sample mass (~10 mg dw) of individuals in each functional feeding group was obtained.

Benthic macroinvertebrates were rinsed with distilled and deionized water and live-sorted into the following representative families for each functional feeding group (Wallace and Webster, 1996): Heptageniidae (scrapers); Baetidae, Ephemerellidae, and Hydropsychidae (collector-gatherers); Perlidae, Chloroperlidae, and Perlodidae (predators); Limnephilidae, Tipulidae, and Pteryonarcyidae (shredders). The most commonly sampled invertebrates across streams included Heptageniidae, Baetidae, Perlidae, Hydropsychidae, and Ephemerellidae. If present, periphyton was collected from the surface of ~10 rocks at each sampling interval and stored as a slurry in stream water.

All blood and stream samples were frozen at the field sites in liquid nitrogen tanks until long-term storage at -20 °C. In 2015, a small number of invertebrate and blood samples from 4 streams inadvertently thawed inside the liquid nitrogen tank for up to 1-2 weeks. I compared isotopic values from thawed and unthawed samples and did not find any effect of thawing on invertebrate or dipper blood isotopes or Hg. Thawing had no effect on the C:N ratio of dipper blood ($p=0.52$) or the relationship between dipper blood and feather Hg ($p=0.67$). A search of the literature for studies on changes to stable isotope ratios in decaying biological material also supports the assumption that thawing does not strongly affect isotopic values. Leaf litter left to decay for several months showed a small initial enrichment in ^{13}C, followed by a decrease of only 0.4 ‰ after 59 months (Melillo *et al.*, 1989). Decaying leaf litter showed a similar trend of initial enrichment in ^{15}N, followed by a slight depletion, with negligible changes of ± 1‰ (Melillo *et al.*, 1989).

3.2.2 Stable isotope analysis of river bird and stream samples

To estimate the proportional contribution of different invertebrate functional feeding groups to the dipper diet, determine dipper trophic position, and study the relationship between stable isotopes and Hg bioaccumulation, dipper whole blood and invertebrates were analyzed for stable isotopes of carbon ($^{13}C/^{12}C$), nitrogen ($^{15}N/^{14}N$), and sulfur ($^{34}S/^{32}S$). The stable isotope ratios of a sample (R_{sample}, the ratio of heavy to light isotopes, e.g.,$^{15}N/^{14}N$, expressed as $\delta^{15}N$) is measured by isotope ratio mass spectrometry and expressed in parts per thousand deviations (‰)

from the isotope ratio of a standard reference material ($R_{standard}$). Thus, R_{sample} is calculated according to $\delta X = (R_{sample} / R_{standard} - 1) \times 1000$, where X is the heavy isotope (e.g. ^{15}N). International standard reference materials are atmospheric N_2 (Air) for $\delta^{15}N$, Vienna Peedee belemnite (VPDB) for $\delta^{13}C$, and Vienna Canon Diablo Troilite (VCDT) for $\delta^{34}S$ (Bond and Hobson, 2012).

Benthic macroinvertebrates, sorted by family, and periphyton were rinsed with ultrapure water (distilled and deionized) and any remaining debris or small invertebrates were removed from periphyton slurries with fine forceps. All invertebrate, periphyton, and whole blood samples were freeze dried for at least 48 hours until dry. Invertebrates were ground to a fine powder using a small mortar and pestle. Approximately 1 mg dried, homogenized invertebrate and whole blood, or 5 mg dried periphyton were weighed into tin capsules for combined $\delta^{13}C$ and $\delta^{15}N$ stable isotope analysis. For $\delta^{34}S$ analysis, 2-3 mg invertebrate and whole blood or 5 mg periphyton were weighed into tin capsules. Lipids were not extracted from the whole blood samples, as avian blood has low lipid content (<5%) and $\delta^{13}C$ is not affected by lipid extraction prior to analysis (Bearhop *et al.*, 2002). Further, unnecessary lipid extraction may compromise samples by causing ^{15}N-enrichment (Bearhop *et al.*, 2002).

All samples were analyzed at the UC Davis Stable Isotope Facility using a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK). Lab references for $\delta^{13}C$ and $\delta^{15}N$ were calibrated against National Institute of Standards and Technology (NIST) Standard Reference Materials IAEA-N1, IAEA-N2, IAEA-N3, USGS-40, and USGS-41. The long-standing measurement accuracy of these standard reference materials is ± 0.2 S.D. ‰ ($\delta^{13}C$) and ± 0.3 S.D. ‰ ($\delta^{15}N$). Precision between duplicate lab reference samples for $\delta^{13}C$ and $\delta^{15}N$ was $\leq$ 0.15 S.D. ‰ and $\leq$ 0.28 S.D. ‰, respectively, for all samples (Appendix 10). Lab references for $\delta^{34}S$ ($^{34}S/^{32}S$) were calibrated against National Institute of Standards and Technology (NIST) Standard Reference Materials IAEA S-1, IAEA S-2, and IAEA S-3 with a long-term accuracy of ± 0.4 S.D. ‰. Precision between duplicate lab reference samples $\delta^{34}S$ was $\leq$ 0.62 S.D. ‰ for all samples (Appendix 11).

Since there are no published turnover values for stable isotopes in dipper tissues, I estimated turnover (represented by half-life) from a variety of diet-change experiments for aquatic birds and passerines. Turnover rates of $\delta^{13}C$ and $\delta^{15}N$ in avian blood are fairly rapid, indicating recent dietary conditions. Whole blood of the Great Skua (*Catharacta skua*) has a half-life of 14.4 days for δ^{15}N and 15.7 days for δ^{13}C (Bearhop *et al.*, 2002). Similarly, the δ^{13}C half-life in captive Japanese Quail (*Coturnix japonica*) is 11.4 days (Hobson and Clark, 1992). The Garden Warbler (*Sylvia borin*) has a half-life of 11 ± 0.8 (S.D.) days for δ^{15}N and 5.0 ± 0.7 (S.D.) to 5.7 ± 0.8 (S.D.) for δ^{13}C (Hobson and Bairlein, 2003). Dunlin (*Calidris alpina pacifica*) have reported half-lives of 11.2 ± 0.8 (S.D.) days for δ^{13}C and 10.0 ± 0.6 (S.D.) days for δ^{15}N (Ogden *et al.*, 2004). The turnover rate of δ^{34}S is reportedly similar to carbon and nitrogen (Vander Zanden *et al.*, 2015). Dippers have a lower metabolic rate than non-aquatic passerines of the same size (Murrish, 1970), so half-lives are likely intermediate between those of the Garden Warbler and Greater Skua; however birds in the above experiments were studied in captivity and may have lower metabolic rates than their wild counterparts. Therefore, whole blood isotopic values represent fairly recent dietary information, likely 15-30 days for both δ^{15}N and δ^{13}C, based on the half-lives reported above.

3.2.3 Hg analysis of river bird and stream samples

Breast feathers were washed with a 2:1 chloroform: methanol solution for 24 hours to remove surface lipids, rinsed three times with ultrapure water, and air dried in a fume hood for 48 hours (Hobson and Bairlein, 2003). Freeze dried dipper whole blood (~10 mg dw) and feathers (~10 mg dw) were analyzed for total Hg using a Direct Mercury Analyzer (DMA-80, Milestone Microwave Laboratory Systems, Shelton, Connecticut, USA) at the University of Saskatchewan. Periphyton, predatory invertebrates, and sediment (~50 mg dw) from a subset of sites were analyzed to characterize longitudinal patterns within one regulated stream based on results of the dipper sample analyses.

Calibration curves were made by plotting the absorbances of the certified reference material (CRM), TORT-3 (National Research Council, Ottawa, Ontario, Canada) of varying mass against the mass of Hg in nanograms (ng) (Jardine *et al.*, 2012). In 2014, recoveries of the CRMs analyzed intermittently with the samples were 99 ± 4.0 % and 94 ± 1.0% (mean ± S.D.) for DORM-4 (n=10) and IAEA85 (n=5), respectively. Blank correction did not improve the performance of CRMs and therefore blank values were not used to adjust sample values. In 2015, recoveries of the CRMs analyzed intermittently with the samples were 99 ± 3.0 % and

93 ± 3.0 % (mean ± S.D.) for DORM-4 (n=10) and IAEA85 (n=5), respectively.

Since turnover time has not been calculated for MeHg in dipper tissues, I followed the approach of Rimmer *et al.* (2005), and based our half-life estimates on published values from waterbirds. Feathers represent past dietary exposure during feather growth (Hobson and Clark, 1992; Bearhop *et al.*, 2002), which occurs once during the late summer or early fall moult in dippers. MeHg half-lives have been published for the whole blood of Great Skua (*Catharacta skua*; Bearhop *et al.*, 2000) at 31.5-63 days, ~74 days for Mallard (Heinz and Hoffman, 2004), and 44–65 days for Cory's Shearwater (*Calonectris diomedea*; Monteiro and Furness 2001). The MeHg half-life for dipper whole blood is likely less than these published values for waterbirds, as passerines have a higher metabolic rate. Dippers, however, have a lower metabolic rate than other passerines as an adaptation for life in cold waters (Murrish, 1970). Therefore, I estimated MeHg half-life in dipper whole blood as ~30 days, which was used a conservative turnover estimate for Bicknell's Thrush (Rimmer *et al.*, 2010). MeHg concentrations in feathers indicate the amount deposited during active feather growth (Wolfe *et al.*, 1998). Feathers collected in the early fall will indicate fairly recent MeHg exposure, since this coincides with the timing of moult. Body feathers were analyzed in this study, since they provide the most representative sample for estimating whole bird Hg content (Furness *et al.*, 1986), and I was interested in the influence of river regulation on the ratio of blood:feather MeHg.

Throughout this study, mercury content was analyzed as total Hg (THg), but values in dippers may be interpreted as dominantly MeHg. The ratio of THg: MeHg in the whole blood of four passerine species was close to 1:1 (Rimmer *et al.*, 2004) and all Hg in seabird feathers is in the organic MeHg form (Thompson and Furness, 1989). Hg in American Dipper eggs and feathers is also close to 100 % MeHg (Henny *et al.*, 2002). Invertebrate, periphyton, and feather Hg are reported as ng/g dry weight. Whole blood samples were weighed before and after drying to obtain the moisture content and convert dry weight to wet weight (Appendix 42). Whole blood Hg is reported in ng/g dw when modeled against feather, invertebrate, and periphyton Hg (also reported in ng/g dw), but reported in ng/g ww when comparing with blood isotopes and avian Hg data from the literature.

3.2.4 Statistical analyses

3.2.4.1 Comparing dipper blood isospace and trophic position between regulated and unregulated streams

Dipper trophic position was calculated by subtracting Heptageniidae $\delta^{15}N$ (baseline of the foodweb at each stream) from dipper whole blood $\delta^{15}N$, dividing by a diet-tissue trophic discrimination factor of 2.67 ± 0.25 ‰ (Hobson and Barlein, 2003; Pearson *et al.*, 2003; Evans-Ogden *et al.*, 2004), and adding 2 (since Heptageniidae are at trophic level 2 as primary consumers), using the trophic position (TP) equation adapted from Jardine *et al.* (2006):

$$TP = [(\text{Dipper Whole Blood } \delta^{15}N - \text{primary consumer } \delta^{15}N)/2.67^{1}] + 2 \text{................ (Equation 3.1)}$$

[1] 2.67 represents an average diet-tissue change in $\delta^{15}N$ observed in insectivorous passerines (Hobson and Barlein, 2003; Pearson *et al.*, 2003; Evans-Ogden *et al.*, 2004).

A series of linear mixed effects models was run using lmer, package *lme4* (Bates *et al.*, 2015, R version 3.2.3) to test for effects of stream type, elevation, salmon, and the interaction between type and elevation on dipper trophic position and blood isotope values ($\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$). For all of these models, stream, year, and watershed were included as random effects (unless S.D. was <0.001, in which case they were excluded from the models) to account for the influence of these factors on stream isotopic profiles and non-independence of dippers. I was unable to test the interaction between stream type and salmon presence, since none of the regulated streams supported anadromous salmon upstream of the powerhouse.

Principal components analysis (PCA) of stable isotopes is effective in identifying niche partitioning among consumers (e.g. Stewart *et al.*, 2003). I applied this method to evaluate effects of river regulation and associated food web changes on a single measure of dipper whole blood isospace. An index of whole blood isospace was created (PCA; prcomp, package *stats*, R version 3.2.3) using trophic position (see calculation below), $\delta^{13}C$, and $\delta^{34}S$. PC1, the combination of linearly-transformed isotopes and trophic position values accounting for the highest amount of variation in the data, explained 71.9 % of the variation in dipper blood isospace. Linear mixed effects models were run using package *lme4* (Bates *et al.*, 2015, R version 3.2.3) to look at fixed effects of stream type, elevation, salmon, and the interaction between type and elevation on PC1. Stream, year, and watershed were included as random effects.

3.2.4.2 Stable isotope mixing models

Bayesian mixing models were run in MixSIAR (Stock and Semmens, 2015), a graphical user interface for R (R Core Team, 2015), to estimate the proportional contribution of each invertebrate foraging guild to dippers inhabiting regulated and unregulated streams. Stable isotopes of carbon, sulfur, and nitrogen were all used in these mixing models, since the inclusion of all three isotopes produced model results with the best diagnostics and source discrimination. Stream was included as a fixed effect in these stable isotope mixing models, enabling the comparison of diet among streams, while accounting for site-specific dietary sources (Semmens *et al.*, 2009). The mean and standard deviations of carbon, nitrogen, and sulfur isotopes of each invertebrate foraging guild were calculated for each stream transect and included as prey sources in the mixing models with samples from both years pooled. Since only 10 resident fish were captured across all streams over the 2 years (almost exclusively Coastrange Sculpin, *Cottus aleuticus*, and Rainbow Trout, *Oncorhynchus mykiss*), the isotopic signature of this source was pooled across all streams as a composite freshwater fish sample.

Since I did not sample any salmon fry or eggs, but observed adult salmon at some streams, published Pacific salmon fry stable isotope values from other watersheds were included at each stream as a representative source of marine derived nutrients. Salmon δ^{13}C (-20.1 ± 0.2 ‰, n=8) and δ^{15}N (13.6 ± 0.2 ‰, n=8) were obtained from whole salmon fry isotope values from the Chilliwack River, British Columbia (Morrissey *et al.,* 2004b), while Alaskan sockeye (*Oncorhynchus nerka)* eggs were used as an estimate of salmon δ^{34}S (18.7 ± 0.4 ‰, n=7) (Godbout *et al.*, 2010). These literature values are appropriate, since there is little variation in δ^{34}S in marine ecosystems, with marine fish averaging 16.8 ± 0.7 ‰ (Nehlich, 2015) and the value of seawater sulfate being highly conserved at ~21 ‰ (Peterson and Fry, 1987). Marine diet sources are also heavily enriched in ^{13}C and ^{15}N compared to freshwater and terrestrial sources (Peterson and Fry, 1987).

By pooling invertebrate and fish samples across years, I was able to incorporate variability and uncertainty into the mixing models, which is a requirement for MixSIAR (Phillips *et al.*, 2014). Sources were distinct on a stream-by-stream basis and combining foraging guilds was not necessary. At a few streams, an inadequate number of shredder samples was collected; therefore, I included a pooled "shredder" signature across that stream type (regulated or unregulated) as the shredder source at these streams, in order to incorporate variability in the signature.

Separate diet-tissue trophic enrichment factors (TEFs) for each isotope were incorporated into the mixing models to account for isotopic fractionation (changes in the isotopic ratio between dippers and their prey) (Hobson and Clark, 1992). TEFs of δ^{13}C and δ^{15}N were obtained from averaging results from three captive studies on three species of primarily insectivorous birds. Diet-whole blood TEFs were 1.3 ‰ for δ^{13}C and 2.9 ‰ for δ^{15}N in Dunlin (*Calidris aplina*) (Evans-Ogden *et al.*, 2004), 1.7 ‰ for δ^{13}C and 2.4 ‰ for δ^{15}N in Garden Warbler (*Sylvia borin*) (Hobson and Bairlein, 2003), and 2.2 ‰ for δ^{13}C, 2.7 ‰ for δ^{15}N in Yellow Warbler (*Setophaga petechia)* (Pearson *et al.*, 2003); therefore, I used the mean ± S.D. TEFs for these species in Bayesian mixing models: 1.73 ± 0.45 ‰ for δ^{13}C and 2.67 ± 0.25 ‰ for δ^{15}N. TEFs for stable isotopes of sulfur are not as well established as carbon and nitrogen, so I used the McCutchan *et al.* (2003) estimate for consumers with high protein diets (1.9 ± 1.14‰), which experience more trophic enrichment in ^{34}S. This is similar to the δ^{34}S TEF value of 0.5 ± 2.4 ‰ estimated for animal consumers in a recent literature review of sulfur stable isotopes (Nehlich, 2015), which concluded that there is no known discrete difference between consumer tissues and diet in δ^{34}S.

Mean and standard deviations of prey consumption estimates from the MixSIAR posterior distribution models were used in subsequent modeling to look at effects of stream type, elevation, and salmon on estimated diet proportions. Separate models were run for each prey source (invertebrate functional feeding groups, resident fish, and anadromous salmon). In cases where watershed and year did not explain substantial variation in diet proportions (standard deviation < 0.001), they were excluded from the models as random factors, and simple general linear models (glm, package *stats*, R version 3.2.3) were used to compare the proportion of each source between stream types, with mean prey consumption estimates for each stream modeled in response to steam type, elevation, salmon presence, and stream type*elevation. When at least one random effect (watershed or year) accounted for variation in the diet proportion, linear mixed effects models were run using lmer, package *lme4* (Bates *et al.*, 2015, R version 3.2.3), also with stream type, elevation, salmon presence, and the interaction between stream type*elevation as fixed effects. Diet proportions were arcsine square-root transformed to improve normality.

3.2.4.3 Comparing invertebrate isotope profiles upstream and downstream of regulated and unregulated streams

A linear mixed effects model (lmer, package *lmerTest*, Kuznetsova *et al.*, 2015, R version 3.2.3) was run for each stream type (regulated and unregulated) to test the *a priori* hypothesis of distinct invertebrate isotopic profiles in habitats modified by RoR flow diversion. Pooled invertebrate signatures at each sampling interval were calculated as the grand mean of the mean of each foraging guild (collector-gatherers, scrapers, shredders, and predators) collected at that location. Resident fish were excluded from the pooled estimate, as they were not collected at each stream. Stream and watershed were included as random effects to account for non-independence of invertebrates sampled at the same stream and to account for watershed-level effects on stream isotope profiles. For unregulated streams, sampling year was also included as a random effect, since it did explain some variance in invertebrate isotope signatures. For each model, a *post-hoc* Tukey test was run to compare the pooled invertebrate isotopic profiles between sampling intervals (glht, package *multcomp*, Hothorn et al., 2008, R Version 3.2.3).

3.2.4.4 Comparing dipper blood and feather Hg between regulated and unregulated streams and relating to blood isospace

Linear mixed effects models (lmer, package *lme4*, Bates *et al.*, 2015, R version 3.2.3) were run to evaluate the influence of blood stable isotopes (δ^{34}S, δ^{13}C, and trophic position), stream type, elevation, salmon, and the interaction between type and elevation on dipper blood and feather Hg. Stream, sampling year, and watershed were included as random effects to account for non-independence of dippers sampled at the same stream, watershed-level effects on isotope profiles, and potential year-effects. If a random effect did not explain substantial variation in the response variable (S.D.<0.001), it was excluded from the model.

Correlations were calculated to compare the relationship between dipper blood Hg and stable isotopes between the two stream types (regulated and unregulated). The correlation between blood and feather Hg was also compared between stream types, as a mechanism for comparing residency time on the stream. Strong blood:feather Hg correlations indicate uniform Hg exposure, and likely constant foraging location, from the time since feather moult in the late summer to the time of fall sampling.

A general linear model (glm, package *stats*, R version 3.2.3) was constructed to test for stream-level differences in dipper blood and feather Hg and isospace by treating stream as a fixed effect. *Post-hoc* Tukey HSD tests (glht, package *multcomp*, Hothorn et al., 2008, R Version 3.2.3) were run to test pairwise differences in dipper blood and feather Hg, blood δ^{34}S, δ^{13}C, and trophic position between individual streams. I also tested for significant differences in dipper blood and feather Hg and blood isotopes between watersheds, by running a linear mixed effects model with watershed as a fixed effect and stream and year trapped as random effects. If a random effect did not explain substantial variation in the response variable (S.D.<0.001), it was excluded from the model. *Post-hoc* Tukey HSD tests (ghlt, package *multcomp*, Hothorn et al., 2008, R Version 3.2.3) were run to test pairwise differences in dipper blood and feather Hg, blood δ^{34}S, δ^{13}C, and trophic position between the three watersheds.

3.2.4.5 Relationship between dipper diet and Hg exposure

Multiple regressions were run to test whether the mean diet proportion of each prey type was related to mean dipper blood or feather Hg for each stream type (regulated/unregulated). The mean proportion of each prey source at each stream, estimated from Bayesian Mixing Models, was modeled against mean dipper blood or feather Hg at each stream.

3.2.4.6 Longitudinal gradient in periphyton and invertebrate Hg at Douglas Creek

Mercury was also analyzed in predatory invertebrates (Perlidae and Perlodidae) and periphyton collected along a longitudinal gradient at one stream, Douglas Creek. Samples were collected at locations 500 m upstream of the dam, within the headpond, directly below the dam, 500 m downstream of the dam, and 2 km downstream of the powerhouse to evaluate whether the headpond was a source of elevated MeHg production. Perlidae (predatory stonefly larvae) have a higher MeHg:THg ratio than other benthic macroinvertebrates, estimated by one study at ~100 % MeHg (Henny *et al.*, 2005).

3.2.4.7 Model Selection

Models were constructed to evaluate a candidate set of potentially biologically important variables and model selection was based on Akaike's Information Criterion adjusted for small sample size (AIC_c, Burnham, and Anderson, 2002). Model selection tables were generated using the package *MuMIn* (Barton, 2016) in R. Linear Models were run using maximum likelihood (ML) estimation and parameter estimates from the best-fitting models were calculated using restricted maximum likelihood estimation (REML) for mixed effects models and maximum likelihood estimation for general linear models. When multiple models were competitive ($AIC_c \leq 2$), conditional model-averaged parameter estimates were calculated using the package *MuMIn* (Barton, 2016), whereby parameters are only averaged over models in which they occur. If a random effect did not explain substantial variation in the response variable (standard deviation<0.001), it was excluded from the model. Models with weight>0 and the null (intercept-only) are presented for comparison. Elevation was included as a continuous variable in all models and stream type refers to the categories "regulated" or "unregulated".

3.3 RESULTS

3.3.1 American dipper diet at regulated and unregulated streams: evidence from multiple stable isotopes

3.3.1.1 Dipper blood isospace and trophic position

Linear mixed-effects models of dipper blood isospace supported an effect of stream type (β =2.44, adj. S.E.=1.63, p=0.13, Fig 3.1), and to a lesser extent, salmon presence (β =0.045, adj. S.E.=2.21, p=0.98, Fig. 3.2, Table 3.1), although these differences were not significant by Frequentist standards (p>0.05). This model support for separation between stream types is most-likely driven by significantly lower blood δ^{34}S in dippers captured at regulated streams compared to unregulated streams (β =-2.42, S.E.=0.95, p=0.029; Figure 3.3, Appendix 13). There was no model support for an effect of anadromous salmon on blood δ^{34}S (Appendix 13). Further, the relationship between trophic position and blood δ^{34}S was weak (Adj. R-sq=0.076, Fig. 3.4).

There was some model support for lower blood δ^{13}C at regulated streams (β=-0.28, Adj. S.E.=0.77, p=0.71), but models did not support effects of elevation or salmon presence (Appendices 15-17) on dipper blood δ^{13}C. Models of dipper trophic position also showed no strong effects of stream type, salmon presence, nor elevation, with the null model accounting for 99% of the model selection weight (Appendices 18-20). Across stream types, dippers were feeding at similar trophic position, regardless of salmon presence.

Table 3.1 Model selection results testing for differences in dipper whole blood stable isotope space (PC1 of $\boldsymbol{\delta}^{13}$C , $\boldsymbol{\delta}^{34}$S and trophic position (based on $\boldsymbol{\delta}^{15}$ N) between regulated and unregulated streams. A linear mixed effects model was run using the package *lme4* in R. Stream type, elevation, salmon, and the interaction between type*elevation were included as fixed effects. Stream, watershed, and year were included as random effects.

Response	**Model Structure**	**AICc**[1]	**Δ AICc**	**Deviance**[2]	**Model Weight**	**df**
PC1	**Type+salmon**	**433.6**	**0**	**418.39**	**0.60**	**7**
	type	**434.7**	**1.03**	**421.74**	**0.36**	**6**
	null	439.0	5.36	428.34	0.041	5

[1] Akaike's Information Criterion, corrected for small sample sizes

[2] -2 (Log Likelihood)

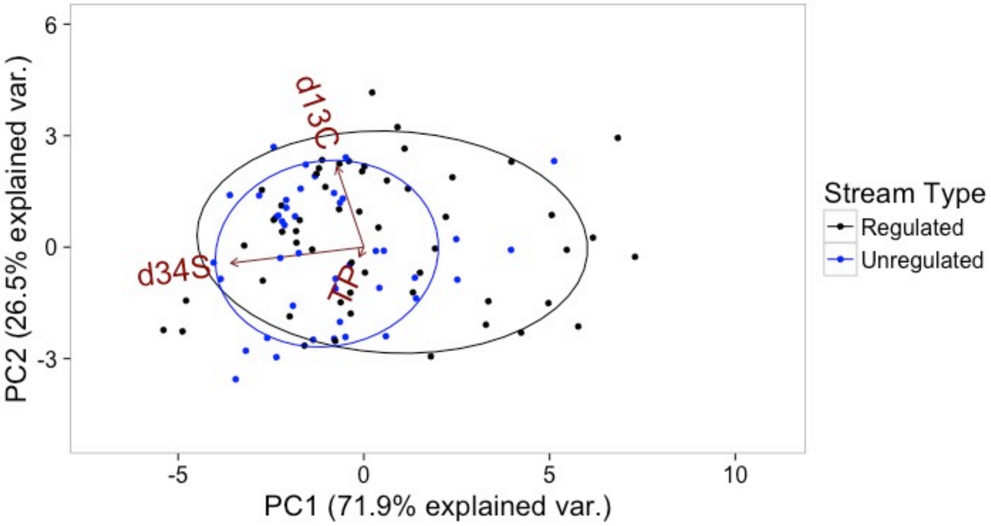

Figure 3.1 PCA plot of dipper whole blood isospace (TP=trophic position, δ^{13}C, and δ^{34}S), grouped by stream type (regulated and unregulated, n=99). There was a strong effect of stream type on PC1, driven by significantly lower blood δ^{34}S in dippers captured at regulated streams (β=-2.42, SE=0.95, p=0.029).

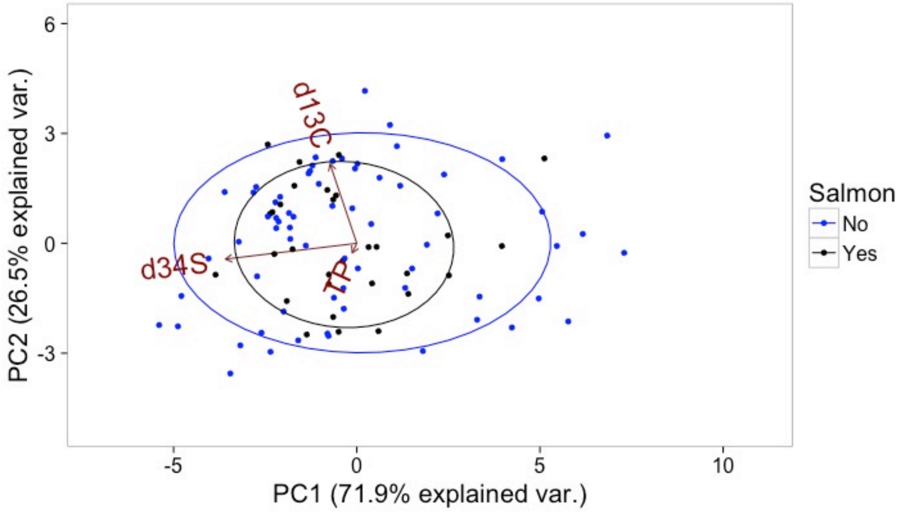

Figure 3.2 PCA plot of dipper whole blood isospace (TP=trophic position, δ^{13}C, and δ^{34}S) grouped by streams with and without anadromous salmon (n=96). There was some model support for effects of salmon on blood isospace, but this factor was not significant (p=0.98).

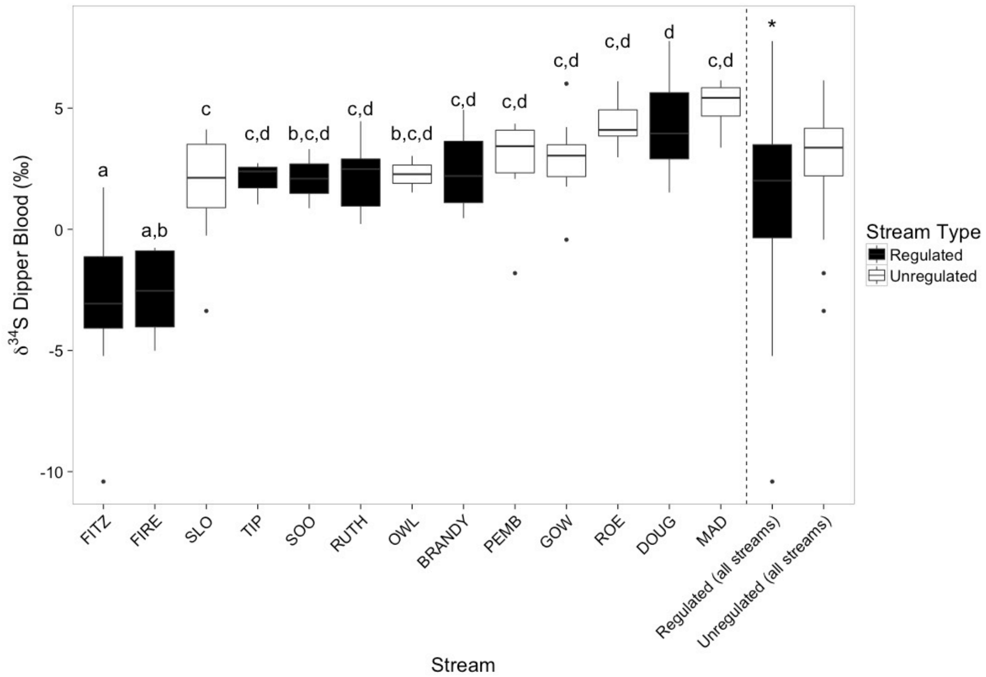

Figure 3.3 Comparing American Dipper whole blood δ^{34}S between regulated and unregulated stream types. Dippers foraging at regulated streams had significantly lower blood δ^{34}S (β =-2.42, S.E.=0.95, p=0.029). Streams sharing a common letter are not significantly different with respect to dipper blood δ^{34}S, as estimated from a *post-hoc* Tukey HSD tests among individual streams.

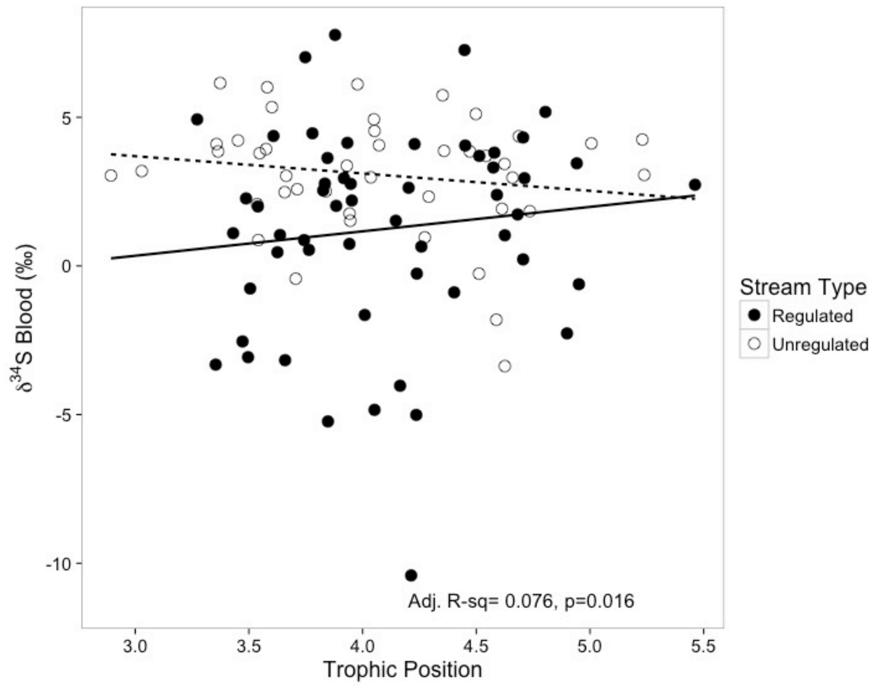

Figure 3.4 Relationship between dipper blood trophic position (TP) and δ^{34}S. There was no significant effect of TP on blood δ^{34}S (p=0.32) and no significant interaction between TP and stream type (p=0.22).

3.3.1.2 Changes in stream invertebrate stable isotope signatures upstream and downstream and results of Bayesian stable isotope mixing models

While there was no difference in invertebrate signatures upstream and downstream of free-flowing streams, habitats modified by RoR dams showed distinct invertebrate isotope signatures (Fig. 3.5). Invertebrates sampled immediately below RoR dams were significantly depleted in ^{34}S (β=-1.33 ± 0.43, p=0.010) and significantly enriched in ^{13}C (β=1.14 ± 0.40, p=0.025), compared to invertebrates sampled 500 m upstream of the dams (Table 3.2). Headpond invertebrates showed the same trend as invertebrates sampled below dams, but the difference with upstream habitats was not significant (Table 3.2). Mean stream invertebrate signatures at unregulated streams were not significantly different between locations for carbon, nitrogen, or sulfur (Table 3.3).

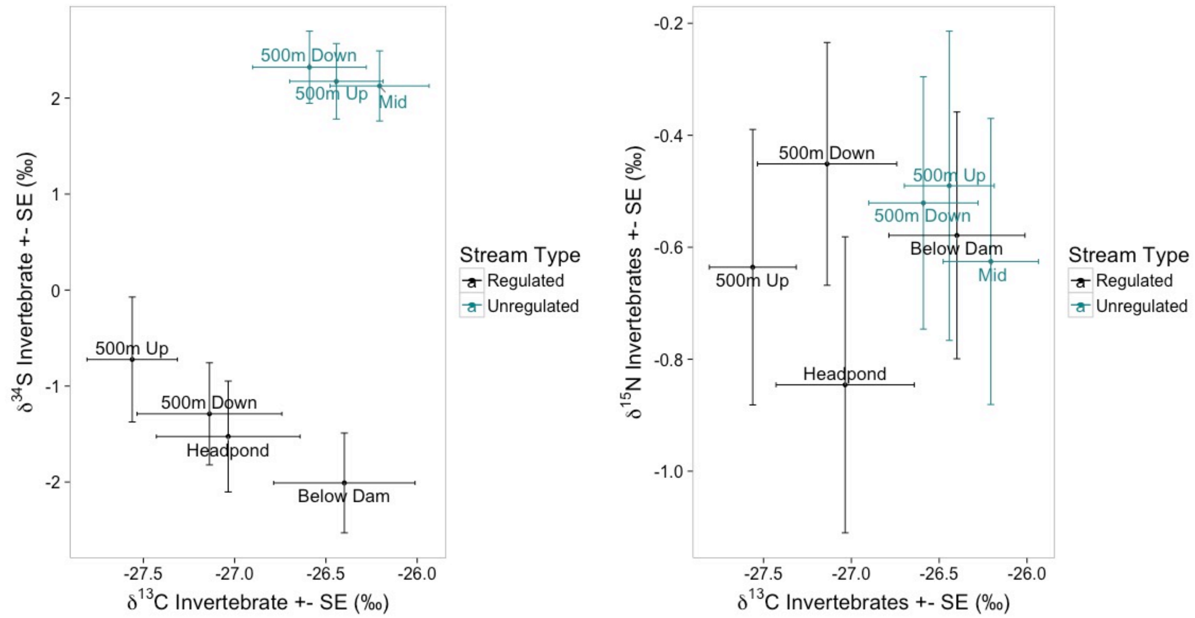

Figure 3.5 Carbon- Sulfur (Left) and Carbon-Nitrogen (Right) stable isotope plots, comparing stream invertebrate isotope profiles (mean ± SE) sampled upstream and downstream of seven regulated and seven unregulated streams. Invertebrate signatures represent the grand mean of the means across four foraging guild (collector-gatherers, scrapers, shredders, and predators) collected at multiple sampling intervals for each river.

The isotopic profile of basal invertebrates (collector-gatherers and scrapers) supported the observed trends in dipper isospace. Across all streams, the δ^{13}C and δ^{15}N signature of scraping and collector-gathering invertebrates were similar, while basal invertebrates at regulated streams showed consistently lower δ^{34}S (Figs 3.6, 3.7). In the absence of ^{13}C- and ^{15}N-enrichment, this suggests that the observed δ^{34}S signature at these streams is not related to salmon presence and is either a product of a) stream geomorphology and hydrology or b) activity of anaerobic sulfate-reducing bacteria.

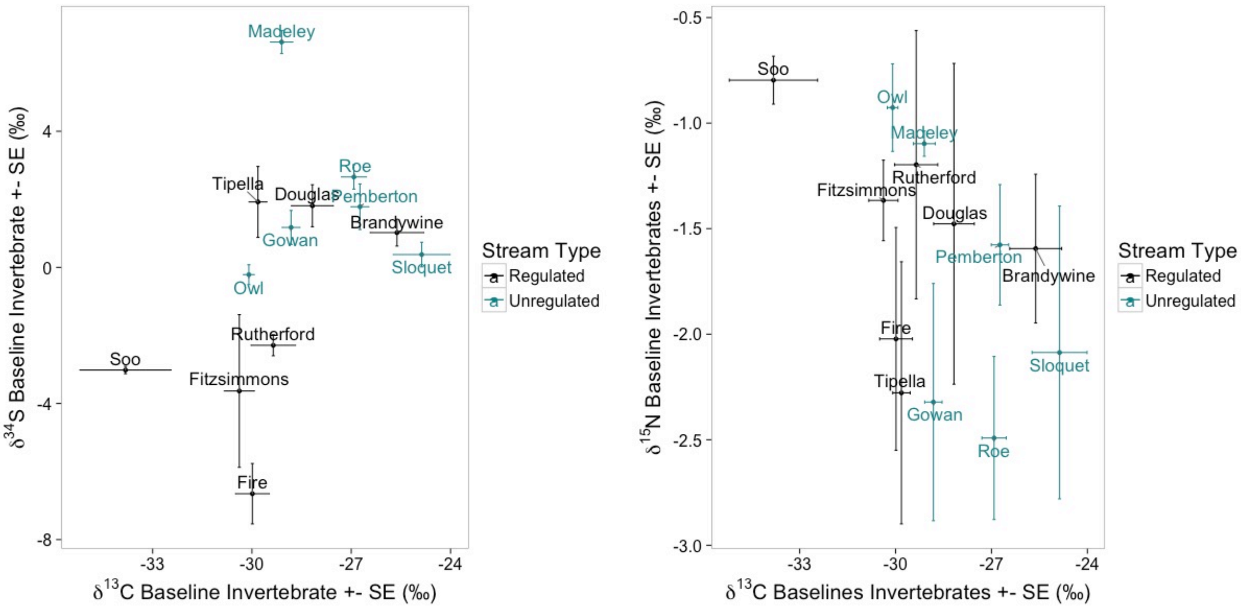

Figure 3.6 Stable isotope biplots of Carbon-Sulfur (LEFT panel) and Carbon-Nitrogen (RIGHT panel) values of baseline scraping invertebrates (Heptageniidae) at regulated and unregulated streams in southwestern British Columbia.

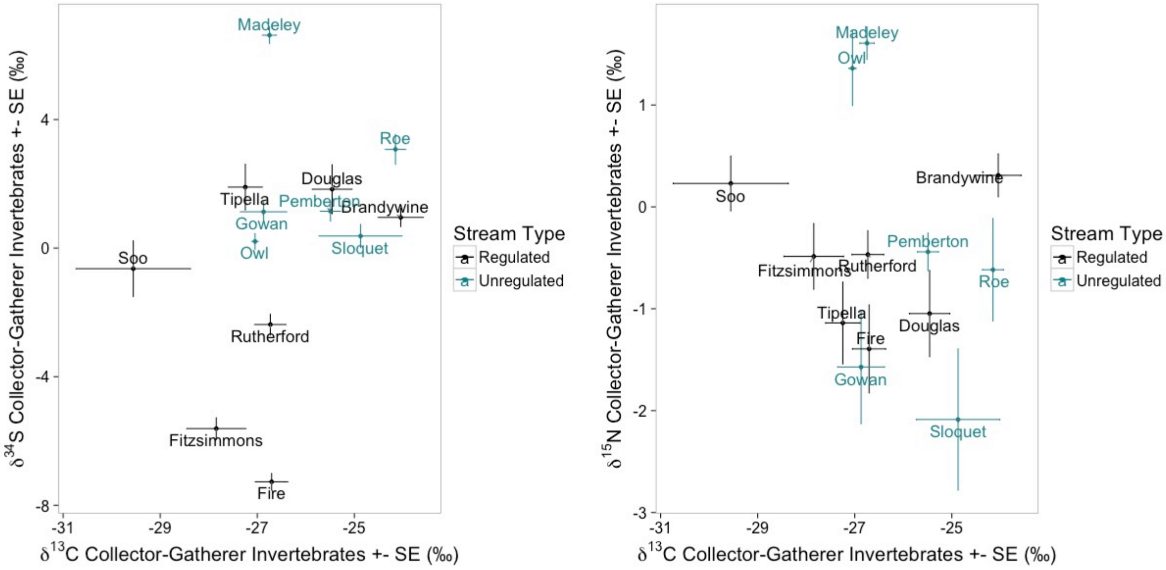

Figure 3.7 Stable isotope biplots of Carbon-Sulfur (LEFT panel) and Carbon-Nitrogen (RIGHT panel) values of baseline collector-gathering invertebrates (Baetidae/Ephemerellidae) at regulated and unregulated streams in southwestern British Columbia.

Table 3.2 Estimates (± S.E.) of *post-hoc* Tukey contrasts comparing invertebrate δ^{34}S, δ^{13}C, and δ^{15}N values sampled upstream and downstream of **RoR-regulated streams**. Positive estimates indicate enrichment in the heavier isotope (^{34}S, ^{13}C, ^{15}N), while negative estimates indicate depletion. Significant differences between sampling intervals are bolded.

	δ^{34}S (‰)		δ^{13}C (‰)		δ^{15}N (‰)	
Stream reach comparison	**Estimate (± SE)**	**p-value**	**Estimate (± SE)**	**p-value**	**Estimate (± SE)**	**p-value**
500m Down - Below Dam	0.51 ± 0.42	0.62	-0.75 ± 0.39	0.22	0.17 ± 0.30	0.94
Headpond-Below Dam	0.50 ± 0.44	0.66	-0.88 ± 0.40	0.12	-0.22 ± 0.30	0.89
Below Dam-500m Up Dam	**-1.33 ± 0.43**	**0.010***	**1.12 ± 0.40**	**0.023***	0.037 ±0.30	0.99
Headpond-500m Down	-0.014 ± 0.43	1.00	-0.13 ± 0.40	0.99	-0.39 ± 0.30	0.57
500m Up- 500m Down	0.82 ± 0.42	0.22	-0.37 ± 0.40	0.79	-0.21 ± 0.30	0.90
500m Up-Headpond	0.83 ± 0.44	0.23	-0.24 ± 0.40	0.93	0.18 ± 0.30	0.94

Table 3.3 Estimates (± SE) of *post-hoc* Tukey contrasts comparing invertebrate δ^{34}S, δ^{13}C, and δ^{15}N values sampled upstream and downstream of unregulated streams. Positive estimates indicate enrichment in the heavier isotope (^{34}S, ^{13}C, ^{15}N), while negative estimates indicate depletion. Significant differences between sampling intervals are bolded.

	δ^{34}S (‰)		δ^{13}C (‰)		δ^{15}N (‰)	
Stream reach comparison	**Estimate (± SE)**	**p-value**	**Estimate (± SE)**	**p-value**	**Estimate (± SE)**	**p-value**
Mid-500m Down Dam	0.12 ± 0.19	0.81	0.32 ± 0.32	0.57	-0.089 ± 0.33	0.96
500m Up Dam-500m Down Dam	-0.072 ± 0.18	0.92	0.16 ± 0.32	0.87	0.026 ± 0.33	1.0
500m Up Dam-Mid	-0.19 ± 0.18	0.56	-0.16 ± 0.32	0.88	0.11 ± 0.34	0.94

TEF-adjusted dipper blood isotope values fell within the range of the isotopic values of stream-specific invertebrate foraging guilds, pooled freshwater fish sources, and values from the literature for Pacific salmon, suggesting no missing dietary sources (Fig. 3.8, see Appendices 21-33 for individual stream isotope biplots). At regulated streams, mean dipper diet consisted of 30 ± 8.1 % predatory invertebrates, followed by 23 ± 4.7 % resident fish, 21 ± 9.4 % shredders, 16 ± 3.0 % collector-gatherers, 8 ± 3.5 % scrapers, and only 2 ± 2.5 % Pacific salmon (Table 3.4, Fig. 3.9). Mean dipper diet was similar at unregulated streams, dominated by resident fish (30 ± 18.4 %), predatory invertebrates (29 ± 14.5 %), collector-gatherers (18 ± 6.3 %), and shredders (15 ± 4.6 %), with minimal contributions from scrapers (7 ± 3.1 %) and Pacific salmon (1 ± 0.5 %).

Bayesian mixing models estimated similar dipper diet between regulated and unregulated streams (Table 3.4, Appendices 34,35), but slightly higher shredder consumption at regulated streams (β=8.52e-02, Adj. S.E.=6.96e-02, p=0.15) compared to unregulated streams (Appendices 35, 37). There was no model support for differences in the proportion of resident fish, predators, collector-gatherers, scrapers, or salmon between stream types (Table 3.5, Appendices 36-41). Elevation was a predictor of the proportion of shredders and collector-gatherers to dipper diet, with trends of higher shredder consumption at higher elevation streams (β=1.73e-04, Adj SE=1.0e-04, p=0.086; Appendix 37) and higher collector-gatherer consumption at lower elevation streams (β =-9.91e-05, Adj SE= 6.34e-05, p=0.12; Appendix 40). There was moderate model support for increased resident fish consumption at salmon-bearing streams (β=0.12, Adj. S.E.= 0.094, p=0.21; Appendix 38) (Table 3.5). Overall, dipper diet was dominated by invertebrates and resident fish at both stream types, with minimal contributions from Pacific salmon.

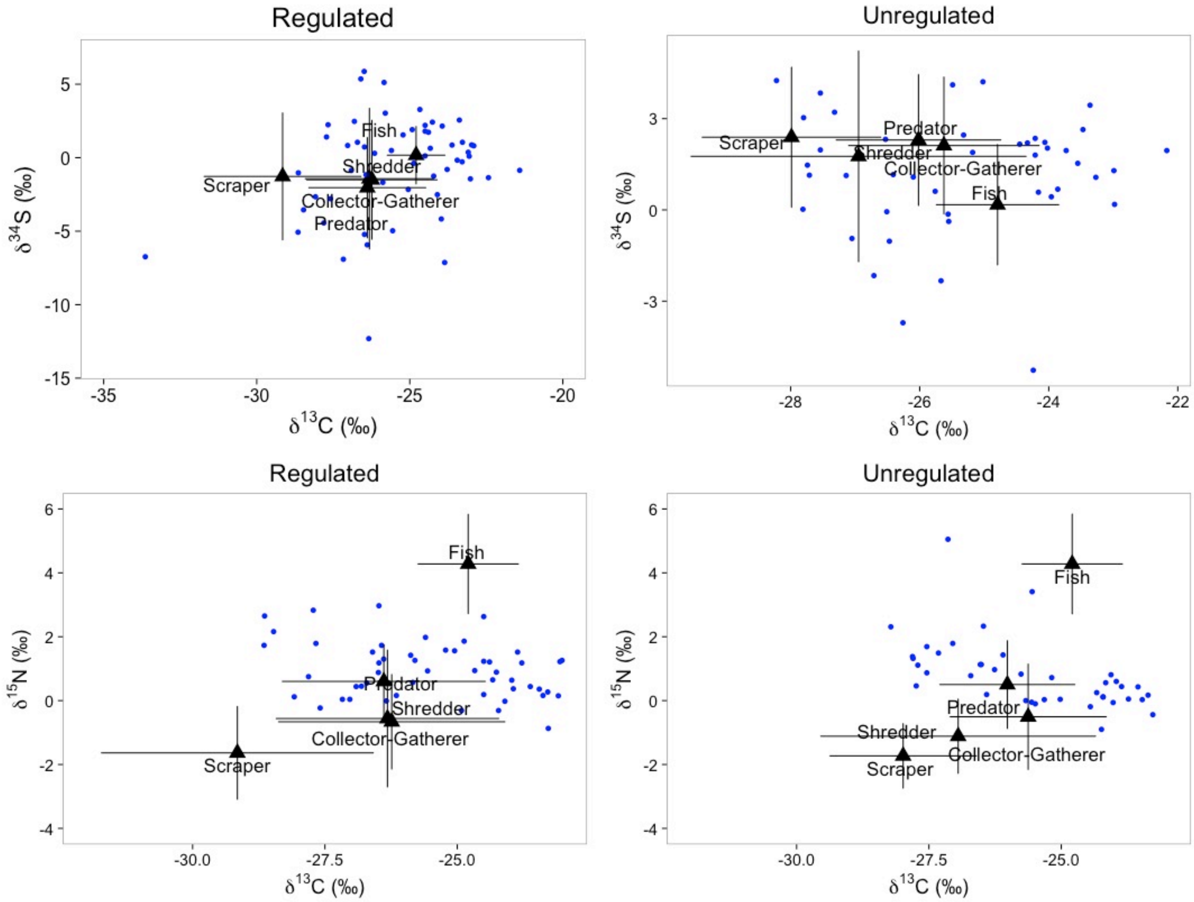

Figure 3.8 Stable isotope biplots of a) Carbon-Sulfur and b) Carbon-Nitrogen food webs at regulated (LEFT panel) and unregulated (RIGHT panel) streams in southern British Columbia. Individual TEF-adjusted dipper blood isotope values are represented as blue points, while the black triangles and lines represent invertebrate foraging guilds (collector-gatherers, scrapers, shredders, and predators) and resident fish source means ± S.D. Anadromous salmon, although included as a source in the mixing models, were excluded from these figures to facilitate easier visual distinction between invertebrate foraging guilds, as salmon values were heavily enriched in all three isotopes compared to the dippers.

Table 3.4 Summary statistics of estimated diet proportions of invertebrate foraging guilds, resident fish, and anadromous salmon for adult dippers, averaged across stream types and pooled across years. The grand mean, S.D., min, and max values of the mean diet proportions are presented for regulated and unregulated streams. Diet proportions at each stream were estimated using Bayesian mixing models in MixSIAR using multiple stable isotopes (δ^{13}C, δ^{15}N, δ^{34}S), with separate prey samples collected at each stream.

Regulated Streams (n = 56 dippers)					**Unregulated Streams** (n = 40 dippers)				
Source	Grand Mean	S.D.	Min	Max	**Source**	Grand Mean	S.D.	Min	Max
Predator	0.30	0.081	0.15	0.39	**Resident Fish**	0.30	0.184	0.09	0.39
Resident Fish	0.23	0.047	0.15	0.31	**Predator**	0.29	0.145	0.16	0.50
Shredder	0.21	0.094	0.10	0.37	**Collector**	0.18	0.063	0.12	0.28
Collector	0.16	0.030	0.12	0.20	**Shredder**	0.15	0.046	0.08	0.22
Scraper	0.08	0.035	0.03	0.14	**Scraper**	0.07	0.031	0.04	0.13
Salmon[**]	0.02	0.015	0.01	0.05	**Salmon**[**]	0.01	0.005	0.01	0.02

[**] based on literature isotope values (not measured in these study streams)

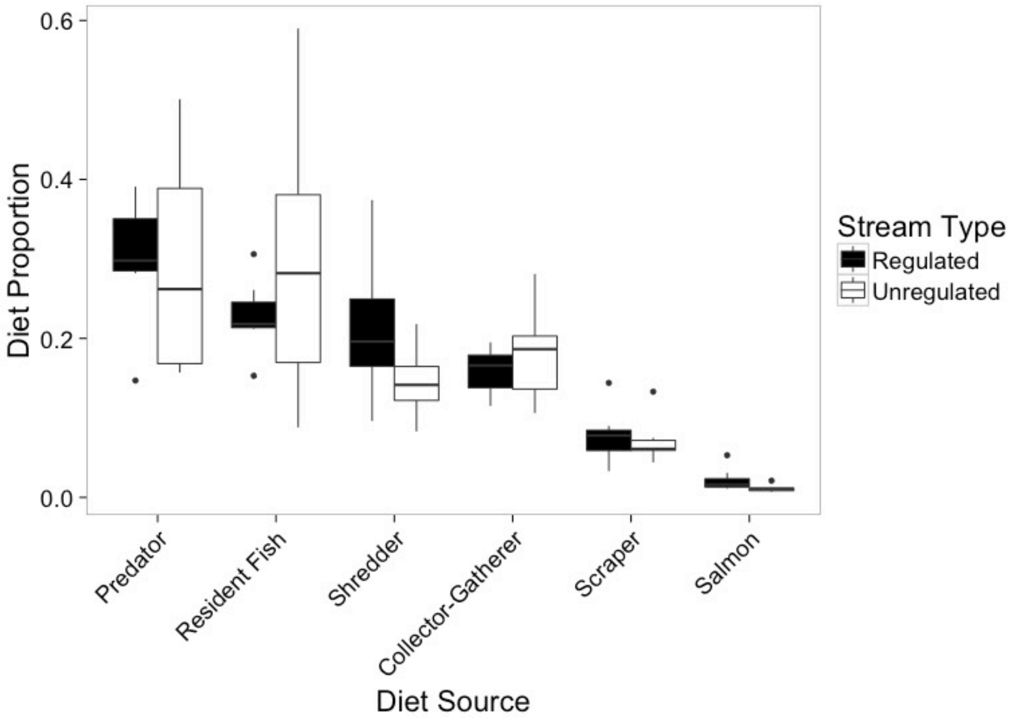

Figure 3.9 Summary of the mean proportional contribution of invertebrate and fish prey sources to the diet of American Dippers captured at regulated (n=56 dippers) and unregulated (n= 0 dippers) streams during the autumns of 2014 and 2015. A Bayesian Mixing model in MixSIAR estimated the mean and credible intervals of the proportional contribution of each source at each stream using three stable isotopes (δ^{13}C, δ^{15}N, δ^{34}S). Mean diet proportions for each stream type were calculated from the MixSIAR output and this information was used in a series of general linear models to test for differences in dipper diet between stream types. Middle, lower, and upper horizontal lines represent the median, 25 % and 75 % credible intervals of the mean contribution of each prey source to dippers sampled at regulated and unregulated streams. Vertical lines represent the 95 % confidence intervals of the means for each stream type.

Table 3.5 Model-averaged estimates of factors predicting the proportion of each prey source to dipper diet at regulated and unregulated streams. The predictive capacity of each factor was determined from a series of general linear models and linear mixed effects models with mean prey consumption estimates for each stream modeled in response to steam type*elevation and salmon presence. Separate models were run for each of the six prey sources. Only fixed effects in competitive models (ΔAICc<2 from top model) are presented.

	Fixed Effects				Watershed included as Random Effect?
Diet Source	Stream Type	Elevation	Salmon Presence	Type* Elevation	
Shredders	β=8.5e-02 ± 5.96e-02, p=0.15	β =1.73e-04 ± 1.0e-04 (p=0.086)	X	X	No
Salmon	X	X	X	X	Yes
Resident Fish	X	X	β=0.12 ± 0.094, (p=0.21)	X	No
Scrapers	X	X	X	X	Yes
Collector-gatherers	X	β =-9.91e-05 ± 6.34e-05 (p=0.12)	X	X	No
Predators	X	X	X	X	No

*positive estimates indicate a higher proportion of that diet source at regulated, higher elevation, and salmon-bearing streams. Negative estimates indicate a higher proportion of that diet source at free-flowing, lower elevation, non-salmon bearing streams. X=no model support for effects of this variable on estimated diet proportions.

3.3.2 Effects of river regulation by run-of-river dams on dipper Hg exposure and body condition and the influence of diet

Mean dipper blood Hg was 466.0 ± 81.3 ng/g ww at regulated and 382.6 ± 50.4 ng/g ww at unregulated streams (Appendix 42). There was no model support for effects of stream type, salmon, elevation, trophic position, or blood δ^{13}C on dipper whole blood Hg (Table 3.6). Although blood δ^{34}S was a significant positive predictor of blood Hg (β=0.029, Adj. S.E.=0.010, p=0.004), the inclusion of this parameter did not improve fit over the null model, suggesting no major influence on blood Hg (Table 3.6). Blood Hg varied by individual stream (Fig. 3.10) and was typically below the threshold causing reproductive impairment in avian species (1000 ng/g ww; Ackerman *et al.*, 2016), with the exception of dippers sampled at Douglas Creek, where blood Hg was recorded at up to 1948.1 ng/g wet weight (mean 987.8 ± 167.2 ng/g ww). Only one other stream, the relatively low-elevation and salmon-bearing stream, Sloquet Creek, supported one dipper with blood Hg above the published toxicity thresholds of 1000 ng/g (Ackerman *et al.*, 2016), measuring 1069.7 ng/g ww. Otherwise, a relatively low mean of 354.5 ± 82.9 ng/g ww was measured in dippers at Sloquet Creek. Blood Hg was significantly lower at Brandywine Creek than all other streams, except Fitzsimmons Creek, another regulated stream (Fig. 3.10). Trophic position (r=0.58, p<0.001, n=53) and blood δ^{34}S (r=0.43, p=0.0012, n=53) were the strongest correlates with blood Hg at regulated streams, while blood δ^{13}C was a weak negative correlate (r=-0.17, p=0.23, n=53; Fig. 3.12). The correlations between blood Hg and all stable isotopes were relatively weak at unregulated streams (r=0.22, p=0.17, n=39 with δ^{34}S, r=0.24, p=0.13, n=39 with TP, and r=-0.039, p=0.81, n=39 with δ^{13}C; Fig. 3.13).

Table 3.6 Model selection results testing for differences in dipper whole blood Hg (log10) between regulated and unregulated streams using a linear mixed effects model. Stream type, elevation, salmon, blood δ^{34}S, blood δ^{13}C, trophic position, and interactions between type*elevation were included as fixed effects and stream and watershed were included as random effects.

Response	**Model Structure**	**AICc**[1]	**Δ AICc**	**Deviance**[2]	**Model Weight**	**df**
Blood Hg ($\log_{10}$)	**null**	**2.4**	**0**	**-6.02**	**0.73**	**4**
	Blood δ^{34}S	**4.4**	**2.01**	**-6.23**	**0.27**	**5**

[1] Akaike's Information Criterion, corrected for small sample sizes

[2] -2 (Log Likelihood)

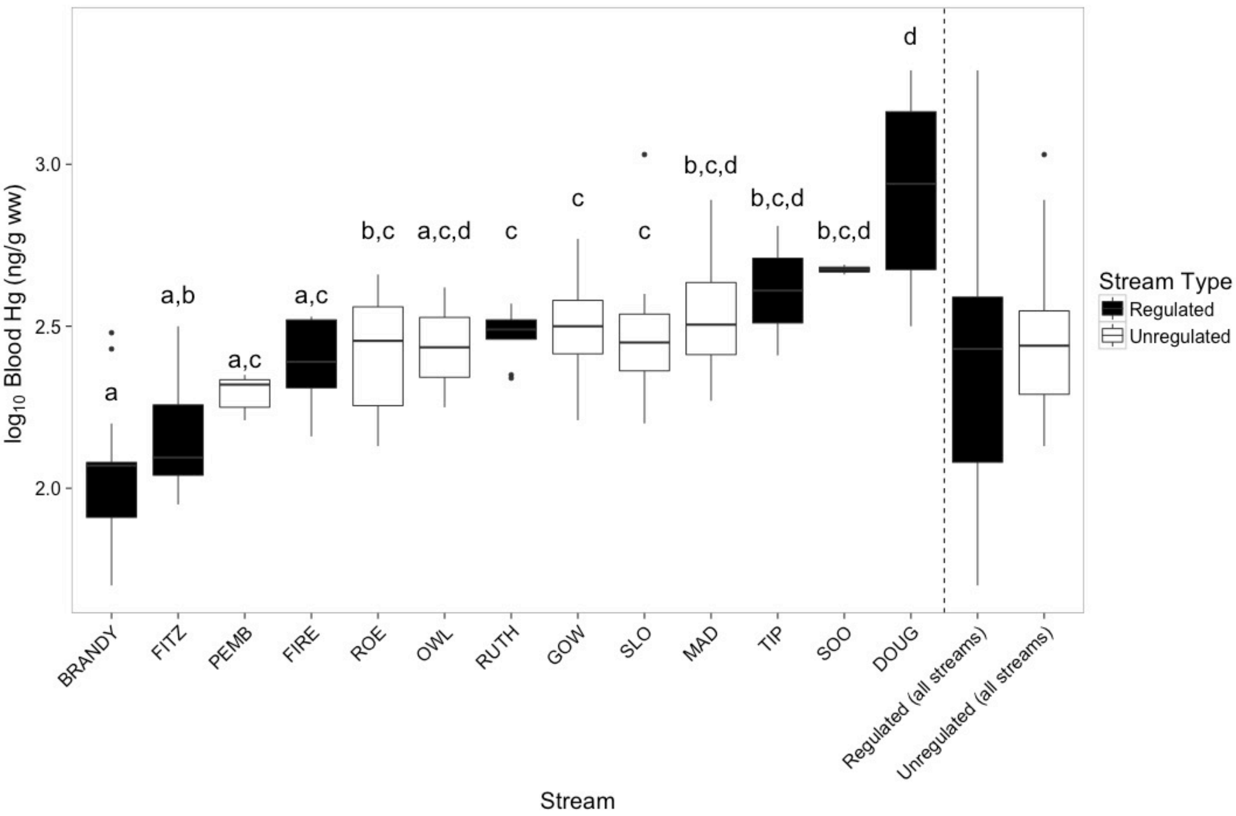

Figure 3.10 American Dipper whole blood ($\log_{10}$) Hg concentrations (ng/g ww) at regulated (n=53) and unregulated streams (n=39) in order of increasing mean Hg. There was no significant difference in blood Hg concentration between stream types (regulated/unregulated) overall, but there were some significant differences between individual streams. Streams sharing a common letter are not significantly different in blood Hg (p-value>0.05 from *post-hoc* Tukey test). At Douglas Creek, dippers had blood Hg exceeding published toxicity benchmarks (987.8 ± 167.2 ng/g ww).

Mean feather Hg concentration was 1564.6 ± 367.2 ng/g dw at regulated and 1149.0 ± 152.1 ng/g dw at unregulated streams (Fig. 3.11, Appendix 42). Although feather Hg concentration was significantly higher in birds with higher blood δ^{34}S (β=0.040, Adj. S.E.=0.011, p<0.001), the inclusion of blood δ^{34}S did not improve model fit over the null model, suggesting no major influence on feather Hg (Fig. 3.12). Feather Hg concentration was not explained by stream type, elevation, nor the presence of anadromous salmon (Table 3.7), but Douglas (mean 3338.6 ± 819.0 ng/g dw) and Madeley Creeks (mean 2311.1 ± 802.6) both supported dippers with relatively high feather Hg concentrations (Fig. 3.11; Appendix 44).

Across all individual dippers, blood δ^{34}S was a fairly strong correlate with feather Hg ($r=0.46$, $p<0.001$, $n=59$ for regulated streams and $r=0.48$, $p<0.0012$, $n=38$ for unregulated streams; Fig. 3.12). Trophic position was correlated with feather Hg at regulated streams ($r=0.48$, $p<0.001$, $n=59$), but not unregulated streams ($r=0.12$, $p=0.47$, $n=38$). Blood δ^{13}C showed a weak negative correlation with feather Hg at unregulated streams ($r=-0.28$, $p=0.092$, $n=38$), but not at regulated streams ($r=-0.060$, $p=0.66$, $n=59$; Fig. 3.12).

Table 3.7 Model selection results testing for differences in dipper feather Hg (log10) between regulated and unregulated streams using a linear mixed effects model. Stream type, elevation, salmon, blood δ^{34}S, blood δ^{13}C, trophic position, and interactions between type*elevation were included as fixed effects and stream and year were included as random effects. Models with weight>0 and the null (intercept-only) are presented for comparison.

Response	**Model Structure**	**AICc**[1]	**Δ AICc**	**Deviance**[2]	**Model Weight**	**df**
Feather Hg ($\log_{10}$)	Blood δ^{34}S	**25.4**	**0**	14.79	**0.59**	**5**
	null	26.2	0.71	17.73	0.41	4

[1] Akaike's Information Criterion, corrected for small sample sizes

[2] -2 (Log Likelihood)

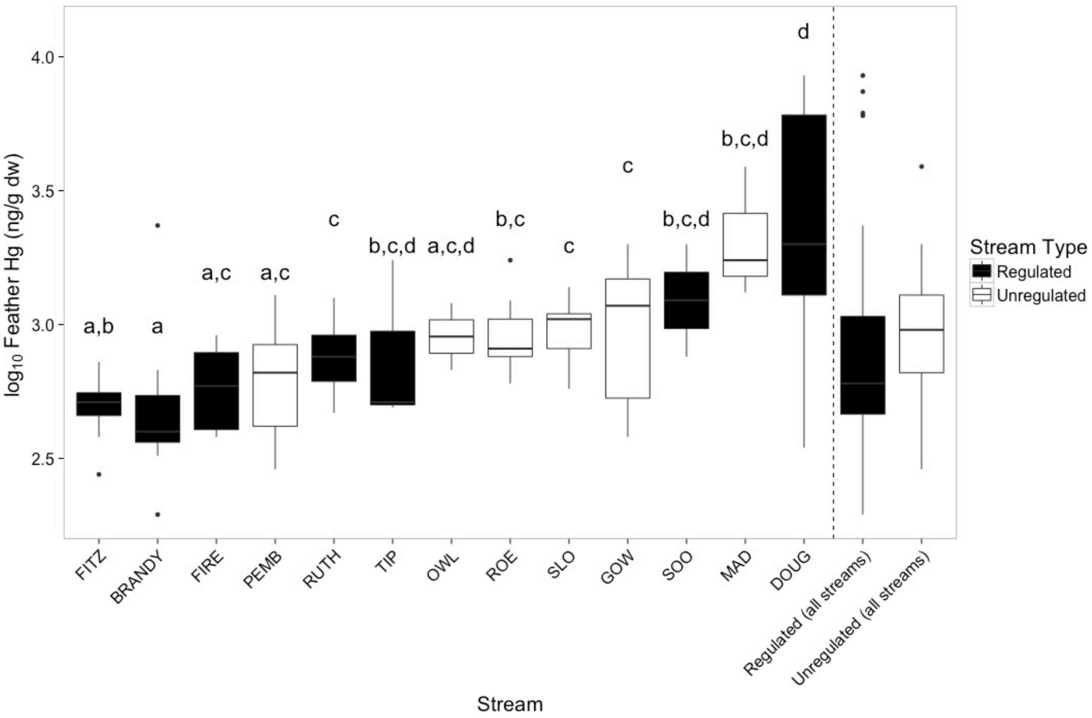

Figure 3.11 Comparing American Dipper feather (log$_{10}$) Hg concentrations (ng/g dw) between regulated (n=59) and unregulated (n=38) streams. There was no model support for effects of stream type, salmon, or elevation on feather Hg. Streams sharing a common letter are not significantly different in feather Hg (p-value>0.05 from *post-hoc* Tukey test).

Blood and feather Hg were strongly correlated in individuals at both regulated (r=0.78, p<0.001, n=53) and unregulated streams (r=0.58, p<0.001, n=38) suggesting that dietary Hg exposure did not change between fall sampling and the late summer moult (Figure 3.13).

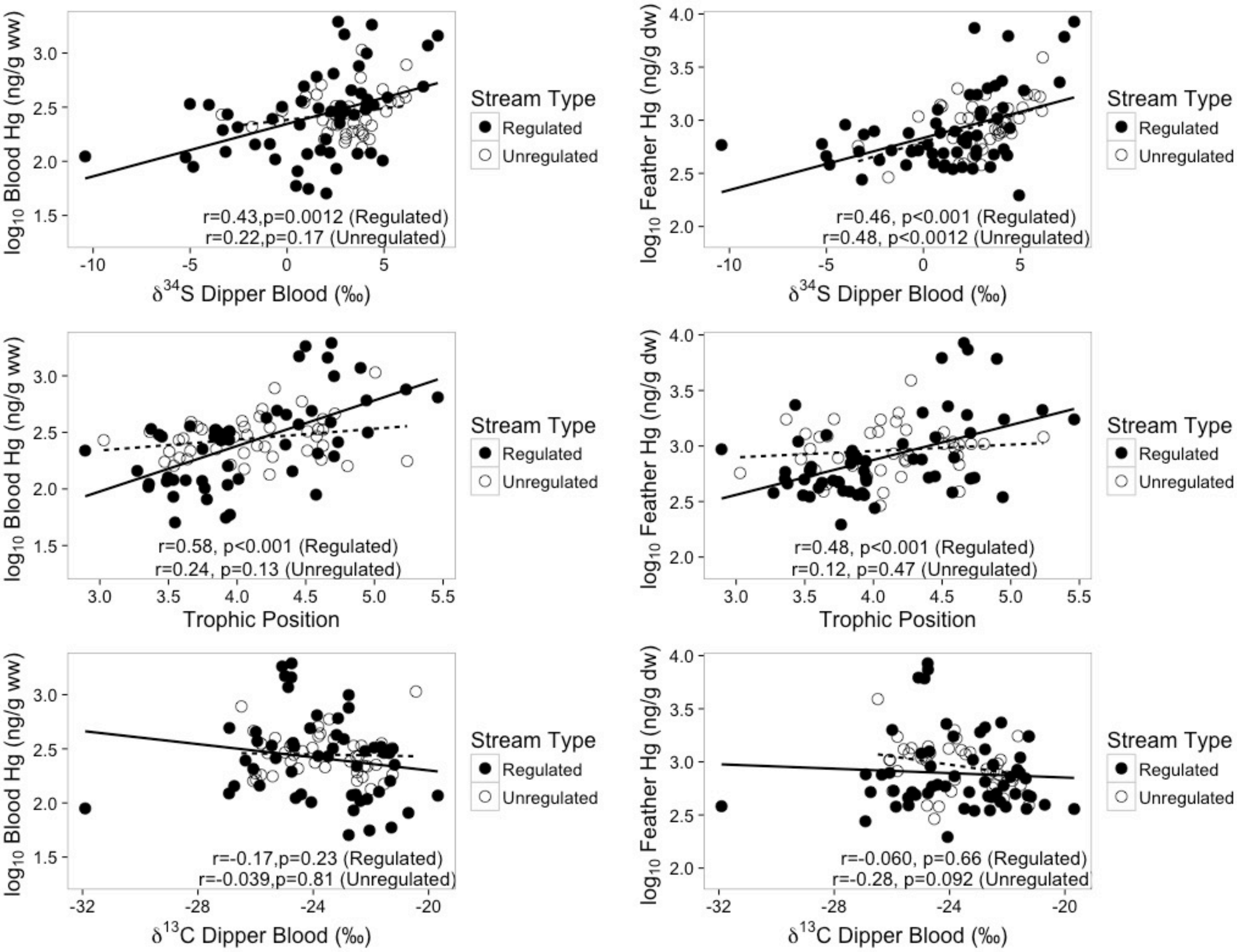

Figure 3.12 Pairwise multiple correlation analysis of trophic position, blood δ^{34}S, and blood δ^{13}C with American Dipper blood and feather Hg. Pearson correlation coefficients (r) were calculated for each stream type.

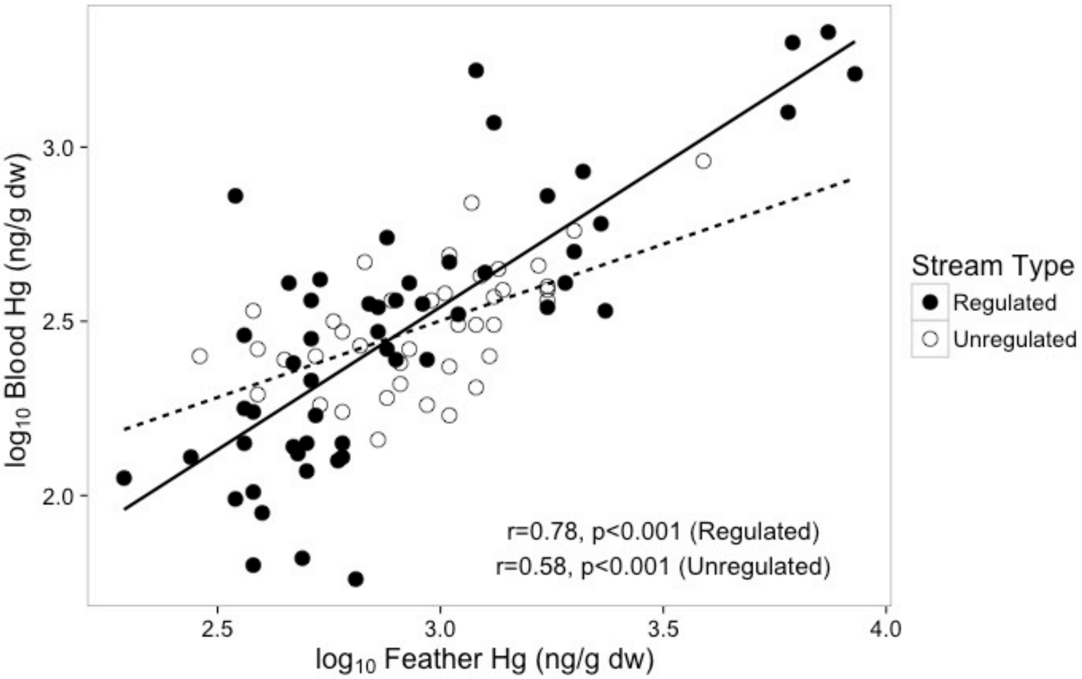

Figure 3.13 Relationship between American Dipper individual whole blood and feather Hg at regulated and unregulated streams. The high correlation between blood and feather Hg at these streams suggests consistent Hg exposure and limited movement between the summer feather moult and autumn blood sampling, particularly at regulated streams.

I did not observe any significant correlations between blood Hg and dipper body condition (Equation 2.1) or morphometrics (Fig. 3.14). There were no significant correlations between feather Hg and body condition or morphometrics. Blood Hg had a weak negative correlation with body condition index at unregulated streams (r=-0.20, p=0.21, n=39) and with wing chord length (r=-0.13, p=0.37, n=53) and tarsus length (r=-0.29, p=0.034, n=53) at regulated streams (Fig. 3.14). An unusual bill deformity was encountered in a hatch-year (HY) dipper at Douglas Creek (Figure 3.15). This young-of-year dipper had a second, smaller bill that exhibited some independent movement from the separate, anatomically normal bill (length=14.8mm). Body condition and other morphometrics in this HY were comparable to other dippers in this study, suggesting no impairment to foraging. This individual had relatively low blood Hg compared to other dippers captured at Douglas Creek (348.4 ng/g ww), but feather Hg (1736.8 ng/g dw) was comparable to other birds captured at this stream and elevated relative to dippers captured at other regulated and unregulated streams.

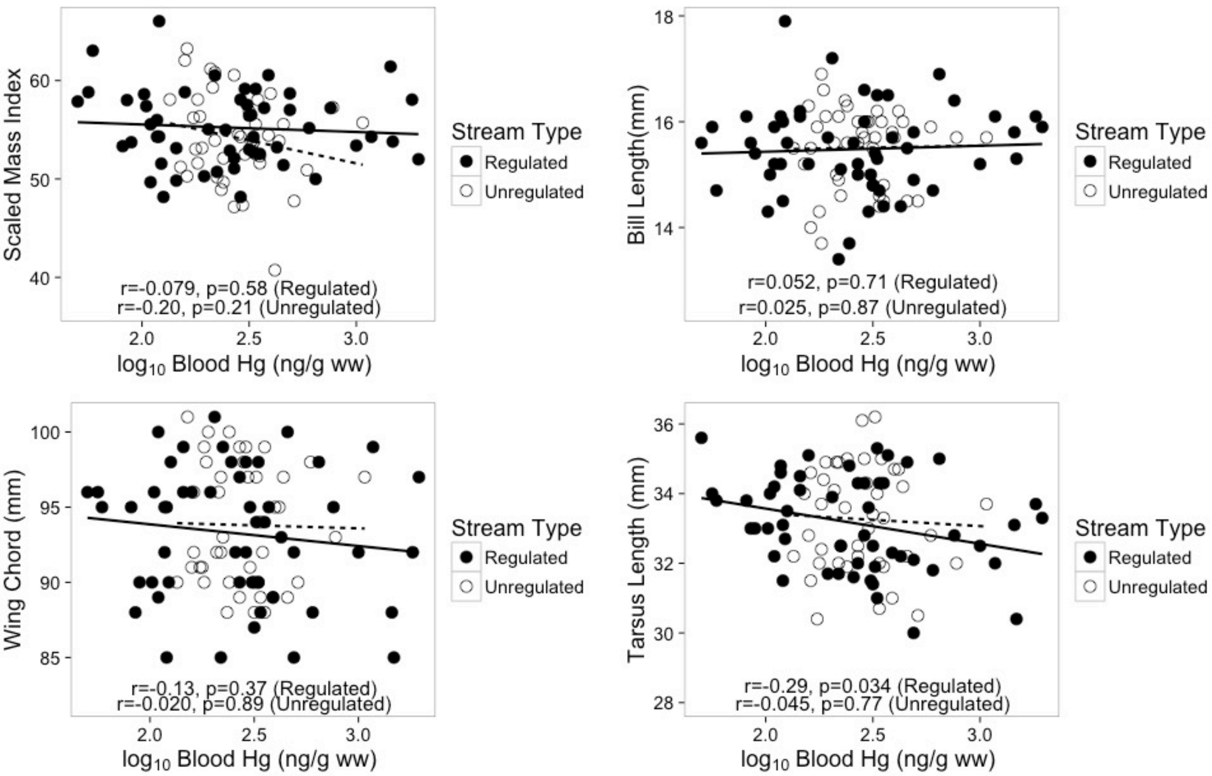

Figure 3.14 American Dipper body condition (represented by a scaled mass index) and morphometrics (wing chord, tarsus, and bill length) as a function of blood Hg ($\log_{10}$) at regulated and unregulated streams.

Figure 3.15 A bill abnormality observed in a hatch-year American Dipper captured at Douglas Creek, a RoR-regulated stream in the Harrison watershed of southwestern British Columbia. The primary bill measured 14.8mm, while the smaller bill was 13.9mm long and consisted of separate upper and lower rhomphotheca (the thin keratin sheath). The smaller bill exhibited independent movement from the separate, anatomically normal bill. Photos by: V. Norbury.

I did not identify any significant relationships or trends between dipper diet and blood or feather Hg concentrations (Figure 3.16).

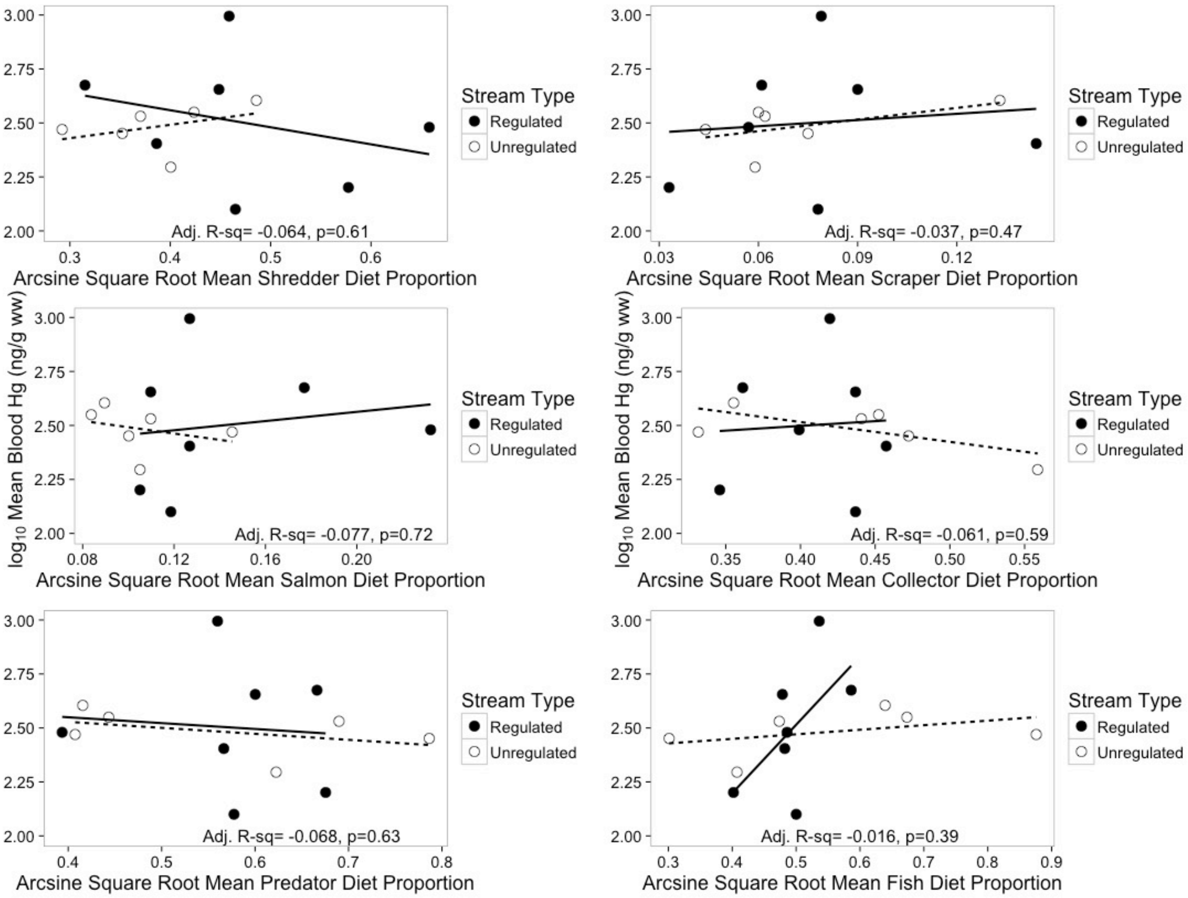

Figure 3.16 The relationship between mean American Dipper blood Hg (log$_{10}$) as a function of mean diet proportions (arcsine square-root). Diet was defined as the proportional contribution of different invertebrate foraging guilds and fish sources (Shredders, Scrapers, Collectors, Predators, Anadromous Salmon, and Resident Fish) to individual birds occupying regulated and unregulated streams. Diet proportions were estimated from Bayesian mixing models in MixSIAR.

3.3.3 Elevated Hg concentrations in dippers foraging at Douglas Creek

Since dippers captured at Douglas Creek (n=12) had significantly higher blood and feather Hg concentrations compared to many other regulated and unregulated streams (Fig. 3.10, 3.11; Appendices 43, 44) and exceeded published toxicity thresholds of 1000 ng/g known to cause reproductive impairments in terrestrial and aquatic birds (Ackerman *et al.*, 2016), I decided to further investigate the potential sources of MeHg at this stream. Dippers at Douglas

Creek were feeding at relatively high trophic position compared with other streams sampled in this study, though not significantly higher than some regulated streams (Tipella Creek, Soo River) or unregulated streams (Owl Creek, Sloquet Creek, Gowan Creek, Madeley Creek) (Fig. 3.17, Appendices 18-20). Blood δ^{34}S was also relatively high at Douglas Creek (Figs. 3.3, 3.17) compared with other regulated streams (Appendix 14). Blood δ^{13}C (Fig. 3.17, Appendices 16-18) and body condition (Fig. 2.7) in dippers at Douglas Creek were comparable to the other streams sampled in this study. Estimated diet proportions for dippers at Douglas Creek were not markedly different from other regulated or unregulated streams (Appendix 35), dominated by predators (28 ± 15 %), resident fish (26 ± 8 %), shredders (20 ± 12 %), and collectors (17 ± 11 %), with minimal contributions from scrapers (7.9 ± 7.2 %) and salmon (1.6 ± 1.6 %).

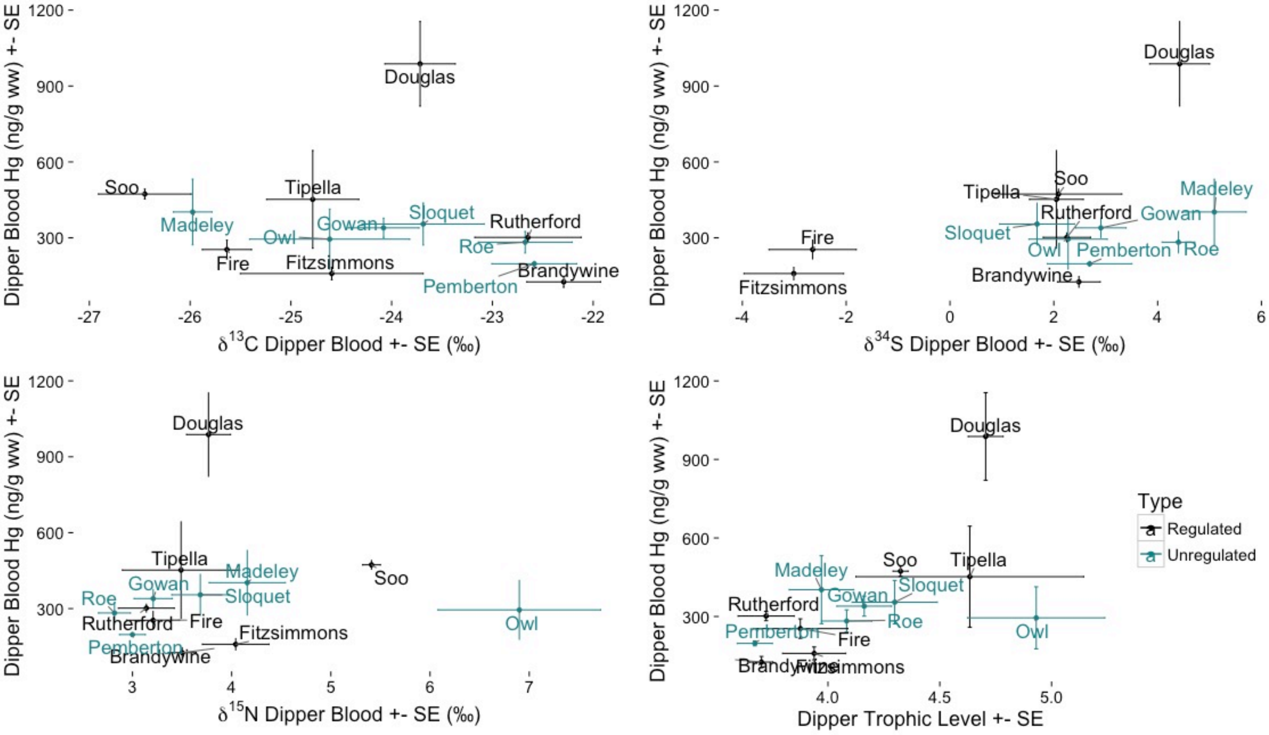

Figure 3.17 Stream-level differences in the relationships between blood stable isotopes of Carbon, Sulfur, and Nitrogen or trophic position with mean blood Hg in American Dippers of Southwestern British Columbia.

To investigate the source of MeHg at Douglas Creek, total Hg was measured in periphyton and benthic macroinvertebrates (Perlidae) sampled along a longitudinal gradient relative to the dam. Headpond periphyton had the highest Hg content of any other periphyton or invertebrate sample taken upstream or downstream of the dam (Figure 3.18). Hg was elevated in Perlidae sampled within the headpond compared with Perlidae sampled 500m upstream of the dam. Elevated Hg was also observed below the dam and 500m downstream, but decreased ~ 2 km downstream from the tailrace to levels similar to those measured 500 m upstream of the dam. Whole body Hg measured 98.54 ng/g dw in one opportunistically captured Coastrange Sculpin 500m upstream of the dam, compared with 180.5 ± 35.2 ng/g dw in headpond periphyton. Periphyton sampled from headponds and immediately below dams was typically more filamentous and abundant than other stream reaches, which had more biofilm-like growth.

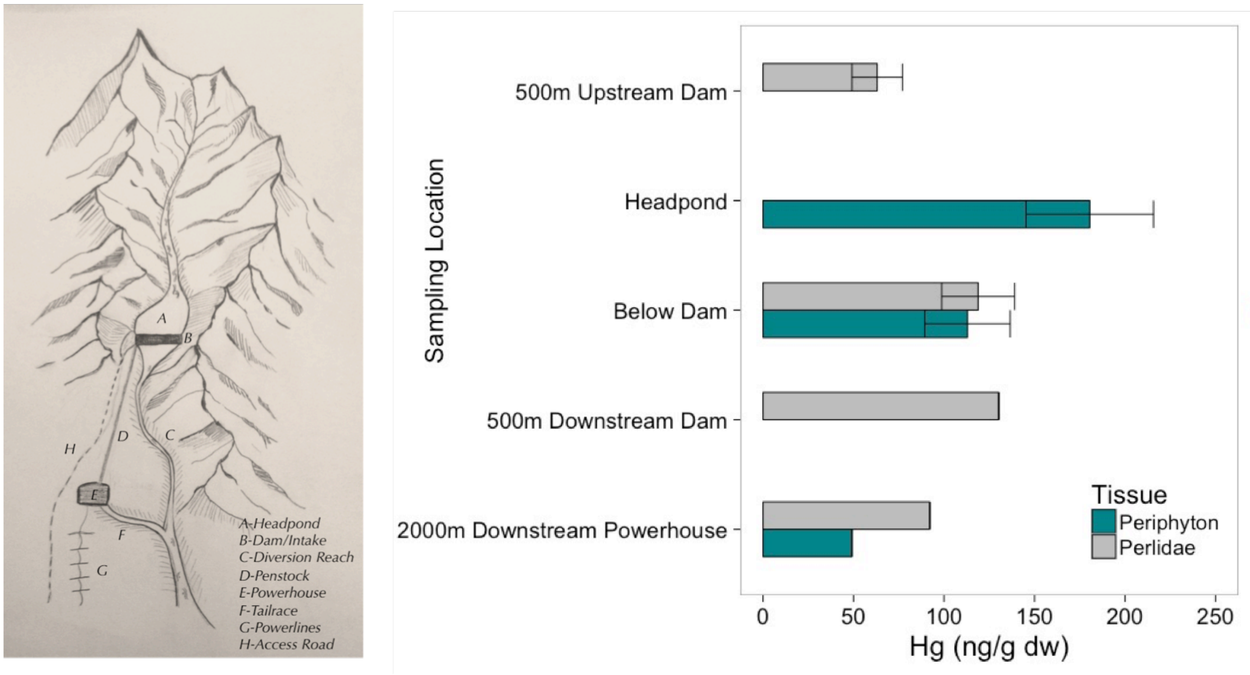

Figure 3.18 Longitudinal patterns in Hg concentrations of Douglas Creek predatory invertebrate (Perlidae) and periphyton samples. A pattern of elevated Hg in periphyton in the headpond and in predatory invertebrates and periphyton below the dam compared with upstream and >500 m downstream was observed. Headpond periphyton samples had higher Hg than any benthic samples from Douglas Creek.

Headpond periphyton was ^{34}S-depleted relative to samples from directly below the dam and 2 km downstream of the powerhouse; unfortunately, I was unable to collect a periphyton sample from 500 m upstream of the dam, as upstream reaches were heavily shaded (Fig. 3.19).

Benthic macroinvertebrates from below the dam were also ^{34}S-depleted compared with 500 m upstream of the Douglas Creek dam. Interestingly, invertebrate samples from 500 m upstream of the dam were ^{34}S-enriched compared with 2 km downstream of the powerhouse, where Pacific salmon were observed, suggesting influences of stream physicochemistry at this site.

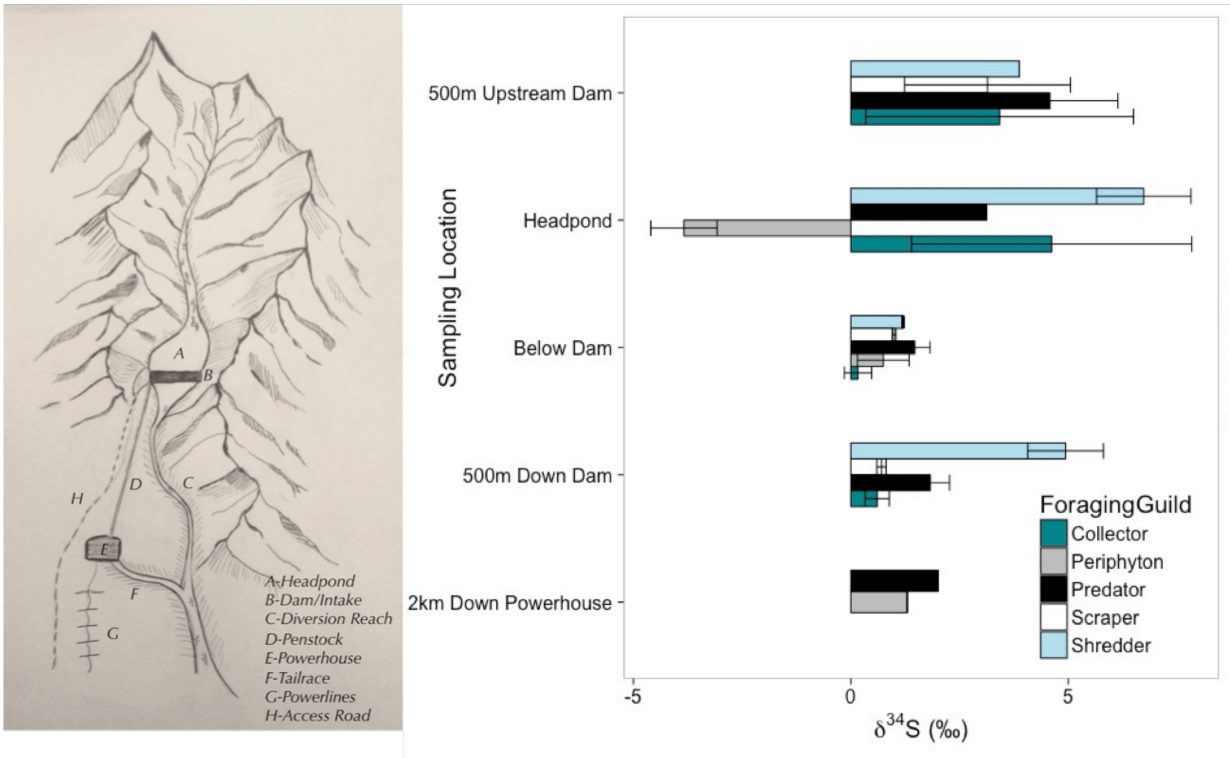

Figure 3.19 Longitudinal patterns in δ^{34}S of Douglas Creek benthic macroinvertebrate foraging guilds and periphyton. Headpond periphyton were ^{34}S-depleted relative to all other samples. Invertebrates sampled below the dam were ^{34}S-depleted relative to 500 m upstream of the dam.

Regulated streams surveyed in this study, including Douglas Creek had near-neutral pH (most-recently measured at 6.08-7.25 in 2013 by Innergex), though average pH measured at Douglas has declined from 7.4 in 2010 to 6.08 in 2013 (data provided by Innergex). Tannins released from flooded forests may decrease stream pH, with negative impacts to dipper productivity related to reduced eggshell thickness (Ormerod *et al.*, 1988) or elevated MeHg bioavailability (Lavoie *et al.*, 2013). Although I did not measure stream pH in this study, it is possible that acidity is a factor influencing MeHg production in these systems, as Common Loon are at highest toxicological risk to MeHg when stream $pH<6.7$ and chick blood $Hg > 1.4$ µg/g dw (Scheuhammer *et al.*, 2016).

There were potential watershed-level effects on dipper Hg exposure and isospace (Fig. 3.20), though it is not possible to disentangle effects of watershed and stream type on these variables, since I was unable to test the watershed*stream type interaction. The Harrison watershed supported dippers with significantly higher blood Hg than the Squamish ($\beta=0.47 \pm 0.17$, $p=0.016$) and Lillooet ($\beta=0.38 \pm 0.15$, $p=0.031$) watersheds, though this may be related to effects of river regulation, since both streams sampled from the Harrison watershed (Douglas and Tipella Creek) were regulated by RoR dams. Though feather Hg was not significantly different between watersheds ($p>0.18$), the Harrison watershed did support dippers with the highest feather Hg concentrations. Dippers in the Harrison watershed were also feeding at significantly higher trophic position than the Squamish ($\beta=0.72 \pm 0.26$, $p=0.017$) and Lillooet ($\beta=0.62 \pm 0.23$, $p=0.019$) watersheds. Blood $\delta^{13}C$ was not significantly different between the three watersheds ($p>0.75$), but dippers in the Squamish watershed had significantly higher blood $\delta^{34}S$ ($\beta=3.31 \pm 1.35$, $p=0.038$) and significantly different blood isospace ($\beta=-3.34 \pm 1.40$, $p=0.044$) than the Lillooet watershed.

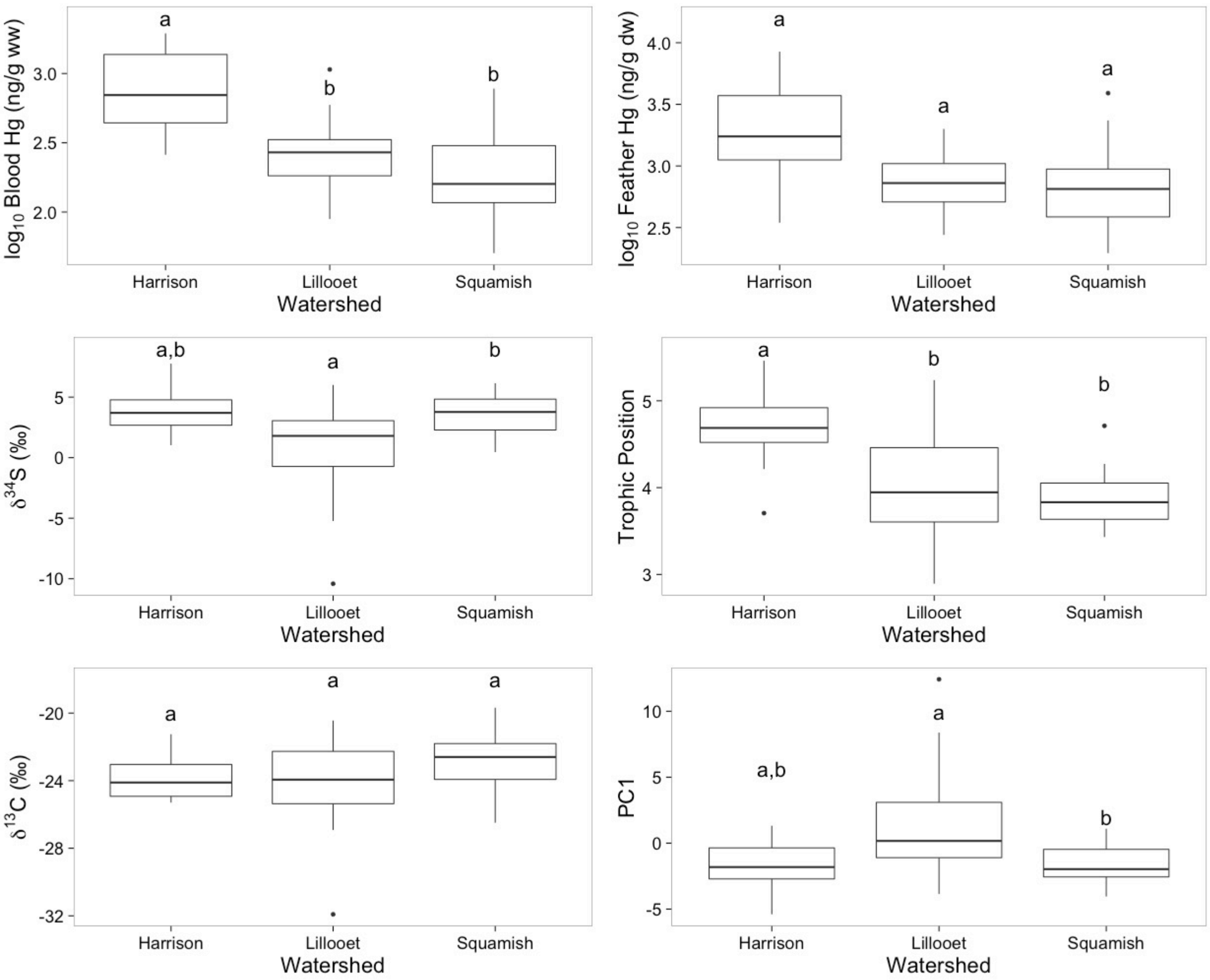

Figure 3.20 Exploring watershed-level differences in American Dipper blood and feather Hg exposure and blood isospace (δ^{13}C, δ^{34}S, and trophic position (see Equation 3.1), represented by PC1, the combination of linearly-transformed isotopes and trophic position accounting for the highest amount of variation in blood isospace). Watersheds sharing a common letter are not significantly different with respect to the measured variable ($p>0.05$), as indicated from a *post-hoc* Tukey HSD test.

3.4 DISCUSSION

3.4.1 Overview

The observation of significantly lower δ^{34}S immediately below RoR dams compared with 500 m upstream of the dam supports the hypothesis that headponds above RoR dams are environments potentially supporting the activity of anaerobic, sulfate-reducing bacteria. By comparison, there was no significant difference in invertebrate δ^{34}S sampled upstream and downstream of unregulated streams. Despite my observation of distinct dipper isospace between stream types (driven by ^{34}S-depletion), I did not observe higher Hg concentrations at regulated streams, with the exception of one regulated stream, Douglas Creek. While blood Hg concentrations remained low at the majority of regulated streams, stream conditions, watershed-level Hg contamination, and foodweb structure (relatively high dipper trophic position) at Douglas Creek likely facilitated the significantly higher blood and feather MeHg measured at this site.

Having predicted an inverse relationship between blood Hg and blood δ^{34}S, I was surprised to find that blood δ^{34}S was a positive predictor of Hg exposure and dippers. Dippers sampled at the regulated stream with the highest Hg concentrations, Douglas Creek, also had relatively high blood δ^{34}S. By comparison, dippers had the lowest Hg concentrations at two regulated streams, Fitzsimmons and Fire, where dipper blood δ^{34}S was also the lowest observed across all study streams. While it is established that Hg increases with δ^{34}S in response to salmon subsidy, I had predicted a negative correlation between blood δ^{34}S and Hg exposure to reflect microbial activity within the headponds. Since salmon had a negligible contribution to dipper diet across all stream types, the positive relationship across sites I observed between blood δ^{34}S and Hg is most-likely driven by a combination of a) the availability of rainbow trout prey and shredding invertebrates contributing to relatively high trophic position of dippers at Douglas and Madeley Creeks, b) stream and watershed sulfur geomorphology, and/or c) the limited extent of the data, with any relationships driven primarily by the stream isotopic and Hg profile at Douglas Creek.

With a low salmon contribution to the dipper diet and the absence of a known anthropogenic Hg point source, some increases in Hg concentrations recorded at Douglas Creek may be explained by active MeHg production within that headpond. My measurement of high Hg and low δ^{34}S in headpond periphyton compared with upstream and downstream of the dam supports the proposed pathway of MeHg production in regulated streams. Increased Hg methylation due to anaerobic, sulfate-reducing conditions may occur at other RoR dams, but my data suggest that most RoR operations in my study area have MeHg concentrations comparable to free-flowing streams. Dippers also did not show predictable responses of increased Hg with depleted δ^{34}S. Stable isotopes of sulfur appear to be a useful tracer of MeHg production at the stream-level, but confounding effects of marine subsidies and geochemistry may restrict the utility of this isotope for comparing MeHg exposure among different water bodies or among birds that forage both upstream and downstream of a single RoR dam. 3.4. Comparing dipper isospace and assimilated diet to nearby watersheds

While dipper whole blood δ^{13}C and trophic position were not significantly different between stream types, δ^{34}S was significantly lower at regulated streams. I did not observe the expected negative relationship between δ^{34}S and blood and feather Hg, likely due to catchment-level differences in stream δ^{34}S and Hg profiles. Although regulated streams had significantly lower invertebrate δ^{34}S signatures overall compared with unregulated streams, Douglas Creek, the site with elevated Hg, had relatively high δ^{34}S. The measurements of consistently lower invertebrate δ^{34}S below RoR dams compared with upstream, however, does support the hypothesis that the source of the depleted dipper blood sulfur is sulfate-reducing bacteria within headponds, rather than a lack of salmon subsidy at these high elevation streams. If salmon presence was the driver of elevated δ^{34}S at regulated streams, I would have expected elevated invertebrate and blood δ^{13}C and δ^{15}N, as both of these isotopes trace salmon-derived lipids that may persist over winter in American Dippers (Morrissey *et al.*, 2012). Therefore, the absence of enrichment in blood δ^{13}C at salmon-bearing streams suggests negligible contribution to the diet of these dippers, as dippers consuming more salmon are known to produce eggs enriched in ^{13}C (Morrissey *et al.*, 2012) and the same pattern would be expected for blood. Since stream biota are highly variable in their δ^{34}S signatures, driven by distinct stream geomorphology and hydrology (Nehlich, 2015), the consistently low invertebrate and dipper blood δ^{34}S observed at regulated streams is compelling evidence for microbial activity occurring under anaerobic conditions in headponds.

Dippers captured at mountain streams in this study were feeding on substantially less salmon (<2 % of diet) than reported in the Chilliwack watershed (mean of 42 ± 7 % for river residents and 22 ± 6 % for tributary migrants, Morrissey *et al.*, 2004b). This could be due, in part, to seasonality, as dippers in this study were sampled during the fall salmon spawn, whereas dippers in the Chilliwack study were sampled during the breeding season (April), which coincides with peak salmon fry abundance (Morrissey *et al.*, 2004b). Salmonid eggs, however, would have been available to dippers during the fall spawn if they inhabited my study streams; therefore, the absence of enrichment in dipper blood δ^{13}C suggests a low salmon contribution, as dippers consuming salmon are known to produce eggs enriched in ^{13}C (Morrissey *et al.*, 2010a; Morrissey *et al.*, 2012). Anadromous Pacific salmon are well-described sources of marine derived nutrients, with tissues consistently enriched in ^{13}C, ^{15}N, and ^{34}S (Naiman *et al.*, 2002). Mean dipper blood δ^{13}C at regulated (-23.7 ± 2.1 ‰) and unregulated (-23.7 ± 1.6 ‰) streams resembled the signature of breeding Chilliwack River tributary migrants (-24.6 ± 1.4 ‰), which are known to consume less salmon than Chilliwack River residents that have relatively enriched signatures of -21.6 ± 1.5 ‰ (Morrissey *et al.*, 2004b).

Dippers in this study were primarily feeding on invertebrates and resident freshwater fish, with the foodweb dominated by terrestrial inputs at both stream types. Mean EPT invertebrate δ^{13}C signatures ranged from -27.6 ± 1.9 ‰ upstream to -26.4 ± 2.9 ‰ below dam at regulated streams and -26.2 ± 1.7 ‰ to -26.6 ± 2.0 ‰ at unregulated streams, which is close to -28‰, the highly conserved value of terrestrial leaf litter (France, 1995a). All stream riparian zones were dominated by mixedwood canopy (primarily Western Hemlock, Wester Red Cedar, Douglas Fir, Bigleaf Maple) and deciduous shrub understory, resulting in fairly high leaf litter inputs during the time of fall sampling. I also observed retention of leaf litter and woody debris in some of the RoR headponds, particularly the larger ones, such as Douglas Creek and Soo River. In comparison, Chillwack River resident EPT larvae δ^{13}C was -25.4 ± 1.1 ‰, reflecting the significant anadromous salmon subsidy to this river (Morrissey *et al.*, 2004b). Similar to dippers in this study, Chilliwack tributaries supported EPT larvae with an average δ^{13}C value of -27.7 ± 0.9 ‰ (Morrissey *et al.*, 2004b). Further support for allochthonous inputs dominating at these streams is the relatively low contribution of scraping invertebrates (Heptageniidae) to the dipper diet, averaging only 8 ± 3.5 % at regulated streams and 7 ± 3.1 % at unregulated streams.

Stable isotope mixing models also supported a slightly higher mean proportion of shredders in the diet of dippers foraging at regulated streams (21 ± 9.4 %) than unregulated streams (15 ± 4.6 %). I expected to see a higher proportion of shredding invertebrates (*e.g.* Limnephiliidae) at regulated streams, as they are characteristic of a) pool habitat and b) terrestrial inputs, and likely to respond to nutrient retention (leaf litter) or the influx of nutrients in the headponds. Limnephiliids are also reportedly tolerant of Hg contamination (Henny *et al.*, 2005). The estimated increase in shredder consumption at regulated streams is consistent with my observation of numerous empty limnephillid cases along headpond perimeters and immediately below the dam cascades on "anthropogenic foraging platforms", where dippers were often observed foraging.

3.4.3 Relevance of dipper Hg concentrations compared with other insectivorous passerines and avian piscivores across North America

Relative to other uncontaminated streams in the Pacific Northwest and Eastern North America, average dipper blood and feather Hg concentrations at mountain streams in the Squamish, Lillooet, and Harrison watersheds are fairly high (Tables 3.8, 3.9). With the exception of Douglas Creek and one sample from the Soo River, dipper blood Hg concentrations remain below published toxicity thresholds of 1000 ng/g (Ackerman *et al.*, 2016; Jackson *et al.*, 2016), known to cause reproductive and physiological impairments in several avian species (Burgess and Meyer, 2008; Franceschini *et al.*, 2009; Jackson *et al.*, 2011; Frederick and Jayasena, 2010) and are low compared with Hg concentrations measured in aquatic and terrestrial passerines consuming invertebrates at historically contaminated rivers across Eastern North America (Table 3.8).

The relatively high Hg concentrations observed in this study compared with other uncontaminated sites across North America, however, challenge the established geographic trend in Hg increasing from west to east across the continent (Evers *et al.*, 1998; Evers *et al.*, 2007; Depew *et al.*, 2013) and support more recent observations of elevated Hg exposure in predatory birds in western North America (Ackerman *et al.*, 2016; Jackson *et al.*, 2016). In the absence of anthropogenic point sources (including RoR dams) and biotransport by anadromous salmon, the Hg concentrations recorded at these streams are best explained by increased atmospheric deposition at high elevation aquatic environments, which is known to influence exposure in piscivorous (Guigueno *et al.*, 2012) and insectivorous (Rimmer *et al.*, 2005) birds.

Blood Hg concentrations are consistently higher in songbirds residing in wetland habitats (freshwater or estuarine) than upland forests (Jackson *et al.*, 2015), but high elevation aquatic habitats may experience even higher exposure. High elevation, heavily forested streams suitable for RoR dams may be sinks for atmospherically-deposited Hg from glacial meltwater or leaf litter. Hg concentrations in the feathers of nestling Osprey (*Pandion haliaetus*) increased with increasing modeled atmospheric deposition and reduced lake size, in response to the accumulation of Hg in glacial meltwater (Guigueno *et al.*, 2012). Bicknell's Thrush (*Catharus bicknelli*) inhabiting montane riparian zones with increased leaf litter inputs experienced higher blood and feather Hg exposure (Rimmer *et al.*, 2005), as leaf litter acts as a pool of Hg that can become methylated under suitable conditions (Miller *et al.*, 2005).

Densely forested, temperate streams may also experience elevated MeHg production through non-vascular plants, including mosses. It is thought that aquatic moss provides the architechture for a biofilm where total Hg is recycled and methylated. This has been demonstrated through laboratory uptake kinetic studies with the aquatic moss, *Fontinalis antipyretica*, which exhibited a high capacity to magnify Hg levels in water, even at very low concentrations (0.1 μg/l) increasing from 0.978 to 4860 ng/g (Diaz *et al.*, 2012). Tsui *et al.* (2009) measured higher MeHg concentrations in streams where the periphyton community shifted to dominance by filamentous algae rather than a benthic biofilm, and suggested that filamentous algal mats harbor more methylating bacteria (with MeHg accounting for 50-100 % of the total Hg). Periphyton growing on the rocky shore of an oligotrophic boreal shield lake also bioconcentrated Hg and are significant sources of MeHg to aquatic consumers, since the epilithic biofilm methylates Hg by housing sulfate-reducing bacteria (Desrosiers *et al.*, 2006). Desrosiers *et al.* (2006) measured methylation rates of periphyton in-lab and discovered that MeHg production rates were reduced by 60 % with the addition of an inhibitor of sulfate-reducing bacteria, by 40 % by an algal inhibitor, and by 40 % with a prokaryote inhibitor, revealing that sulfate reducing bacteria and other microorganisms may contribute to Hg methylation of periphyton. Non vascular plants (mosses, lichen, fungi) typically have higher Hg concentrations than those measured in vascular plants (Moore *et al.*, 1995 in Grigal *et al.*, 2002).

Table 3.8 Comparison of American Dipper whole blood Hg concentrations (mean, range, and S.E.) measured in insectivorous adult passerines (aquatic and terrestrial) across North America. Entries are presented in descending order of mean blood Hg and results from this study are bolded.

Species[1] (n)	Location	Habitat	Mean (range) Blood Hg (ng/g) ww	S.E. Blood Hg ww	Source
REVI (5)	South River, Virginia	Hg-contaminated river	6720	4600	Cristol *et al.,* 2008
CARW (49)	South River, Virginia	Hg-contaminated river	4490	2270	Cristol *et al.,* 2008
TRES (78)	South River, Virginia	Hg-contaminated river	3660	2420	Cristol *et al.,* 2008
CARW (17)	North Fork Hobson River, Virginia	Hg-contaminated river forest floodplain	3380 (620-8380)	1830	Jackson *et al.*, 2011
NESP (24)	North Carolina, USA	Salt Marsh (breeding)	1070	50	Winder & Emslie (2011)
AMDI (12)	**Douglas Creek, British Columbia**	**RoR-regulated mountain stream**	**987.76 (315.38-1948.06)**	**167.23**	**This study**
NOWA (30)	New York City, New York	Riparian	420 (90-2080)	80	Seewagen, 2012
AMDI (53)	**Coastal British Columbia**	**RoR-regulated mountain streams**	**417.55 (50.52-1948.06)**	**74.07**	**This study**
TRES (57)	Shenandoah headwater, Virginia	Hg-contaminated headwater	356	2410	Brasso & Cristol, 2007
AMDI (39)	**Coastal British Columbia**	**Unregulated mountain streams**	**340.73 (134.11-1069.69)**	**42.73**	**This study**
CARW (9)	North Fork Hobson River, Virginia	Uncontaminated river forest floodplain	290 (120-520)	140	Jackson *et al.*, 2011
RWBB (9)	Kenridge Farm, New York	Aquatic	235	71	Gillet & Seewagen (2014)
NESP (13)	Ontario	Wetland (breeding)	220	20	Winder & Emslie (2011)
SWSP (30)	Southern Wisconsin	Wetland	187	106	Strom & Brady (2011)
TRES (67)	Shenandoah headwater, Virginia	Uncontaminated Headwater	170	150	Brasso and Cristol, 2007
NESP (47)	North Carolina, USA	Salt Marsh (wintering)	140	20	Winder & Emslie (2011)
SWSP (40)	Northern Wisconsin	Wetland (acidic)	135	64	Strom & Brandy (2011)
BITH (43)	Mt. Mansfield, Vermont	Montane Forest	94	470	Rimmer et al., 2005
YRWA (13)	Mt. Mansfield, Vermont	Montane Forest	91	55	Rimmer *et al.*, 2005
RWBB (5)	Bronx River, NY	Aquatic	61	16	Gillet & Seewagen (2014)
BLPW (10)	Mt. Mansfield, Vermont	Montane Forest	55	17	Rimmer *et al.*, 2005

[1] Red-Eyed Vireo (REVI), Carolina Wren (CARW), Tree Swallow (TRES), Eastern Phoebe (EAPH), Rough-Winged Swallow (RRSW), Nelson Sparrow (NESP), American Dipper (AMDI), Northern Waterthrush (NOWA), Red-Winged Blackbird (RWBB), Swamp Sparrow (SWSP), Bicknell's Thrush (BITH), Yellow-Rumped Warbler (YRWA), Blackpoll Warbler (BLPW)

3.4.4 Pathways of MeHg exposure in dippers foraging in RoR headponds and free-flowing mountain streams

Elevated MeHg concentrations have been previously documented in American Dippers consuming large amounts of salmon (Morrissey *et al.*, 2005; Morrissey *et al.*, 2012) and in dippers residing on rivers historically contaminated by cinnabar and gold mining activity (Henny *et al.*, 2005) (Table 3.9). Dippers at Douglas Creek had blood and feather Hg exceeding some published toxicity thresholds for birds, despite low salmon consumption and no known anthropogenic Hg point source. American Dippers captured at Douglas Creek had feather Hg concentrations surpassing those reported in feathers from streams historically contaminated by cinnabar and gold mining (Table 3.9). Maximum dipper blood Hg values measured at Douglas Creek exceeded mean concentrations measured in Common Loon blood across North America (1730 ± 60 ng/g, n=644), a high-trophic level bird known to accumulate high levels of MeHg through its piscivorous diet (Evers *et al.*, 2008). By comparison, White-throated Dippers sampled on non-salmon bearing streams had undetectable Hg concentrations in their eggs (Morrissey *et al.*, 2010a). Although the relationship between dipper blood δ^{34}S and Hg was not straightforward in these systems, the most parsimonious explanation for the elevated Hg measured in dippers at Douglas Creek is relatively high levels of atmospherically-deposit Hg, followed by methylation within the headponds by sulfate-reducing bacteria in filamentous periphyton, and increased biomagnification in dippers feeding at a relatively high trophic position.

As a relatively new, large, and low-velocity pool with decaying tree stumps and fine sediment, I suspected Douglas Creek to be a site of high Hg methylation potential. Age alone, however, cannot explain the elevated Hg concentrations at Douglas Creek, as two other creeks in the same watershed were regulated in the same year and Fitzsimmons Creek was regulated one year later (in 2010). Further, the Soo River, the oldest of the dams sampled (commissioned in 1994), supported dippers with relatively high blood Hg. Anaerobic conditions of the Douglas Creek headpond, indicated by ^{34}S-depleted invertebrate signatures below the dam, promote release of Hg from sediment, whereas oxic conditions favour sediment uptake of Hg (Ullrich *et al.*, 2001). Hot springs activity in the coast mountains of B.C. are a likely geological source of Hg (Nriagu, 1989; King *et al.*, 2006) at this stream and other streams in the Harrison watershed. Although further work is required to isolate the characteristics of headponds and stream physicochemistry that influence Hg-methylation at the stream-level, I have evidence to suggest that headponds are a likely site of Hg-methylation.

Table 3.9 Comparison of aquatic invertebrate and American Dipper feather Hg levels from Pacific Northwest streams containing natural and anthropogenic sources of Hg. Streams are presented in descending order of dipper feather Hg and results from this study are bolded.

Location	Hg Point Source	MeHg Source	Source THg (ng/g dw)	Source % MeHg	Source MeHg (ng/g dw)	Mean Feather Hg (ng/g dw)	SE Feather Hg	BMF Feather/ EPT	Source
Douglas Creek, B.C. (RoR-regulated)	**None**	**Perlidae (Below dam)**	**122.6 ± 12.2**[1]	**100**[2]	**122.64**	**3338.6 (346.3-8459.5)**	**819.0**	**27.2**	**This study**
Douglas Creek, B.C. (RoR-regulated)	**None**	**Perlidae (500m up)**	**63.1 ± 14.0**	**100**[2]	**63.07**	**3338.6 (346.3-8459.5)**	**819.0**	**52.9**	**This study**
Douglas Creek, BC (RoR-regulated)	**None**	**Headpond Periphyton**	**180.5 ± 35.2**	__	__	__	__	__	**This study**
Coastal B.C. Regulated streams	**None**	__	__	__	__	**1564.6 (196.2-8459.5)**	**367.18**	__	**This study**
Coast Fork Range, Oregon	Historic Cinnabar (HgS) Mine	Perlidae	201.64	103.6	208.90	1158 (590-2200)	__	5.5	Henny *et al.*, 2005
Coast Fork Range, Oregon	Historic Cinnabar (HgS) Mine	EPT larvae	197.9 (153.4-294.7)	57 (47-71)	111.9 (79.8-210.1)	1158 (590-2200)	__	10.3	Henny *et al.*, 2005
Coastal B.C. Unregulated streams	**None**	__	__	__	__	**1149.0 (290.5-3898.4)**	**152.10**	__	**This study**
Chilliwack River, BC	None	Salmon Fry	35 ± 10	100[2]	35	790	60	22.6	Morrissey *et al.*, 2005
Chilliwack River Tributaries, BC	None	EPT larvae	18 ± 4	56	10.1	580	60	57.4	Morrissey *et al.*, 2005
Row River Range, Oregon	Historic Gold Mine District	Perlidae	35.50	101.7	36.09	375 (296-453)	__	10.4	Henny *et al.*, 2005
Row River Range, Oregon	Historic Gold Mine District	EPT larvae	47.8 (29.7-80.5)	44 (21-85)	21.2 (15.3-30.1)	375 (296-453)	__	17.7	Henny *et al.*, 2005
Middle Fork Range, Oregon	None	EPT larvae	19.3 (12.9-25.2)	68(54-81)	13.1 (10.5-18.0)	267 (231-311)	__	20.4	Henny *et al.*, 2005

[1] Perlidae average from below dam and 500m downstream of the dam from 2014-2015.
[2] Assumed to be 100% MeHg, based on values reported by Henny *et al.*, 2005 for Perlidae.

My measurements of ^{34}S-depleted headpond periphyton with high Hg and nearly 2-fold higher Hg concentrations in predatory invertebrates sampled below the Douglas Creek RoR dam compared with 500 m upstream suggest microbial activity within the headpond. The Hg concentrations in periphyton sampled in the Douglas Creek headpond (180.5 ± 35.2 ng/g dw) surpass concentrations recorded in stream invertebrates inhabiting historic gold mining districts of Oregon (29.67–80.46 ng/g dw) and rival concentrations measured in stream invertebrates downstream of a historic cinnabar (HgS) mine in Oregon (153.40–294.65) (Henny *et al.*, 2005). Predatory invertebrates (Perlidae) below the Douglas Creek dam had similar Hg concentrations to Perlidae downstream of the historic cinnabar mine and over 3-fold higher than Perlidae downstream of the historic gold mine. Perlidae upstream of Douglas Creek also had higher Hg concentrations than recorded in the historic Oregon gold mine district, also suggesting a natural or anthropogenic Hg point source upstream of the Douglas Creek RoR dam that is becoming methylated in the headpond and accumulating in predatory dippers.

The relatively high trophic position of dippers foraging at Madeley and Douglas Creek and the positive correlation between trophic position and Hg exposure is consistent with the literature on MeHg biomagnification. This could be reflecting increased availability of resident trout to the dipper diet. At Madeley Creek, there is a large rainbow trout population in the lake upstream (British Columbia Fisheries Inventories Data Queries). Though my data showed no significant effect of trophic position on blood δ^{34}S (likely due to low variability in TP across streams), trophic position is a positive predictor of δ^{34}S, with a slight enrichment of δ^{34}S per trophic level and even higher enrichment in animals with high-protein diets (McCutchan *et al.*, 2003; Nehlich, 2015). Any changes in TP at Douglas Creek could confound the effect of microbial activity on the dipper δ^{34}S signal. Improved foraging efficiency on invertebrates and resident trout eggs and fry within the Douglas Creek headpond and directly below the dam likely contributed to MeHg bioaccumulation in dippers at this regulated stream.

The relatively high dipper trophic position, blood Hg, and feather Hg concentrations measured at Douglas Creek is consistent with the findings of Fanny *et al.* (2013), who suggested that the combined stressors of altered flow and metal contamination cause significant shifts in invertebrate community structure compared to altered flow regime in the absence of contamination. I suspect that characteristics of stream and riparian physicochemistry (including elevated deposition of inorganic Hg), age since indundation, dam operation, and headpond features may contribute to variation in Hg levels in foodwebs of run of river streams.

3.4.5 Body condition and morphometrics

With no significant difference in Hg exposure between regulated and unregulated streams and limited diet shifts, it is not surprising that body condition and morphometrics were uniform across stream types. The bill deformity observed in a hatch-year dipper at Douglas Creek is peculiar, since this individual had fairly high feather Hg concentrations, but low blood Hg. It is possible that, due to its age, most of the blood Hg obtained through its diet was depurated into its growing feathers, which is a mechanism for chicks to prevent MeHg toxicity (Fournier *et al.*, 2002; Kenow *et al.*, 2003; Condon and Cristol, 2009; Kenow *et al.*, 2010). Though speculative at this point, it is also possible that elevated MeHg observed in AHY dippers at this stream could produce teratogenic effects in dipper offspring. Egg-injection studies have demonstrated the capacity for MeHg to cause bill deformities in young birds (Heinz *et al.*, 2011; Braune *et al.*, 2012), but other contaminants that were not measured in this study, including selenium, also cause bill deformities (Hoffman *et al.*, 1988; Ohlendorf *et al.*, 1988).

3.4.6 Toxicological effects

While I have identified increased MeHg production potential in a RoR reservoir, uncertainty remains over whether there will be any long-term toxicological effects to reproduction or behaviour at Douglas Creek. Henny (2005) observed high nesting success in American Dippers residing on contaminated streams in Oregon (with mean feather Hg measured at 1158 (range 590-220) ng/g dw downstream of historic cinnabar mines and 375 (range 296-453) ng/g dw downstream of historic gold mines). Feather Hg concentrations in dippers at Douglas Creek (mean 3338.6 ± 819.0, range 346.3-8459.5), however, are substantially higher than those measured at these historically-contaminated sites. Tree swallows breeding along experimentally flooded reservoirs (mean blood Hg increased in nestlings increased from 1210 ± 150 ng/g ww before inundation to 2200 ± 102 ng/g ww post-flood) actually benefitted from inundation through benefits of earlier nest initiation, larger eggs, and faster growth in response to increased availability of emerging dipteran prey (Gerrard and St. Louis, 2001). Thus, Gerard and Louis (2001) concluded that reservoirs do not act as ecological traps for tree swallows nesting in riparian shrub communities modified by hydroelectric resevoirs, despite increased Hg exposure.

Unlike Tree Swallows that breed near reservoirs, feed on emerging insects, and therefore only experience transient exposure to Hg, dippers are stream obligates that may experience prolonged exposure to contaminants, as indicated by the high correlation between blood:feather Hg in the dippers of this study. Although adverse effects thresholds for adult Common Loons have been established at 3000 ng/g ww in blood (Evers *et al.*, 2008), passerines are considered more sensitive to MeHg toxicity (Heinz *et al.*, 2009), and negative effects to behaviour and reproduction have been documented at or near 1000 ng/g ww in whole blood (Frederick and Jayasena, 2010; Jackson *et al.*, 2011; Ackerman *et al.*, 2016). With a natural history intermediate between passerines and piscivorous water birds, such as the Common Loon, the sensitivity of dippers to MeHg is also likely intermediate between these taxa. Further research on their productivity and survival is necessary to address dipper response to MeHg contamination at the concentrations measured in this study.

3.4.7 Summary

Although I identified increased shredder consumption and significantly lower dipper blood δ^{34}S at regulated streams, dipper mercury exposure was not consistently or significantly different between regulated and unregulated streams. I did, however, discover that dippers residing at high-elevation mountain stream habitats experience higher mercury exposure than passerine species residing at lower elevations, presumably related to increased atmospheric deposition at high elevation, densely forested streams. I also identified one case (Douglas Creek) where a low-flow habitat modified by a RoR dam led to enhanced MeHg bioaccumulation, with periphyton as a likely source of sulfate-reducing bacterial activity. Under the combined conditions of a) high-protein prey availability and b) elevated atmospheric deposition of Hg that can be methylated by sulfate reducing bacteria, American Dippers can experience exposure to MeHg of potential toxicity concern. Although at this point I have not observe any differences in body condition between stream types, future work is needed to determine if long-term chronic MeHg toxicity can impair productivity or survival of predatory river birds.

CHAPTER 4: SYNTHESIS

4.1 HABITAT SUITABILITY OF STREAMS WITH RUN-OF-RIVER DAMS AND IMPLICATIONS FOR RIVER ECOTOXICOLOGY

Rivers provide numerous ecological and cultural services for humans and wildlife that are vulnerable to increasing demands for freshwater and renewable energy production. As it stands, nearly 2/3 of the world's large rivers are altered by dams (World Commission on Dams, 2000; Nilsson *et al.*, 2005), and an unknown number of small rivers are similarly impacted across the globe. With demonstrated negative impacts of flow abstraction on stream-dependent organisms through changes to physical habitat and contaminant exposure, streams that provide valuable ecological services cannot be taken for granted. The overarching goal of this study was to determine if flow-regulation by RoR dams alters American Dipper habitat use, diet, and exposure to MeHg. Using stable isotopes and the American Dipper as a high-trophic level bioindicator, I was able to characterize slight diet changes related to flow diversion, demonstrate MeHg production within RoR headponds, and measure MeHg biomagnification through to high-trophic level stream obligates under suitable conditions. By colour-banding and monitoring dipper populations across seasons, I documented higher adult occupancy, density and year-round residency at regulated streams and identified headponds as potential breeding habitat for a variety of waterfowl. With likely benefits of improved foraging under low-flow conditions, but potential for elevated MeHg exposure, I hypothesized habitats modified by RoR dams may act as ecological traps for resident river birds and breeding waterfowl.

At the outset of this project, I was unable to predict the response of dippers to flow abstraction, since there were both potential benefits and costs to reduced flow. Having identified clear short-term benefits to foraging and year-round habitat availability associated with flow diversion by RoR dams, the question still remains over whether these benefits are outweighed by the costs of long-term exposure to MeHg. The data presented in this thesis suggest that dippers are residing year-round at regulated streams possibly to exploit consistent and more easily attainable food resources, as a strategy to secure nesting sites, and/or to save energy from migration. Further, some rivers regulated by RoR dams provide seasonal habitat for breeding waterfowl, in particular Harlequin Ducks. I have also provided support for increased atmospheric deposition of Hg at high elevation, densely forested streams, consistent with the observations in another alpine passerine, the Bicknell's Thrush (Miller *et al.*, 2005; Rimmer *et al.*, 2005). Collectively, the features of high levels of atmospherically deposited Hg, favourable conditions for the activity of sulfate-reducing bacteria, and improved foraging efficiency at low flows in RoR headponds have the potential to facilitate substantial MeHg biomagnification in apex stream predators. This is not surprising, given beaver impoundments (Roy *et al.*, 2009a,b), experimental reservoirs (Gerrard and St. Louis, 2001) and conventional reservoirs (Rosenberg *et al.*, 1997), typically at lower elevation than my study streams, have the same effect on MeHg cycling.

In the first data chapter, I discussed three mechanisms by which RoR dams may create habitats that act as ecological traps for dippers. D'Amico's (2011) hypothesis of non-adaptive foraging under altered flow regime seems not to apply at RoR facilities with a reduced and stabilized hydrograph. In fact, dippers appear to have adapted well to foraging in these low-flow habitats, to the extent that they use features of the dam itself (cascade) as foraging platforms and feed on increasingly available limnephiliids (shredding invertebrates characteristic of lentic habitats). This is consistent with the earlier prediction that flow stabilization may decrease the energetic demands of foraging (D'Amico *et al.*, 2000). With similar diets and no difference in body condition measured between regulated and unregulated streams, I do not see this as a mechanism for an ecological trap. The second proposed mechanism of increased nest failure (by flooding or predation) requires further investigation through a long-term productivity study involving many more marked birds. I have, however, identified several species of waterbirds, woodpeckers, and passerines breeding within headponds, especially the larger Soo River, that can be studied to test this hypothesis.

The third proposed mechanism for elevated MeHg exposure is supported by my measurements at Douglas Creek, but not at some of the smaller RoR dams, such as Brandywine and Fitzsimmons Creeks. These two regulated streams, which were also the two lowest-capacity projects, supported dippers with the lowest observed blood Hg concentrations compared with all other regulated and unregulated streams. This suggests that aspects of regulatory technique (such as water retention time in the headpond) are likely influencing MeHg production potential at the stream-level. Nevertheless, long-term exposure to MeHg could have long-term impacts for the productivity of resident river birds and breeding waterbirds that experience transient exposure that coincides with the likely timing of peak MeHg production in the summer. Before concluding that RoR reservoirs act as ecological traps through the mechanism of MeHg toxicity, however, one must first demonstrate negative impacts to productivity and fitness, which will require a longer-term study.

At a theoretical level, results of this study contribute to a growing body of literature on the ecosystem-level impacts of flow abstraction to smaller streams, MeHg-cycling at high elevation streams with and without flow abstraction, and dipper biology at higher elevation, third-order streams. I have also provided support for the utility of sulfur isotopes for tracing microbial activity in streams modified by flow abstraction and contributed to our understanding of avian MeHg exposure in western North America and the aquatic-terrestrial connectivity of MeHg cycling. Though Ackerman *et al.* (2016) conducted a thorough review on avian Hg exposure across western North America and identified several hotspots of contamination, alpine stream environments remain underrepresented, despite the potential for elevated MeHg production.

4.2 RECOMMENDATIONS FOR SUSTAINABLE HYDROELECTRICITY GENERATION AND FUTURE RESEARCH

At an applied level, I have accrued multiple pieces of evidence supporting dippers as sentinels of stream health at RoR dams, including year-round residency at these streams, shifts in diet, and the detection of MeHg in their tissues. I recommend dippers as an effective bioindicator for changes to stream ecosystems impacted by flow abstraction and the application of stable isotopes in tracing food web changes and contaminant biomagnification. It should be noted, however, that dippers may experience more benefits to anthropogenic river regulation than resident and migratory fish, as they often respond positively to habitat disruptions involving infrastructure, such as bridges that provide nest sites (Loegering and Anthony, 2006). They will, however, reflect changes to the invertebrate community and contaminant biomagnification potential that can be used to assess risk for other species. With additional support for the aquatic-terrestrial connectivity of contaminants and flow abstraction, monitoring the response of this ideal indicator of interface ecological integrity would be valuable for current and future RoR projects in the Pacific Northwest and range of other dipper species. In addition to monitoring dipper populations, I recommend monitoring Hg and MeHg concentrations and the sulfur isotopic profile of stream-dependent organisms before and after RoR-regulation. To prevent MeHg production within RoR headponds, I recommend selecting sites with low levels of atmospherically-deposited Hg and maintaining adequate flow within headponds to prevent anaerobic conditions.

Current long-term monitoring guidelines for RoR dams in British Columbia emphasize the protection of fish and fish habitat (Lewis *et al.*, 2012), but the complexity of these guidelines, lack of data for older facilities, and power producer non-compliance with monitoring recommendations has left the effects of RoR-regulation on salmonids and salmonid habitat in BC largely inconclusive (Connors *et al.*, 2014). Dippers are arguably more easily and effectively monitored than fish, especially on high-elevation, steep mountain streams. I argue that the application of stable isotopes and non-lethal sampling of a high-trophic level bioindicator offers simplification to current monitoring guidelines for RoR projects in British Columbia.

As a short-term study over a large region, there are limitations to the conclusions that can be drawn from my research, but I hope to have initiated further investigation into MeHg production in RoR headponds and avian habitat use. The main question I would like to see addressed is whether year-round residency at high elevation streams has the same costs to dipper fitness as those experienced by altitudinal migrants; or, if flow stabilization has removed these costs and created the ultimate strategy, where there are no costs of delayed nesting (associated with altitudinal migration) or traditional costs of year-round residency at lower elevation (increased competition for nest sites and reduced annual survival).

I have identified several key areas for future research on the ecotoxicological impacts of RoR dams. Ideally, a before-after-control-impact study would address these questions, but with many RoR dams in place across North America, all within the range of the American Dipper, extending this study spatiotemporally could also be a reasonable approach.

1) A long-term productivity study of American Dippers at regulated and unregulated streams would be valuable for comparing the relative impacts of nest predation (by predation and flooding), and MeHg concentrations in adults, eggs, and developing young between regulated and free-flowing streams. Quantifying year-round dipper movement

through radio telemetry methods is also recommended, along with comparing the body condition of these dippers to those benefiting from large salmon subsidies, such as those in the Chilliwack watershed.

2) Further investigation into the relationship with MeHg-cycling and features of stream physicochemistry (e.g. pH) and regulation techniques (especially the retention time of water in the headpond) is highly recommended. Additionally, the relationship between dam age and MeHg cycling requires further investigation. The recently commissioned (November 2015) Tretheway Creek project in the Harrison watershed (same as Douglas Creek) would be an interesting stream to monitor.
3) A more in-depth characterization of the resident fish and invertebrate community composition upstream and downstream of impoundments is recommended to supplement diet information obtained from stable isotope analysis.
4) I recommend conducting winter surveys at these streams to compare dipper density between regulated and unregulated streams, as dippers are known to occupy stream reaches kept ice-free by hydroelectric plants (Price and Bock, 1983). Collecting a winter blood and feather sample would enable further comparison of residency between regulated and unregulated streams. I would expect a higher winter ratio of blood: feather Hg at regulated streams if dippers are indeed taking advantage of ice-free pools, rather than migrating to lower elevation reaches.
5) Habitat characteristics of the Soo River, combined with the relatively high Hg concentrations measured in the two dippers sampled at this stream, lead me to suspect elevated MeHg production within this headpond. The Soo River headpond covers a significant area, decaying trees are abundant, and there is an obvious sedimentation problem, to the point that silt needs to be manually removed from the intake area (Pers. Obs). A variety of avian species were observed breeding within the novel wetland. I recommend sampling resident river birds, breeding waterbirds, and passerines from this headpond for Hg and stable isotopes.
6) Explore Hg stable isotope fractionation as a method of tracing the activity of sulfate-reducing bacteria in headponds, which has been used effectively for other microbial pathways (Kritee *et al.*, 2008).

7) Explore the utility of bryophytes for tracing MeHg production at RoR headponds, which are demonstrated indicators of metal contamination in streams (Diaz *et al.*, 2012) and more easily collected and ubiquitous at these mountain streams than periphyton.
8) A comparison of seasonal variation in MeHg exposure between the American Dipper and Pacific Wren would be a very interesting future study to investigate a) MeHg exposure in high elevation, resident passerines and b) the effects of aquatic vs. terrestrial diets and trophic position on MeHg exposure.

4.3 CONCLUDING REMARKS

In 2014 and 2015, many watersheds in southern British Columbia experienced severe streamflow droughts (Coulthard *et al.*, 2016), defined as a sustained period of below-average stream discharge (Van Loon and Laaha, 2015). These droughts occurred as a result of record-breaking low snowpack and historic high summer temperatures, regardless of the wet winters (Coulthard *et al.*, 2016). Using Mountain Hemlock (*Tsuga mertensiana*) tree ring growth, which is sensitive to annual maximum snow depth as a results of its influence on length of growing season, and a paleoenvironmental record of seasonal drought as predictors in a dendrohydrological model, Coulthard *et al.* (2016) reconstructed summer streamflow for several basins in southern B.C. for the past ~350 years. They concluded that although the droughts of 2014 and 2015 were not as severe as those reconstructed for the mid-17th century, if the low-flow magnitudes anticipated under climate change co-occur with lowest possible natural flows, streamflow drought severities in small watersheds in south coastal British Columbia could exceed those experienced in the past ~350 years (Coulthard *et al.*, 2016).

Further, Coulthard *et al.* (2016) argue that current water management strategies in southern B.C., based on worst-case scenarios from historical streamguage data, likely underestimate the potential magnitude of natural droughts. This means that the minimum in-stream flow recommendations for independent power producers in B.C., which are based on fish-bearing status and historic flow data from gauge sites (Hatfield *et al.*, 2003), could also be flawed by the use of short-term (recommended minimum of 20 years) streamflow data. Under the simultaneous stressors of climate change-related drought and naturally high atmospheric Hg deposition, regulation of mountain streams may further exacerbate any effects of drought or MeHg exposure to stream-dependent organisms.

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APPENDIX

Appendix 1. Seasonal American Dipper density counts (mean ± S.E.) at regulated and unregulated streams in coastal British Columbia. Counts (# dippers/km) were adjusted by detection probabilities calculated from double-observer surveys and the number of banded birds sighted is indicated in brackets.

Stream	**Type**	**Fall 2014**	**Pre-Freshet**	**Post-Freshet**	**Fall 2015a**	**Fall 2015b**
Brandywine	Regulated	14.48 ± 0.48 (4)	1 ± 0.050 (1)	7 ± 0.60 (2)	4.13 ± 0.14 (4)	2.35 ± 0.23 (1)
Madeley	Unregulated	0	2.15 ± 0.10 (0)	1 ± 0.086 (0)	0	0
Fitzsimmons	Regulated	3.10 ± 0.10 (2)	0	1 ± 0.086 (0)	0	0
Roe	Unregulated	5.17 ± 0.17 (3)	1 ± 0.050 (0)	1 ± 0.086 (0)	3.10 ± 0.10 (2)	0
Rutherford	Regulated	5.17 ± 0.17 (1)	2.15 ± 0.10 (0)	1 ± 0.086 (0)	4.13 ± 0.14 (0)	0
Pemberton	Unregulated	4.14 ± 0.14 (1)	2.15 ± 0.10 (0)	2 ± 0.17 (0)	2.07 ± 0.069 (1)	0
Douglas	Regulated	7.24 ± 0.24 (1)	2.15 ± 0.10 (0)	1 ± 0.086 (0)	3.10 ± 0.10 (0)	3.53 ± 0.35 (3)
Gowan	Unregulated	0	0	1 ± 0.086 (0)	0	1.18 ± 0.57 (0)
Fire	Regulated	3.10 ± 0.10 (2)	1 ± 0.050 (0)	2 ± 0.17 (0)	0	0
Sloquet	Unregulated	2.07 ± 0.069 (1)	2.15 ± 0.10 (0)	0	1.03 ± 0.034 (0)	0
Soo	Regulated	NA	1 ± 0.050 (0)	1 ± 0.086 (0)	0	2.35 ± 0.23 (1)
Owl	Unregulated	NA	1 ± 0.050 (0)	2 ± (0)	0	0
Tipella	Regulated	2.07 ± 0.069 (0)	2.15 ± 0.10 (1)	0	0	0
Roger	Unregulated	NA	0	1 ± 0.086 (0)	0	1.18 ± 0.57 (0)
Regulated (average)		5.86 ±1.88 (2.07-14.48)	1.38 ±0.31 (0-2.15)	2.16 ±1.03 (0-8.15)	1.62 ±0.78 (0-4.14)	1.18 ±0.57 (0-3.53)
Unregulated (average)		2.27 ±1.05 (0-5.17)	1.23 ±0.36 (0-2.15)	1.33 ±0.30 (0-2.33)	0.89 ±0.47 (0-3.10)	0.34 ±0.22 (0-1.18)

Appendix 2. Estimates of *post-hoc* Tukey contrasts comparing mean American Dipper densities (# dippers/km) at regulated and unregulated streams between seasons. Significant differences are bolded.

Linear Hypothesis	**Estimate**	**S.E.**	**z value**	**Pr(>|z|)**
Fall 2015A-Fall 2014=0	-1.12	0.29	-3.91	**<0.001**
Fall 2015B-Fall 2014=0	-1.65	0.35	-4.71	**<0.001**
Post-freshet-Fall 2014=0	-0.91	0.27	-3.42	**0.01**
Pre-freshet-Fall 2014=0	-1.12	0.29	-3.91	**<0.001**
Fall 2015B-Fall 2015A=0	-0.53	0.46	-1.17	0.74
Post-freshet-Fall 2015A=0	0.21	0.39	0.54	0.98
Pre-freshet-Fall 2015A=0	0.00	0.41	0.00	1.00
Post-freshet-Fall 2015B=0	0.74	0.47	1.56	0.48
Pre-freshet-Fall 2015B=0	0.53	0.46	1.16	0.75
Pre-freshet-Post-freshet=0	-0.21	0.40	-0.53	0.98

Appendix 3. Multi-state occupancy model selection results comparing occupancy of banded and unbanded American Dippers between regulated and unregulated streams (with counts from Roger Creek omitted).

Model	**AIC$_c$[1]**	**ΔAIC$_c$**	**AIC$_c$ Weights**	**Model Likelihood**	**k[2]**	**Deviance[3]**
Ψ1(.)Ψ2(.)ρ1(.)ρ2(.)δ(.)[4]	156.07	0	0.85	1	5	91.53
Ψ1(.)Ψ2(g) ρ1(.)ρ2(.)δ(.)	159.83	3.76	0.13	0.15	6	87.86
Ψ1(g)Ψ2(.) ρ1(.)ρ2(.)δ(.)	163.50	7.43	0.021	0.024	6	91.53

[1] Akaike's Information Criterion, corrected for small sample sizes

[2] Number of parameters

[3] -2 (Log Likelihood)

[4] This model allows estimation of the following parameters: Ψ1, probability that a site is occupied regardless of band state; Ψ2: probability that a site is occupied by a banded bird; φ1, probability that occupancy was detected given true state=1(unbanded); φ2, probability that occupancy was detected given true state=2 (banded); and, δ, probability that banded birds were observed, given detection of occupancy. Effects of stream type (g) are indicated for each parameter, while (.) indicates no effect of stream type.

Appendix 4. Multi-state occupancy model selection results comparing occupancy of banded and unbanded American Dippers between regulated and unregulated streams (assuming the re-sighted bird at Roger Creek was banded).

Model	**AIC_c[1]**	**ΔAIC_c**	**AIC_c Weights**	**Model Likelihood**	**k[2]**	**Deviance[3]**
Ψ1(.)Ψ2(.)ρ1(.)ρ2(.)δ(.)[4]	163.90	0	0.84	1	5	94.68
Ψ1(.)Ψ2(g) ρ1(.)ρ2(.)δ(.)	167.78	3.88	0.12	0.14	6	92.07
Ψ1(g)Ψ2(.) ρ1(.)ρ2(.)δ(.)	170.40	6.50	0.033	0.039	6	94.68

[1] Akaike's Information Criterion, corrected for small sample sizes

[2] Number of parameters

[3] -2 (Log Likelihood)

[4] This model allows estimation of the following parameters: Ψ1, probability that a site is occupied regardless of band state; Ψ2: probability that a site is occupied by a banded bird; φ1, probability that occupancy was detected given true state=1(unbanded); φ2, probability that occupancy was detected given true state=2 (banded); and, δ, probability that banded birds were observed, given detection of occupancy. Effects of stream type (g) are indicated for each parameter, while (.) indicates no effect of stream type

Appendix 5. Comparison of parameter estimates (±S.E.) for multi-state occupancy models (with stream type differences in the occupancy rate of banded dippers) including and excluding the unregulated stream without any banded American Dippers (Roger Creek). Estimated parameters include: Ψ1, probability that a site is occupied regardless of band state; Ψ2: probability that a site is occupied by a banded bird; ρ1, probability that occupancy was detected given true state=1(unbanded); ρ2, probability that occupancy was detected given true state=2 (banded); and, δ, probability that banded birds were observed, given detection of occupancy.

Model Structure	**Ψ1**	**Ψ2**	**ρ1**	**ρ2**	**δ**	**Likelihood Ratio Test Result[1]**
Assume resight unbanded	Reg, Unreg= 1±0	Reg=1±0 Unreg= 0.50±0.22	Reg, Unreg= 0.44± 0.12	Reg, Unreg= 0.70 ± 0.066	Reg, Unreg= 0.50±0.086	χ^2=4.83, df=1, **p=0.028**
Omit Roger Creek	Reg, Unreg= 1±0	Reg=1±0 Unreg= 0.57±0.23	Reg, Unreg= 0.43±0.14	Reg, Unreg= 0.70 ± 0.066	Reg, Unreg= 0.50±0.086	χ^2=3.67, df=1, **p=0.057**
Assume resight banded	Reg, Unreg= 1±0	Reg=1±0 Unreg= 0.66±0.22	Reg, Unreg= 0.43±0.15	Reg, Unreg= 0.68±0.065	Reg, Unreg= 0.50±0.084	χ^2=2.62, df=1, p=0.11

[1] Maximum likelihood test result for the effect of stream type differences on the occupancy rate of banded birds (Ψ2)

Appendix 6. Seasonal changes in the number of marked and unmarked dippers sighted at each regulated and unregulated stream. Numbers represent total counts (# birds/km) with the number of marked birds re-sighted in brackets. Adjusted double observer counts were rounded to the nearest whole number. Regulated streams are marked with an asterisk.

	Stream													
Time	Brandy*	Mad	Fitzs*	Roe	Ruth*	Pem	Owl	Soo*	Roger	Gow	Fire*	Tip*	Slo	Doug*
Fall 2014 Trap 1	7	2	6	5	3	1	NA	NA	NA	4	4	1	4	5
Fall 2014 Count (marked)	14 (4)	0	3 (2)	5 (3)	5 (1)	4 (1)	NA	NA	NA	0	3 (2)	2 (0)	2 (1)	7 (1)
Fall 2014 Trap 2	2	0	2	1	0	1	NA	NA	NA	0	0	0	0	0
Total Marked before spring 2015	9	2	8	6	3	2	NA	NA	NA	4	4	1	4	5
Pre-freshet Count (marked)	1 (1)	2 (0)	0	1 (0)	2 (0)	2 (0)	1 (0)	1 (0)	0	0	1 (0)	2 (1)	2 (0)	2 (0)
Post-freshet Count (marked)	7 (2)	1 (0)	1 (0)	1 (0)	1 (0)	2 (0)	2 (0)	1 (0)	1 (0)	1 (0)	2 (0)	0	0	1 (0)
Fall 2015 Trap 1	6	1	3	2	7	5	2	2	0	2	2	1	4	3
Total Marked before fall 2015 Survey 1 (from 2014 and 2015)	15	3	11	8	10	7	2	2	0	6	6	2	8	8
Fall 2015A Survey (marked)	4 (4)	0	0	3 (2)	4 (0)	2 (1)	0	0	0	0	0	0	1 (1)	3 (0)
Fall 2015 Trap 2	0	1	0	0	0	0	0	0	0	0	0	1	1	4
Total Marked before fall 2015 Survey B from 2015	6	2	3	2	7	5	2	2	0	4	2	2	5	7
Total Marked before fall 2015 B Survey (from 2014 and 2015)	15	4	11	8	10	7	2	2	0	10	6	3	9	12
Fall 2015 B Survey (marked)	2 (1)	0	0	0	0	0	0	2 (1)	1 (0)	1 (0)	0	0	0	3 (3)

Appendix 7. Proportion of after-hatch-year (AHY) American Dippers trapped at each regulated and unregulated stream during fall 2015 (n=54 dippers).

Stream	Type	Proportion AHY Trapped	N	Anadromous Salmon Present	Elevation (m)
Brandywine	Regulated	0.50	6	No	828
Madeley	Unregulated	0	2	No	851
Fitzsimmons	Regulated	0.67	3	No	995
Roe	Unregulated	0.33	3	No	708
Rutherford	Regulated	0.57	7	No	742
Pemberton	Unregulated	0.20	5	No	262
Douglas	Regulated	0.43	7	No	370
Gowan	Unregulated	0.43	7	Yes	140
Fire	Regulated	1	2	No	384
Sloquet	Unregulated	0.33	6	Yes	55
Soo	Regulated	0.50	2	No	589
Owl	Unregulated	0	2	Yes	366
Tipella	Regulated	0.50	2	No	338

Appendix 8. Proportion of female after-hatch-year (AHY) American Dippers trapped at each regulated and unregulated stream during fall 2015 (n=23 AHY dippers captured during fall 2015). Streams with only hatch-year (HY) captures in 2015 were excluded from this table.

Stream	Type	Proportion AHY Females	N	Anadromous Salmon Present	Elevation (m)
Brandywine	Regulated	0.67	3	No	828
Fitzsimmons	Regulated	0.50	2	No	995
Roe	Unregulated	1	1	No	708
Rutherford	Regulated	0.50	4	No	742
Pemberton	Unregulated	1	1	Yes	262
Douglas	Regulated	0.33	3	No	370
Gowan	Unregulated	0.33	3	Yes	140
Fire	Regulated	0.50	2	No	384
Sloquet	Unregulated	0	2	Yes	55
Soo	Regulated	0	1	No	589

Appendix 9. Estimates of *post-hoc* Tukey contrasts comparing American Dipper body condition (represented by a scaled mass index) between regulated and unregulated streams. Significant comparisons are presented in bold.

Linear Hypothesis	Estimate	S.E.	z value	Pr(>|z|)	Linear Hypothesis	Estimate	S.E.	z value	Pr(>|z|)
DOUG-BRANDY=0	-1.44	1.49	-0.97	1.00	**SLO-FITZ=0**	2.22	1.69	1.32	0.98
FIRE-BRANDY=0	-4.08	1.86	-2.19	0.57	**SOO-FITZ=0**	0.99	2.96	0.33	1.00
FITZ-BRANDY=0	-4.40	1.53	-2.87	0.16	**TIP-FITZ=0**	-0.99	2.51	-0.39	1.00
GOW-BRANDY=0	-5.55	1.53	-3.63	**0.02**	**MAD-GOW=0**	2.80	2.25	1.24	0.99
MAD-BRANDY=0	-2.75	2.17	-1.27	0.99	**OWL-GOW=0**	-5.20	2.96	-1.75	0.86
OWL-BRANDY=0	-10.75	2.90	-3.70	**0.01**	**PEMB-GOW=0**	5.36	1.86	2.88	0.15
PEMB-BRANDY=0	-0.19	1.77	-0.11	1.00	**ROE-GOW=0**	2.65	1.73	1.53	0.94
ROE-BRANDY=0	-2.90	1.63	-1.78	0.84	**RUTH-GOW=0**	2.40	1.69	1.42	0.97
RUTH-BRANDY=0	-3.15	1.57	-2.00	0.71	**SLO-GOW=0**	3.37	1.69	2.00	0.71
SLO-BRANDY=0	-2.18	1.57	-1.38	0.97	**SOO-GOW=0**	2.14	2.96	0.72	1.00
SOO-BRANDY=0	-3.41	2.90	-1.18	0.99	**TIP-GOW=0**	0.16	2.51	0.07	1.00
TIP-BRANDY=0	-5.39	2.44	-2.21	0.56	**OWL-MAD=0**	-8.00	3.34	-2.39	0.42
FIRE-DOUG=0	-2.64	1.93	-1.37	0.98	**PEMB-MAD=0**	2.56	2.42	1.06	1.00
FITZ-DOUG=0	-2.96	1.61	-1.84	0.81	**ROE-MAD=0**	-0.15	2.32	-0.07	1.00

GOW-DOUG=0	-4.11	1.61	-2.55	0.32	**RUTH-MAD=0**	-0.40	2.28	-0.18	1.00
MAD-DOUG=0	-1.31	2.23	-0.59	1.00	**SLO-MAD=0**	0.57	2.28	0.25	1.00
OWL-DOUG=0	-9.31	2.95	-3.16	**0.07**	**SOO-MAD=0**	-0.66	3.34	-0.20	1.00
PEMB-DOUG=0	1.26	1.83	0.68	1.00	**TIP-MAD=0**	-2.64	2.95	-0.90	1.00
ROE-DOUG=0	-1.46	1.70	-0.86	1.00	**PEMB-OWL=0**	10.56	3.09	3.42	**0.03**
RUTH-DOUG=0	-1.71	1.65	-1.04	1.00	**ROE-OWL=0**	7.85	3.02	2.60	0.29
SLO-DOUG=0	-0.73	1.65	-0.44	1.00	**RUTH-OWL=0**	7.59	2.99	2.54	0.32
SOO-DOUG=0	-1.97	2.95	-0.67	1.00	**SLO-OWL=0**	8.57	2.99	2.87	0.16
TIP-DOUG=0	-3.95	2.49	-1.59	0.93	**SOO-OWL=0**	7.34	3.86	1.90	0.78
FITZ-FIRE=0	-0.31	1.96	-0.16	1.00	**TIP-OWL=0**	5.36	3.52	1.52	0.95
GOW-FIRE=0	-1.47	1.96	-0.75	1.00	**ROE-PEMB=0**	-2.71	1.94	-1.40	0.97
MAD-FIRE=0	1.33	2.49	0.54	1.00	**RUTH-PEMB=0**	-2.97	1.90	-1.56	0.93
OWL-FIRE=0	-6.66	3.15	-2.12	0.63	**SLO-PEMB=0**	-1.99	1.90	-1.05	1.00
PEMB-FIRE=0	3.90	2.15	1.82	0.83	**SOO-PEMB=0**	-3.23	3.09	-1.04	1.00
ROE-FIRE=0	1.18	2.03	0.58	1.00	**TIP-PEMB=0**	-5.20	2.66	-1.95	0.74
RUTH-FIRE=0	0.93	1.99	0.47	1.00	**RUTH-ROE=0**	-0.25	1.77	-0.14	1.00
SLO-FIRE=0	1.91	1.99	0.96	1.00	**SLO-ROE=0**	0.72	1.77	0.41	1.00
SOO-FIRE=0	0.67	3.15	0.21	1.00	**SOO-ROE=0**	-0.51	3.02	-0.17	1.00
TIP-FIRE=0	-1.30	2.73	-0.48	1.00	**TIP-ROE=0**	-2.49	2.57	-0.97	1.00
GOW-FITZ=0	-1.15	1.64	-0.70	1.00	**SLO-RUTH=0**	0.98	1.72	0.57	1.00
MAD-FITZ=0	1.65	2.25	0.73	1.00	**SOO-RUTH=0**	-0.26	2.99	-0.09	1.00
OWL-FITZ=0	-6.35	2.96	-2.14	0.61	**TIP-RUTH=0**	-2.23	2.54	-0.88	1.00
PEMB-FITZ=0	4.21	1.86	2.26	0.52	**SOO-SLO=0**	-1.24	2.99	-0.41	1.00

ROE-FITZ=0	1.50	1.73	0.87	1.00	**TIP-SLO=0**	-3.21	2.54	-1.27	0.99
RUTH-FITZ=0	1.24	1.69	0.74	1.00	**TIP-SOO=0**	-1.98	3.52	-0.56	1.00

Appendix 10. Precision between duplicate UC Davis Stable Isotope Facility laboratory reference samples for $\delta^{13}C_{VPDB}$ and $\delta^{15}N_{Air.}$

Tissue	**Year**	**Reference ID**	**Reference Name**	$\delta^{13}C_{VPDB}$ (‰)	$\delta^{15}N_{Air}$ (‰)	**S.D. ($\delta^{13}C$ ‰)**	**S.D. ($\delta^{15}N$ ‰)**
Whole blood	2014	G-13	Bovine Liver	-21.69	7.72	0.15	0.080
Whole blood	2014	G-17	USGS-41 Glutamic Acid	37.63	47.60	0.020	0.28
Whole blood	2014	G-18	Nylon 5	-27.72	-10.31	0.030	0.16
Whole blood	2014	G-20	Glutamic Acid	-16.65	-6.80	0.050	0.090
Whole blood	2015	G-13	Bovine Liver	-21.69	7.72	0.080	0.010
Whole blood	2015	G-18	Nylon 5	-27.72	-10.31	0.060	0.090
Whole blood	2015	G-20	Glutamic Acid	-16.65	-6.80	0.040	0.13
Whole blood	2015	G-21	Enriched Alanine	43.02	41.13	0.090	0.11
Invertebrates	2014	G-13	Bovine Liver	-21.69	7.72	0.040	0.10
Invertebrates	2014	G-17	USGS-41 Glutamic Acid	37.63	47.60	0.12	0.14
Invertebrates	2014	G-18	Nylon 5	-27.72	-10.31	0.080	0.13
Invertebrates	2014	G-20	Glutamic Acid	-16.65	-6.80	0.040	0.14
Invertebrates	2015	G-13	Bovine Liver	-21.69	7.72	0.070	0.11
Invertebrates	2015	G-18	Nylon 5	-27.72	-10.31	0.060	0.12
Invertebrates	2015	G-20	Glutamic Acid	-16.65	-6.80	0.11	0.11
Invertebrates	2015	G-21	Enriched Alanine	43.02	41.13	0.070	0.050

Appendix 11. Precision between duplicate UC Davis Stable Isotope Facility laboratory reference samples for $\delta^{34}S_{VCDT}$

Tissue	**Year**	**Reference ID**	**Reference Name**	**$\delta^{34}S_{VCDT}$ (‰)**	**S.D. ($\delta^{34}S$ ‰)**
Whole blood	2014	Standard 1	Whale Baleen	18.15	0.40
Whole blood	2014	Standard 2	Hair	1.91	0.33
Whole blood	2014	Standard 3	Taurine	-3.94	0.33
Whole blood	2015	CYS1	Cysteine	36.95	0.050
Whole blood	2015	HHS	Hair	2.19	0.33
Whole blood	2015	MMS	Mahi-Mahi Muscle	20.21	0.62
Whole blood	2015	RWB	Whale Baleen	18.54	0.44
Whole blood	2015	TAUR	Taurine	-3.94	0.18
Invertebrates	2014	Standard 1	Whale Baleen	18.15	0.37
Invertebrates	2014	Standard 2	Hair	1.91	0.22
Invertebrates	2014	Standard 3	Taurine	-3.94	0.30
Invertebrates	2015	CYS1	Cysteine	36.88	0.16
Invertebrates	2015	HHS	Hair	1.96	0.24
Invertebrates	2015	MMS	Mahi-Mahi Muscle	20.32	0.43
Invertebrates	2015	PIN	Pintail Feather	-2.56	0.15
Invertebrates	2015	RWB	Whale Baleen	18.30	0.43
Invertebrates	2015	TAUR	Taurine	-3.93	0.28

Appendix 12. Mean ± S.D. of American Dipper isotope ratios (δ^{13}C, δ^{15}N, δ^{34}S) and trophic position in whole blood samples collected at regulated and unregulated streams in coastal British Columbia.

Stream	**Type**	**n Blood** δ^{15}N, δ^{13}C	**n Blood** δ^{34}S	**Mean Blood** δ^{13}C (‰)	**S.D. Blood** δ^{13}C (‰)	**Mean Blood** δ^{15}N (‰)	**S.D. Blood** δ^{15}N (‰)	**Mean Blood** δ^{34}S (‰)	**S.D. Blood** δ^{34}S (‰)	**Mean TP**[1]	**S.D. TP**
Brandywine	Regulated	13	13	-22.29	1.32	3.50	0.51	2.48	1.48	3.70	0.18
Madeley	Unregulated	4	4	-25.98	0.38	4.16	0.77	5.09	1.23	3.97	0.29
Fitzsimmons	Regulated	11	11	-24.59	3.01	4.04	1.12	-3.01	3.18	3.94	0.47
Roe	Unregulated	8	8	-22.67	1.40	2.82	0.48	4.40	0.95	4.08	0.34
Rutherford	Regulated	10	10	-22.65	1.67	3.14	0.89	2.25	1.44	3.72	0.40
Pemberton	Unregulated	7	7	-22.58	1.12	3.00	0.35	2.69	2.16	3.67	0.21
Douglas	Regulated	12	12	-23.72	1.21	3.77	0.77	4.42	2.00	4.71	0.27
Gowan	Unregulated	10	10	-24.08	1.17	3.21	0.64	2.91	1.61	4.16	0.41
Fire	Regulated	6	5	-25.64	0.60	3.21	0.65	-2.65	1.88	3.88	0.52
Sloquet	Unregulated	9	9	-23.69	1.92	3.68	0.91	1.68	2.29	4.30	0.60
Tipella	Regulated	3	3	-24.78	0.79	3.49	1.02	2.05	0.90	4.63	0.88
Owl	Unregulated	2	2	-24.62	1.12	6.90	1.16	2.28	1.07	4.93	0.43
Soo	Regulated	2	2	-26.45	0.65	5.41	0.13	2.09	1.73	4.32	0.05
Regulated		57	56	-23.73	2.08	3.63	0.90	1.28*	3.41	4.05	0.55
Unregulated		40	40	-23.65	1.64	3.46	1.08	3.07	2.00	4.12	0.48

[1] Trophic Position (see equation 3.1)

* American Dipper blood δ^{34}S was significantly lower at regulated streams (β=-2.42, SE=0.95, p=0.029).

Appendix 13. Model selection results testing for differences in American Dipper whole blood δ^{34}S (n=96) between regulated and unregulated streams. A linear mixed effects model was run using the package *lme4* in R. Stream type, elevation, salmon, and the interaction between type*elevation were included as fixed effects. Stream, watershed, and year were included as random effects.

Response	**Model Structure**	**AICc**[1]	**Δ AICc**	**Deviance**[2]	**Model Weight**	**df**
Dipper whole blood δ^{34}S	**Type**	**430.6**	**0**	**417.72**	**0.91**	**6**
	null	435.3	4.64	424.63	0.090	5

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[1] Akaike's Information Criterion, corrected for small sample sizes

[2] -2 (Log Likelihood)

Appendix 14. Estimates of *post-hoc* Tukey contrasts comparing mean American Dipper blood δ^{34}S (n=96) between individual regulated and unregulated streams. Significant differences are bolded.

Linear Hypothesis	**Estimate**	**S.E.**	**z value**	**Pr(>|z|)**	**Linear Hypothesis**	**Estimate**	**S.E.**	**z value**	**Pr(>|z|)**
DOUG-BRANDY=0	1.94	0.78	2.50	0.35	**SLO-FITZ=0**	4.69	0.85	5.53	**<0.01**
FIRE-BRANDY=0	-5.13	1.02	-5.03	**<0.01**	**SOO-FITZ=0**	5.10	1.49	3.42	**0.03**
FITZ-BRANDY=0	-5.49	0.79	-6.92	**<0.01**	**TIP-FITZ=0**	5.06	1.26	4.01	**<0.01**
GOW-BRANDY=0	0.42	0.79	0.53	1.00	**MAD-GOW=0**	2.19	1.13	1.93	0.76
MAD-BRANDY=0	2.61	1.11	2.35	0.45	**OWL-GOW=0**	-0.63	1.49	-0.42	1.00
OWL-BRANDY=0	-0.21	1.47	-0.14	1.00	**PEMB-GOW=0**	-0.22	0.94	-0.23	1.00
PEMB-BRANDY=0	0.21	0.91	0.23	1.00	**ROE-GOW=0**	1.49	0.87	1.71	0.88
ROE-BRANDY=0	1.92	0.84	2.28	0.51	**RUTH-GOW=0**	-0.65	0.85	-0.77	1.00
RUTH-BRANDY=0	-0.23	0.82	-0.28	1.00	**SLO-GOW=0**	-1.23	0.85	-1.45	0.96
SLO-BRANDY=0	-0.81	0.82	-0.99	1.00	**SOO-GOW=0**	-0.82	1.49	-0.55	1.00
SOO-BRANDY=0	-0.39	1.47	-0.27	1.00	**TIP-GOW=0**	-0.86	1.26	-0.68	1.00

TIP-BRANDY=0	-0.43	1.24	-0.35	1.00	**OWL-MAD=0**	-2.82	1.68	-1.68	0.89
FIRE-DOUG=0	-7.07	1.03	-6.85	**<0.01**	**PEMB-MAD=0**	-2.40	1.22	-1.98	0.73
FITZ-DOUG=0	-7.43	0.81	-9.19	**<0.01**	**ROE-MAD=0**	-0.69	1.16	-0.59	1.00
GOW-DOUG=0	-1.52	0.81	-1.88	0.79	**RUTH-MAD=0**	-2.84	1.15	-2.48	0.37
MAD-DOUG=0	0.67	1.12	0.60	1.00	**SLO-MAD=0**	-3.42	1.15	-2.98	0.12
OWL-DOUG=0	-2.15	1.48	-1.45	0.96	**SOO-MAD=0**	-3.00	1.68	-1.79	0.84
PEMB-DOUG=0	-1.73	0.92	-1.88	0.79	**TIP-MAD=0**	-3.04	1.48	-2.06	0.67
ROE-DOUG=0	-0.02	0.85	-0.03	1.00	**PEMB-OWL=0**	0.41	1.55	0.27	1.00
RUTH-DOUG=0	-2.17	0.83	-2.62	0.28	**ROE-OWL=0**	2.13	1.52	1.40	0.97
SLO-DOUG=0	-2.75	0.83	-3.31	0.05	**RUTH-OWL=0**	-0.02	1.50	-0.02	1.00
SOO-DOUG=0	-2.33	1.48	-1.58	0.93	**SLO-OWL=0**	-0.60	1.50	-0.40	1.00
TIP-DOUG=0	-2.37	1.25	-1.90	0.78	**SOO-OWL=0**	-0.19	1.94	-0.10	1.00
FITZ-FIRE=0	-0.36	1.05	-0.35	1.00	**TIP-OWL=0**	-0.23	1.77	-0.13	1.00
GOW-FIRE=0	5.55	1.05	5.31	**<0.01**	**ROE-PEMB=0**	1.71	0.98	1.75	0.86
MAD-FIRE=0	7.74	1.30	5.95	**<0.01**	**RUTH-PEMB=0**	-0.44	0.96	-0.46	1.00
OWL-FIRE=0	4.92	1.62	3.03	0.10	**SLO-PEMB=0**	-1.01	0.96	-1.06	1.00
PEMB-FIRE=0	5.33	1.14	4.70	**<0.01**	**SOO-PEMB=0**	-0.60	1.55	-0.39	1.00
ROE-FIRE=0	7.05	1.08	6.52	**<0.01**	**TIP-PEMB=0**	-0.64	1.34	-0.48	1.00
RUTH-FIRE=0	4.90	1.06	4.61	**<0.01**	**RUTH-ROE=0**	-2.15	0.89	-2.41	0.41
SLO-FIRE=0	4.32	1.06	4.07	**<0.01**	**SLO-ROE=0**	-2.72	0.89	-3.06	0.10
SOO-FIRE=0	4.74	1.62	2.92	0.14	**SOO-ROE=0**	-2.31	1.52	-1.52	0.94
TIP-FIRE=0	4.70	1.42	3.32	**0.04**	**TIP-ROE=0**	-2.35	1.29	-1.82	0.83
GOW-FITZ=0	5.92	0.83	7.16	**<0.01**	**SLO-RUTH=0**	-0.58	0.87	-0.66	1.00

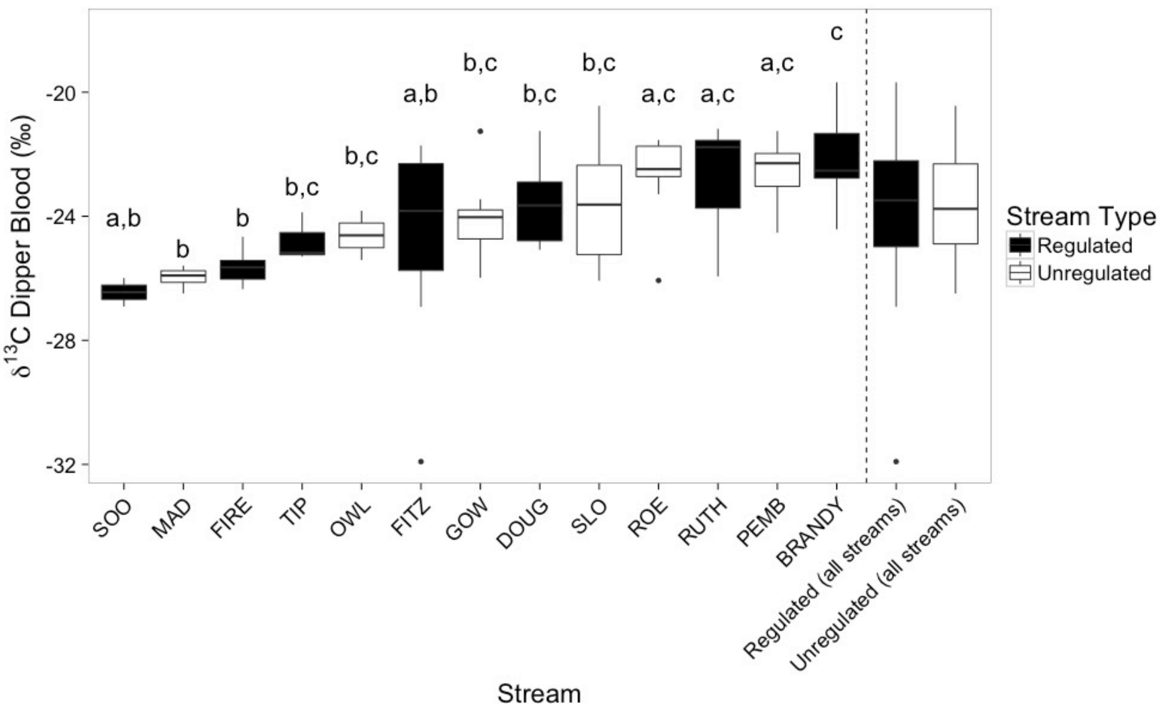
MAD-FITZ=0	8.10	1.13	7.16	**<0.01**	**SOO-RUTH=0**	-0.16	1.50	-0.11	1.00
OWL-FITZ=0	5.28	1.49	3.55	**0.02**	**TIP-RUTH=0**	-0.20	1.28	-0.16	1.00
PEMB-FITZ=0	5.70	0.94	6.08	**<0.01**	**SOO-SLO=0**	0.41	1.50	0.28	1.00
ROE-FITZ=0	7.41	0.87	8.50	**<0.01**	**TIP-SLO=0**	0.37	1.28	0.29	1.00
RUTH-FITZ=0	5.26	0.85	6.21	**<0.01**	**TIP-SOO=0**	-0.04	1.77	-0.02	1.00

Appendix 15. Model selection results testing for differences in American Dipper whole blood $\delta^{13}C$ between regulated and unregulated streams (n=97). A linear mixed effects model was run using the package *lme4* in R. Stream type, elevation, salmon, and the interaction between type*elevation were included as fixed effects. Stream and watershed were included as random effects.

Response	Model Structure	AICc[1]	Δ AICc	Deviance[2]	Model Weight	df
Dipper whole blood $\delta^{13}C$	**null**	**406.9**	**0**	**398.50**	**0.60**	**4**
	type	407.8	0.84	397.12	0.40	5

[1] Akaike's Information Criterion, corrected for small sample sizes

[2] -2 (Log Likelihood)



Appendix 16. Comparing American Dipper whole blood δ^{13}C (‰) between regulated and unregulated streams (n=97). Streams sharing the same letter are not significantly different (p>0.05) from one another.

Appendix 17. Estimates of *post-hoc* Tukey contrasts comparing mean American Dipper blood δ^{13}C (n=97) between individual regulated and unregulated streams. Significant differences are bolded.

Linear Hypothesis	Estimate	S.E.	z value	Pr(>|z|)	Linear Hypothesis	Estimate	S.E.	z value	Pr(>|z|)
DOUG-BRANDY=0	-1.43	0.65	-2.20	0.57	**SLO-FITZ=0**	0.91	0.71	1.28	0.99
FIRE-BRANDY=0	-3.34	0.80	-4.18	**<0.01**	**SOO-FITZ=0**	-1.86	1.24	-1.49	0.95
FITZ-BRANDY=0	-2.30	0.66	-3.47	**0.03**	**TIP-FITZ=0**	-0.19	1.05	-0.18	1.00
GOW-BRANDY=0	-1.79	0.66	-2.70	0.24	**MAD-GOW=0**	-1.90	0.95	-2.01	0.71
MAD-BRANDY=0	-3.68	0.93	-3.98	**<0.01**	**OWL-GOW=0**	-0.54	1.24	-0.43	1.00
OWL-BRANDY=0	-2.32	1.23	-1.89	0.78	**PEMB-GOW=0**	1.50	0.78	1.91	0.77
PEMB-BRANDY=0	-0.29	0.76	-0.39	1.00	**ROE-GOW=0**	1.41	0.73	1.93	0.76
ROE-	-0.38	0.70	-0.54	1.00	**RUTH-**	1.43	0.71	2.03	0.69

BRANDY=0					**GOW=0**			
RUTH-BRANDY=0	-0.35	0.68	-0.52	1.00	**SLO-GOW=0**	0.39	0.71	0.56	1.00
SLO-BRANDY=0	-1.39	0.68	-2.05	0.68	**SOO-GOW=0**	-2.37	1.24	-1.91	0.78
SOO-BRANDY=0	-4.16	1.23	-3.38	**0.04**	**TIP-GOW=0**	-0.70	1.05	-0.67	1.00
TIP-BRANDY=0	-2.49	1.04	-2.40	0.42	**OWL-MAD=0**	1.36	1.40	0.97	1.00
FIRE-DOUG=0	-1.92	0.81	-2.37	0.44	**PEMB-MAD=0**	3.39	1.01	3.34	**0.04**
FITZ-DOUG=0	-0.88	0.68	-1.30	0.98	**ROE-MAD=0**	3.30	0.97	3.39	**0.04**
GOW-DOUG=0	-0.36	0.68	-0.54	1.00	**RUTH-MAD=0**	3.33	0.96	3.48	**0.03**
MAD-DOUG=0	-2.26	0.93	-2.42	0.41	**SLO-MAD=0**	2.29	0.96	2.39	0.43
OWL-DOUG=0	-0.90	1.24	-0.73	1.00	**SOO-MAD=0**	-0.48	1.40	-0.34	1.00
PEMB-DOUG=0	1.13	0.77	1.47	0.96	**TIP-MAD=0**	1.19	1.24	0.96	1.00
ROE-DOUG=0	1.04	0.71	1.46	0.96	**PEMB-OWL=0**	2.03	1.30	1.57	0.93
RUTH-DOUG=0	1.07	0.69	1.55	0.94	**ROE-OWL=0**	1.94	1.27	1.53	0.94
SLO-DOUG=0	0.03	0.69	0.04	1.00	**RUTH-OWL=0**	1.97	1.25	1.57	0.93
SOO-DOUG=0	-2.73	1.24	-2.21	0.56	**SLO-OWL=0**	0.93	1.25	0.74	1.00
TIP-DOUG=0	-1.07	1.04	-1.02	1.00	**SOO-OWL=0**	-1.84	1.62	-1.13	1.00
FITZ-FIRE=0	1.04	0.82	1.27	0.99	**TIP-OWL=0**	-0.17	1.48	-0.11	1.00
GOW-FIRE=0	1.56	0.82	1.89	0.78	**ROE-PEMB=0**	-0.09	0.82	-0.11	1.00
MAD-FIRE=0	-0.34	1.04	-0.33	1.00	**RUTH-PEMB=0**	-0.06	0.80	-0.08	1.00
OWL-FIRE=0	1.02	1.32	0.77	1.00	**SLO-PEMB=0**	-1.10	0.80	-1.38	0.97
PEMB-FIRE=0	3.05	0.90	3.39	**0.04**	**SOO-PEMB=0**	-3.87	1.30	-2.98	0.12
ROE-FIRE=0	2.96	0.85	3.47	0.03	**TIP-PEMB=0**	-2.20	1.12	-1.97	0.73
RUTH-FIRE=0	2.99	0.84	3.58	0.02	**RUTH-ROE=0**	0.03	0.74	0.04	1.00
SLO-	1.95	0.84	2.33	0.47	**SLO-**	-1.01	0.74	-1.36	0.98

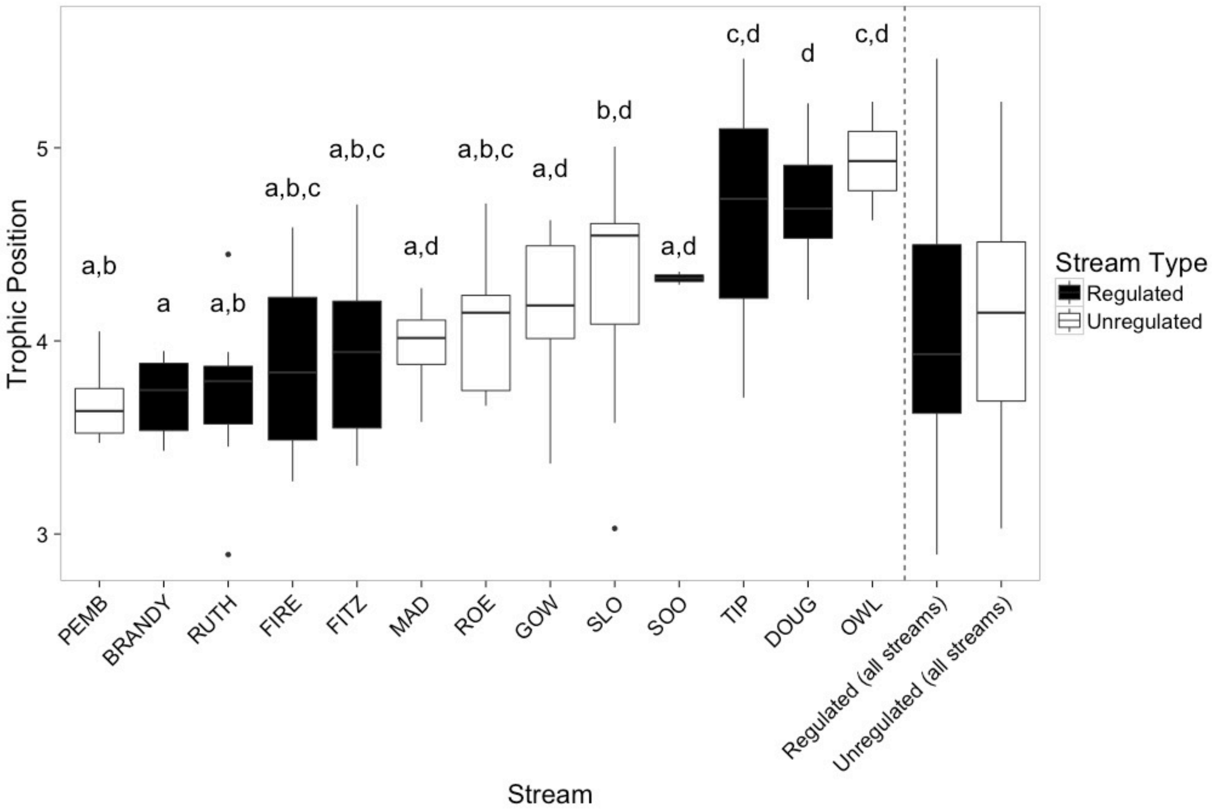
FIRE=0					**ROE=0**			
SOO-FIRE=0	-0.82	1.32	-0.62	1.00	**SOO-ROE=0**	-3.78	1.27	-2.98	0.12
TIP-FIRE=0	0.85	1.14	0.74	1.00	**TIP-ROE=0**	-2.11	1.08	-1.95	0.74
GOW-FITZ=0	0.51	0.69	0.75	1.00	**SLO-RUTH=0**	-1.04	0.72	-1.44	0.96
MAD-FITZ=0	-1.38	0.95	-1.46	0.96	**SOO-RUTH=0**	-3.80	1.25	-3.03	0.10
OWL-FITZ=0	-0.02	1.24	-0.02	1.00	**TIP-RUTH=0**	-2.14	1.07	-2.01	0.71
PEMB-FITZ=0	2.01	0.78	2.57	0.31	**SOO-SLO=0**	-2.76	1.25	-2.20	0.56
ROE-FITZ=0	1.92	0.73	2.64	0.27	**TIP-SLO=0**	-1.10	1.07	-1.03	1.00
RUTH-FITZ=0	1.95	0.71	2.75	0.21	**TIP-SOO=0**	1.67	1.48	1.13	1.00

Appendix 18. Model selection results testing for differences in American Dipper trophic position (n=97) between regulated and unregulated streams. A linear mixed effects model was run using the package *lme4* in R. Stream type, elevation, salmon, and the interaction between type*elevation were included as fixed effects. Stream, watershed, and year were included as random effects.

Response	**Model Structure**	**AICc**[1]	**Δ AICc**	**Deviance**[2]	**Model Weight**	**df**
Dipper trophic position	**null**	**129.2**	**0**	**118.56**	**0.99**	**5**
	Elevation	144.3	15.06	131.36	0.001	6

[1] Akaike's Information Criterion, corrected for small sample sizes

[2] -2 (Log Likelihood)



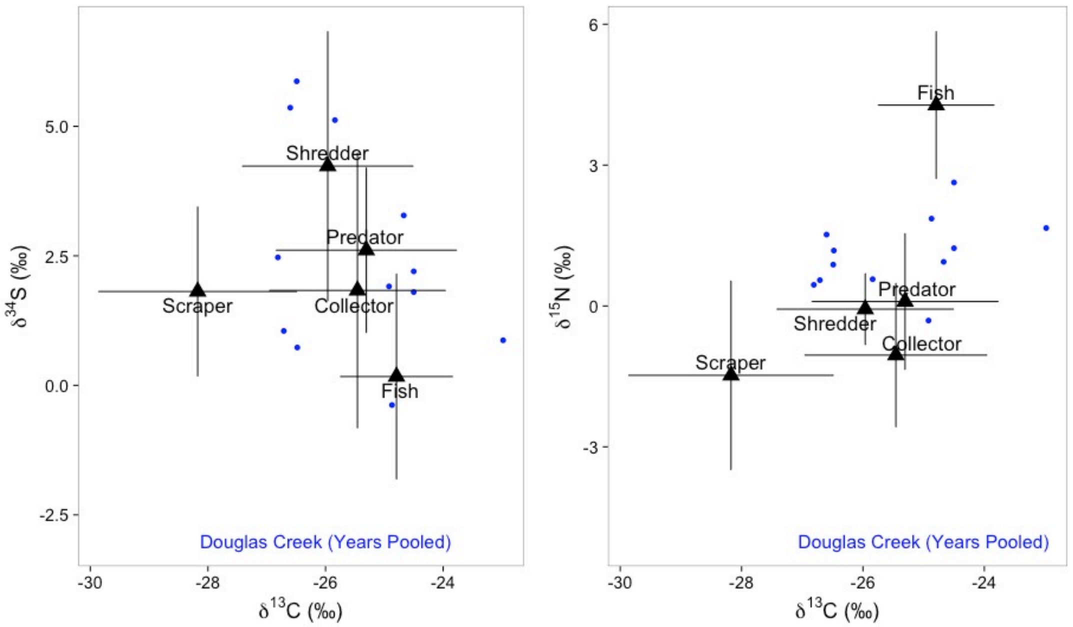
Appendix 19. Comparing American Dipper trophic position between regulated and unregulated streams (n=97). There was no significant difference in dipper trophic position between stream types. Streams sharing the same letter are not significantly different (p>0.05) from one another.

Appendix 20. Estimates of *post-hoc* Tukey contrasts comparing mean American Dipper trophic position (n=97) between individial regulated and unregulated streams. Significant differences are bolded.

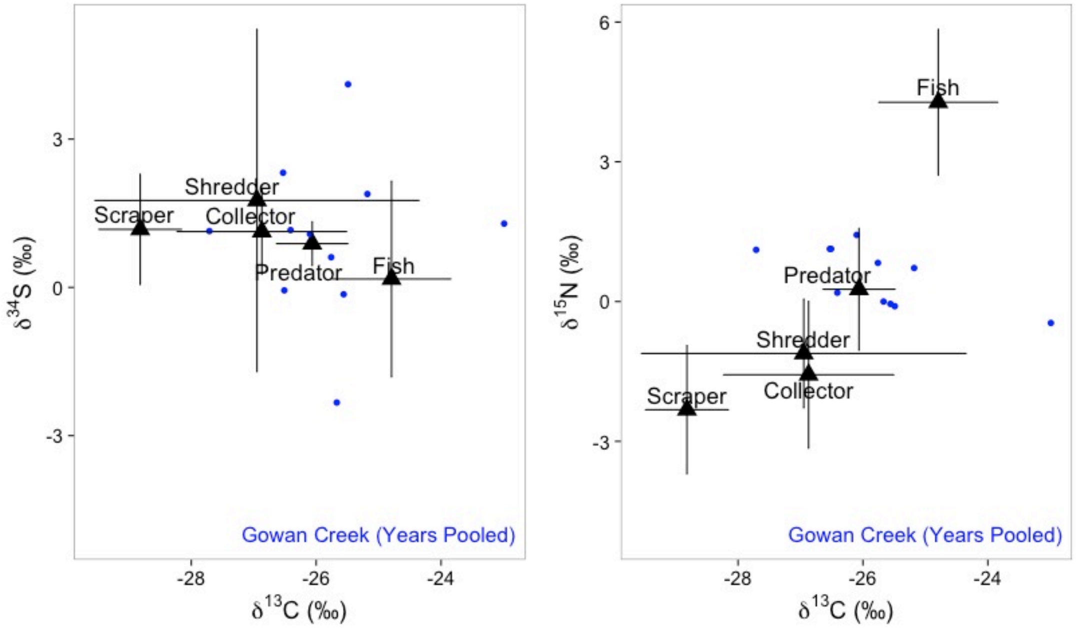
Linear Hypothesis	**Estimate**	**S.E.**	**z value**	**Pr(>|z|)**	**Linear Hypothesis**	**Estimate**	**S.E.**	**z value**	**Pr(>|z|)**
DOUG-BRANDY=0	1.00	0.16	6.18	**<0.01**	**SLO-FITZ=0**	0.36	0.18	2.04	0.69
FIRE-BRANDY=0	0.17	0.20	0.87	1.00	**SOO-FITZ=0**	0.39	0.31	1.24	0.99
FITZ-BRANDY=0	0.24	0.17	1.42	0.97	**TIP-FITZ=0**	0.70	0.26	2.64	0.27
GOW-BRANDY=0	0.46	0.17	2.77	0.20	**MAD-GOW=0**	-0.19	0.24	-0.81	1.00
MAD-	0.27	0.23	1.16	0.99	**OWL-**	0.77	0.31	2.47	0.37

BRANDY=0					**GOW=0**				
OWL-BRANDY=0	1.23	0.31	3.99	**<0.01**	**PEMB-GOW=0**	-0.49	0.20	-2.50	0.35
PEMB-BRANDY=0	-0.03	0.19	-0.16	1.00	**ROE-GOW=0**	-0.08	0.18	-0.43	1.00
ROE-BRANDY=0	0.38	0.18	2.17	0.59	**RUTH-GOW=0**	-0.44	0.18	-2.48	0.36
RUTH-BRANDY=0	0.02	0.17	0.12	1.00	**SLO-GOW=0**	0.14	0.18	0.77	1.00
SLO-BRANDY=0	0.60	0.17	3.50	0.02	**SOO-GOW=0**	0.16	0.31	0.52	1.00
SOO-BRANDY=0	0.62	0.31	2.02	0.70	**TIP-GOW=0**	0.47	0.26	1.79	0.84
TIP-BRANDY=0	0.93	0.26	3.59	0.02	**OWL-MAD=0**	0.96	0.35	2.74	0.22
FIRE-DOUG=0	-0.83	0.20	-4.09	**<0.01**	**PEMB-MAD=0**	-0.30	0.25	-1.17	0.99
FITZ-DOUG=0	-0.77	0.17	-4.54	**<0.01**	**ROE-MAD=0**	0.11	0.24	0.46	1.00
GOW-DOUG=0	-0.54	0.17	-3.21	**0.06**	**RUTH-MAD=0**	-0.25	0.24	-1.03	1.00
MAD-DOUG=0	-0.73	0.23	-3.14	0.08	**SLO-MAD=0**	0.33	0.24	1.37	0.98
OWL-DOUG=0	0.23	0.31	0.73	1.00	**SOO-MAD=0**	0.35	0.35	1.01	1.00
PEMB-DOUG=0	-1.03	0.19	-5.36	**<0.01**	**TIP-MAD=0**	0.66	0.31	2.14	0.61
ROE-DOUG=0	-0.62	0.18	-3.48	**0.03**	**PEMB-OWL=0**	-1.26	0.32	-3.87	**<0.01**
RUTH-DOUG=0	-0.98	0.17	-5.66	**<0.01**	**ROE-OWL=0**	-0.85	0.32	-2.68	0.25
SLO-DOUG=0	-0.41	0.17	-2.35	0.46	**RUTH-OWL=0**	-1.21	0.31	-3.85	**<0.01**
SOO-DOUG=0	-0.38	0.31	-1.23	0.99	**SLO-OWL=0**	-0.63	0.31	-2.02	0.70
TIP-DOUG=0	-0.07	0.26	-0.27	1.00	**SOO-OWL=0**	-0.61	0.41	-1.50	0.95
FITZ-FIRE=0	0.06	0.21	0.30	1.00	**TIP-OWL=0**	-0.30	0.37	-0.80	1.00
GOW-FIRE=0	0.29	0.21	1.39	0.97	**ROE-PEMB=0**	0.41	0.20	2.01	0.70
MAD-FIRE=0	0.09	0.26	0.36	1.00	**RUTH-PEMB=0**	0.05	0.20	0.25	1.00
OWL-FIRE=0	1.05	0.33	3.19	**0.06**	**SLO-PEMB=0**	0.63	0.20	3.13	0.08
PEMB-	-0.20	0.23	-0.90	1.00	**SOO-**	0.65	0.32	2.01	0.71

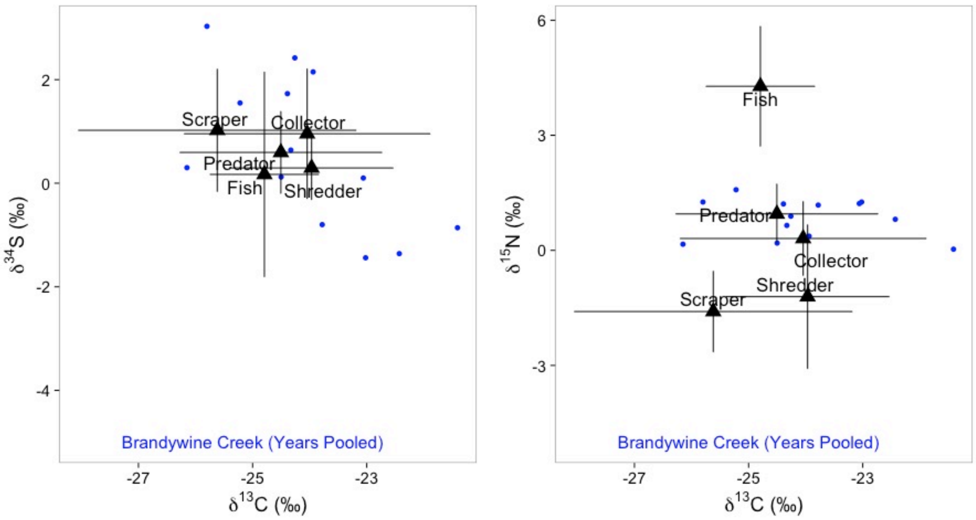
FIRE=0					**PEMB=0**				
ROE-FIRE=0	0.21	0.21	0.97	1.00	**TIP-PEMB=0**	0.96	0.28	3.44	0.03
RUTH-FIRE=0	-0.15	0.21	-0.73	1.00	**RUTH-ROE=0**	-0.36	0.19	-1.94	0.76
SLO-FIRE=0	0.42	0.21	2.02	0.70	**SLO-ROE=0**	0.21	0.19	1.15	0.99
SOO-FIRE=0	0.45	0.33	1.36	0.98	**SOO-ROE=0**	0.24	0.32	0.76	1.00
TIP-FIRE=0	0.76	0.29	2.65	0.26	**TIP-ROE=0**	0.55	0.27	2.04	0.68
GOW-FITZ=0	0.22	0.17	1.30	0.98	**SLO-RUTH=0**	0.58	0.18	3.17	0.07
MAD-FITZ=0	0.03	0.24	0.14	1.00	**SOO-RUTH=0**	0.60	0.31	1.92	0.77
OWL-FITZ=0	0.99	0.31	3.19	**0.07**	**TIP-RUTH=0**	0.91	0.27	3.42	**0.03**
PEMB-FITZ=0	-0.27	0.20	-1.36	0.98	**SOO-SLO=0**	0.03	0.31	0.08	1.00
ROE-FITZ=0	0.15	0.18	0.80	1.00	**TIP-SLO=0**	0.34	0.27	1.26	0.99
RUTH-FITZ=0	-0.21	0.18	-1.21	0.99	**TIP-SOO=0**	0.31	0.37	0.84	1.00



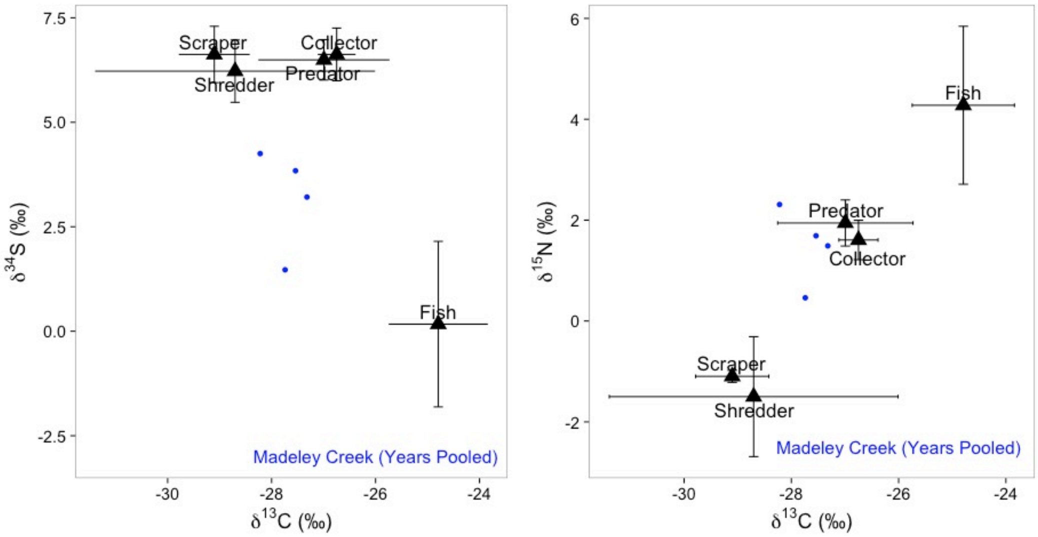
Appendix 21. Carbon-Sulfur (a) and Carbon-Nitrogen (b) stable isotope biplots of the Douglas Creek foodweb (regulated). Individual American Dipper blood isotope values (TEF-adjusted) are represented as blue points, while the black triangles and lines represent invertebrate functional feeding groups and fish source means ± S.D.



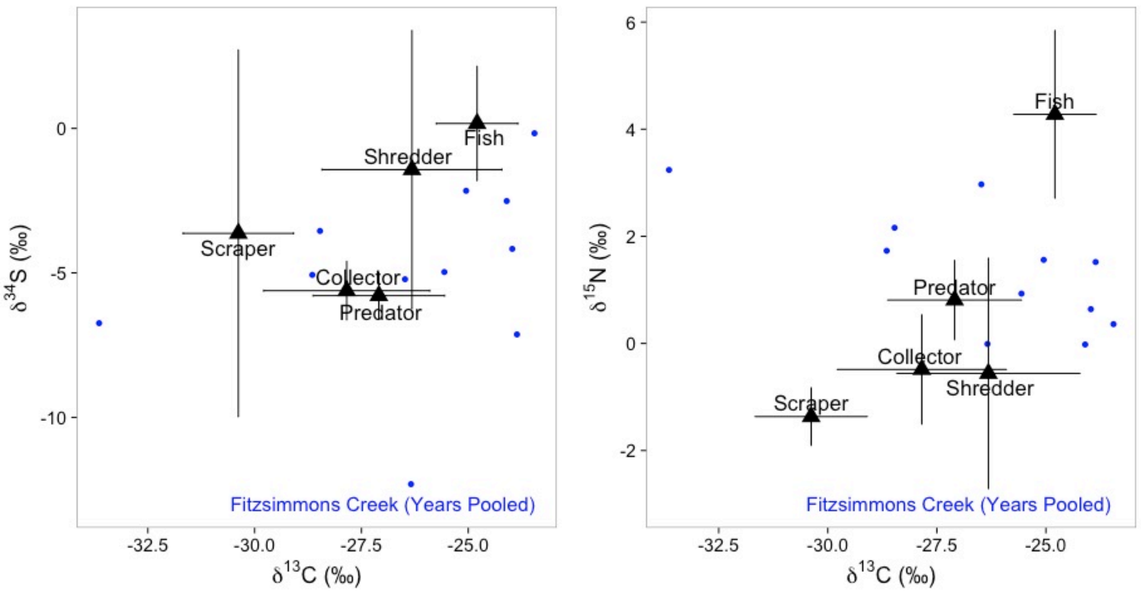
Appendix 22. Carbon-Sulfur (a) and Carbon-Nitrogen (b) stable isotope biplots of the Gowan Creek foodweb (unregulated). Individual American Dipper blood isotope values (TEF-adjusted) are represented as blue points, while the black triangles and lines represent invertebrate functional feeding groups and fish source means ± S.D.



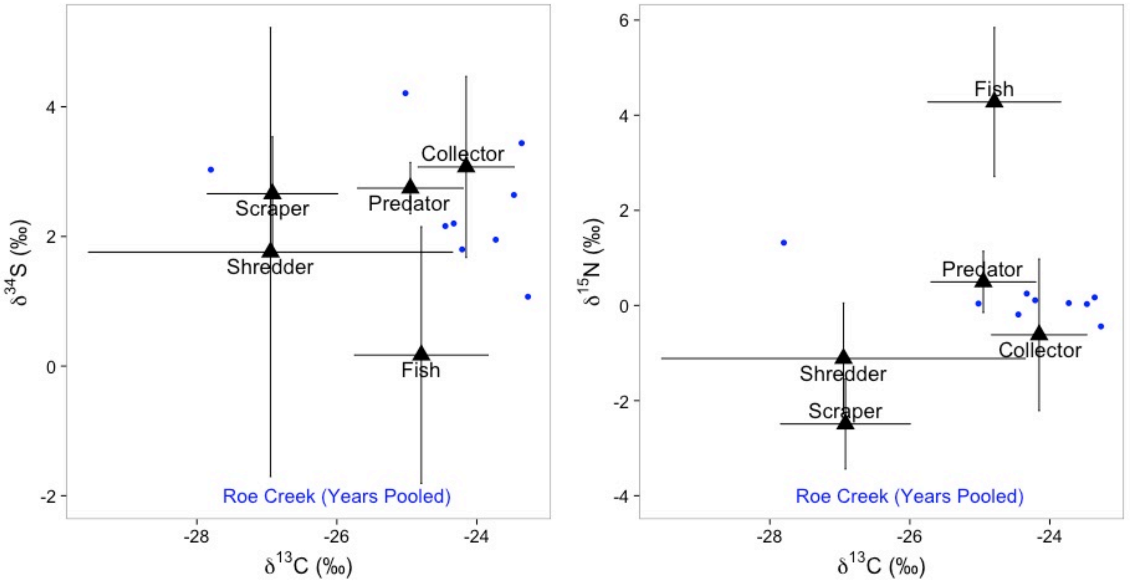
Appendix 23. Carbon-Sulfur (a) and Carbon-Nitrogen (b) stable isotope biplots of the Brandywine Creek foodweb (regulated). Individual American Dipper blood isotope values (TEF-adjusted) are represented as blue points, while the black triangles and lines represent invertebrate functional feeding groups and fish source means ± S.D.



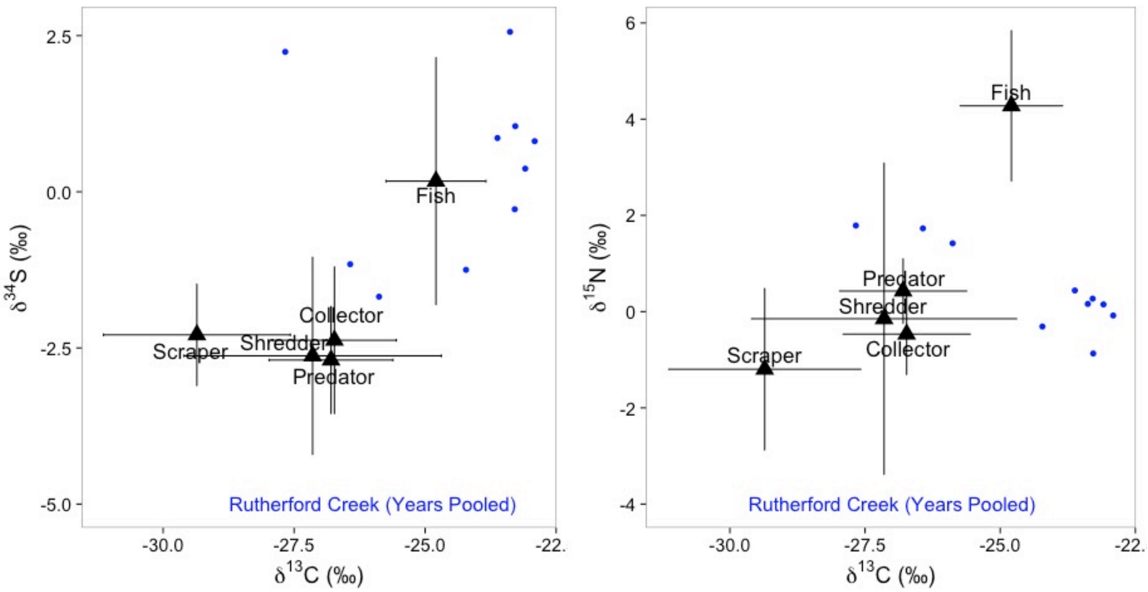
Appendix 24. Carbon-Sulfur (a) and Carbon-Nitrogen (b) stable isotope biplots of the Madeley Creek foodweb (unregulated). Individual American Dipper blood isotope values (TEF-adjusted) are represented as blue points, while the black triangles and lines represent invertebrate functional feeding groups and fish source means ± S.D.



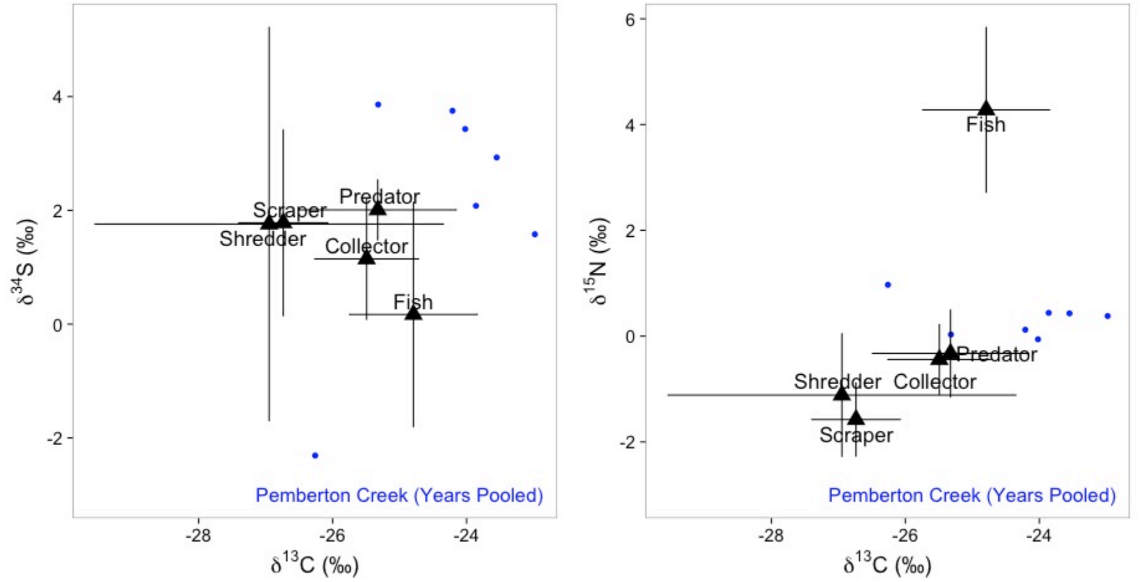
Appendix 25. Carbon-Sulfur (a) and Carbon-Nitrogen (b) stable isotope biplots of the Fitzsimmons Creek foodweb (regulated). Individual American Dipper blood isotope values (TEF-adjusted) are represented as blue points, while the black triangles and lines represent invertebrate functional feeding groups and fish source means ± S.D.



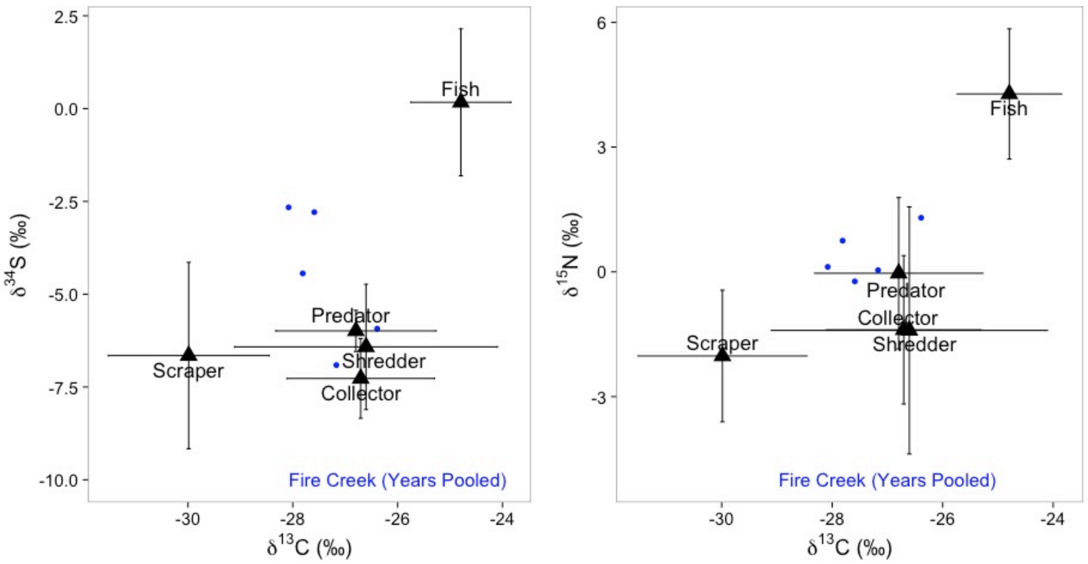
Appendix 26. Carbon-Sulfur (a) and Carbon-Nitrogen (b) stable isotope biplots of the Roe Creek foodweb (unregulated). Individual American Dipper blood isotope values (TEF-adjusted) are represented as blue points, while the black triangles and lines represent invertebrate functional feeding groups and fish source means ± S.D.



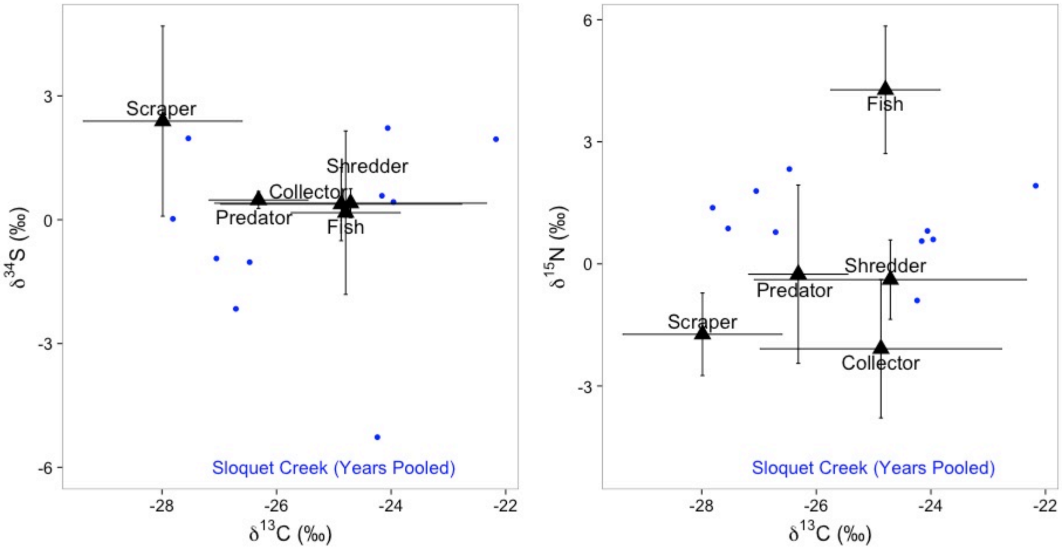
Appendix 27. Carbon-Sulfur (a) and Carbon-Nitrogen (b) stable isotope biplots of the Rutherford Creek foodweb (regulated). Individual American Dipper blood isotope values (TEF-adjusted) are represented as blue points, while the black triangles and lines represent invertebrate functional feeding groups and fish source means ± S.D.



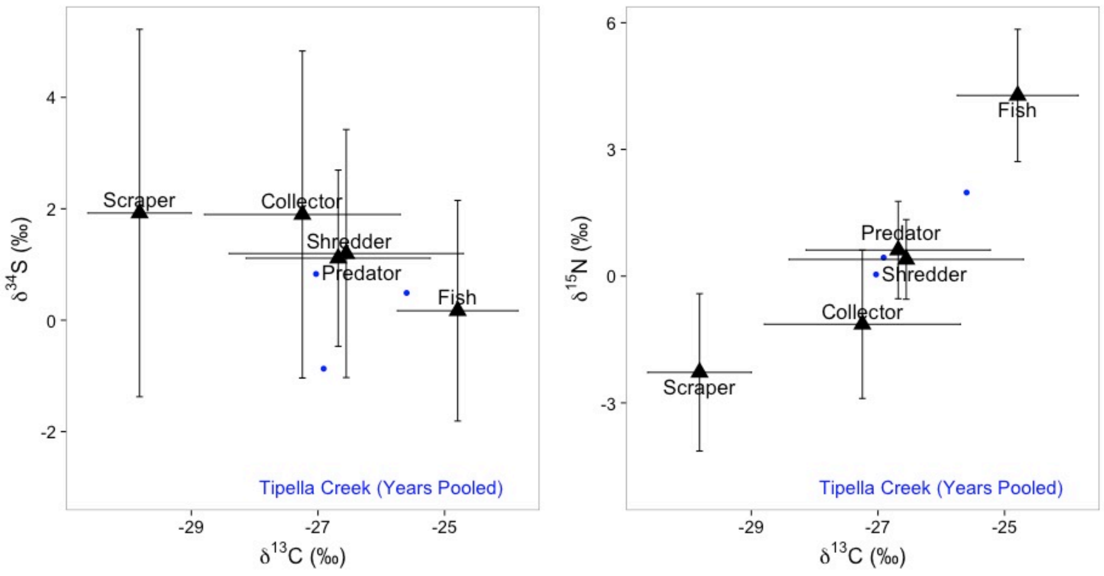
Appendix 28. Carbon-Sulfur (a) and Carbon-Nitrogen (b) stable isotope biplots of the Pemberton Creek foodweb (unregulated). Individual American Dipper blood isotope values (TEF-adjusted) are represented as blue points, while the black triangles and lines represent invertebrate functional feeding groups and fish source means ± S.D.



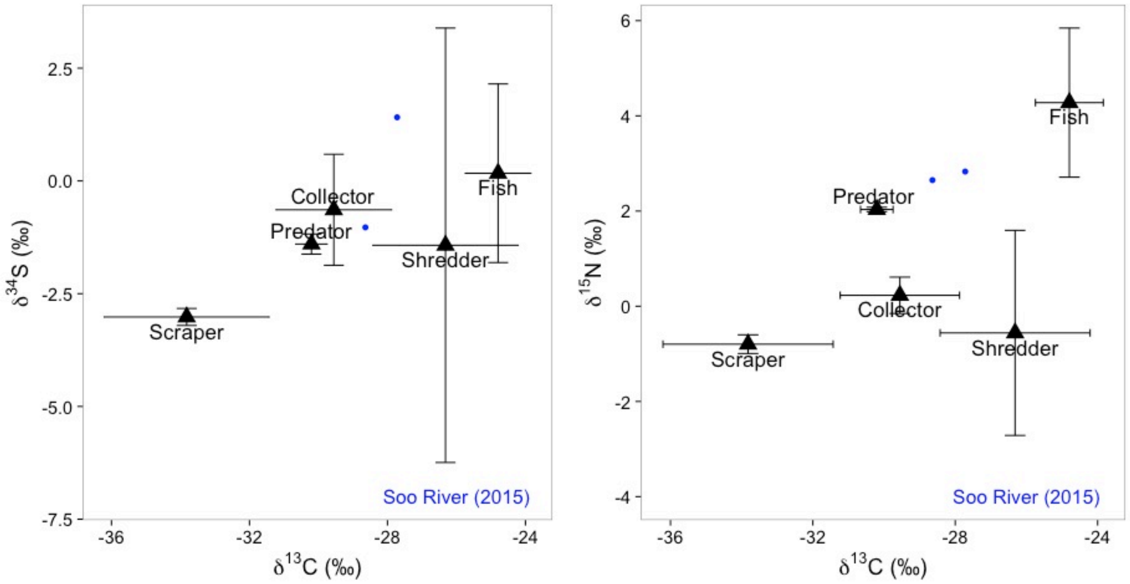
Appendix 29. Carbon-Sulfur (a) and Carbon-Nitrogen (b) stable isotope biplots of the Fire Creek foodweb (regulated). Individual American Dipper blood isotope values (TEF-adjusted) are represented as blue points, while the black triangles and lines represent invertebrate functional feeding groups and fish source means ± S.D.



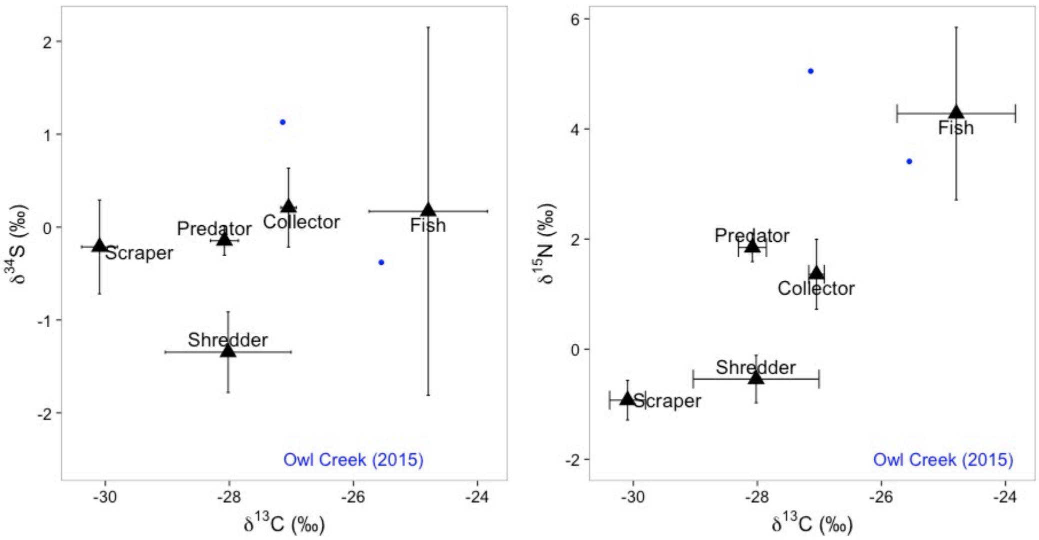
Appendix 30. Carbon-Sulfur (a) and Carbon-Nitrogen (b) stable isotope biplots of the Sloquet Creek foodweb (unregulated). Individual American Dipper blood isotope values (TEF-adjusted) are represented as blue points, while the black triangles and lines represent invertebrate functional feeding groups and fish source means ± S.D.



Appendix 31. Carbon-Sulfur (a) and Carbon-Nitrogen (b) stable isotope biplots of the Tipella Creek foodweb (regulated). Individual American Dipper blood isotope values (TEF-adjusted) are represented as blue points, while the black triangles and lines represent invertebrate functional feeding groups and fish source means ± S.D.



Appendix 32. Carbon-Sulfur (a) and Carbon-Nitrogen (b) stable isotope biplots of the Soo River foodweb (regulated). Individual American Dipper blood isotope values (TEF-adjusted) are represented as blue points, while the black triangles and lines represent invertebrate functional feeding groups and fish source means ± S.D.



Appendix 33. Carbon-Sulfur (a) and Carbon-Nitrogen (b) stable isotope biplots of the Owl Creek foodweb (unregulated). Individual American Dipper blood isotope values (TEF-adjusted) are represented as blue points, while the black triangles and lines represent invertebrate functional feeding groups and fish source means ± S.D.

Appendix 34. Summary (mean ± S.D.) of the stable isotope signature ($\delta^{13}C$, $\delta^{15}N$, $\delta^{34}S$) of American Dipper diet sources (n = 96 dippers) at regulated and unregulated streams. Diet proportions were calculated using a Bayesian Mixing model in the program MixSIAR using stable isotope values ($\delta^{13}C$, $\delta^{15}N$, $\delta^{34}S$) from separate invertebrate samples collected at each stream (n=7 regulated and 7 unregulated). *Indicates when the isotope values were pooled across all sources from that stream type.

	Regulated Streams								**Unregulated Streams**							
Diet Source	Stream	Mean $\delta^{13}C$ (‰)	S.D. $\delta^{13}C$ (‰)	Mean $\delta^{15}N$ (‰)	S.D. $\delta^{15}N$ (‰)	Mean $\delta^{34}S$ (‰)	S.D. $\delta^{34}S$ (‰)	n	Stream	Mean $\delta^{13}C$ (‰)	S.D. $\delta^{13}C$ (‰)	Mean $\delta^{15}N$ (‰)	S.D. $\delta^{15}N$ (‰)	Mean $\delta^{34}S$ (‰)	S.D. $\delta^{34}S$ (‰)	n
Collector	DOUG	-25.46	1.50	-1.05	1.53	1.83	2.65	12	GOW	-26.87	1.36	-1.57	1.58	1.13	0.86	8
Scraper		-28.17	1.68	-1.48	2.01	1.81	1.63	7		-28.82	0.67	-2.32	1.38	1.17	1.12	5
Shredder		-25.96	1.45	-0.07	0.76	4.23	2.60	7		-26.95	2.60	-1.11	1.17	1.76	3.46	9
Predator		-25.31	1.53	0.10	1.45	2.61	1.59	8		-26.06	0.58	0.26	1.31	0.89	0.44	6
Fish		-24.79	0.95	4.28	1.57	0.17	1.98	15		-24.79	0.95	4.28	1.57	0.17	1.98	15
Collector	BRANDY	-24.04	2.16	0.31	0.97	0.96	1.26	19	MAD	-26.75	0.36	1.61	0.39	6.62	0.63	6
Scraper		-25.62	2.44	-1.59	1.06	1.02	1.19	9		-29.10	0.68	-1.10	0.12	6.62	0.67	4
Shredder		-23.97	1.43	-1.21	1.88	0.30	0.62	2		-28.70	2.69	-1.50	1.19	6.22	0.75	4
Predator		-24.50	1.77	0.95	0.78	0.60	0.79	12		-26.99	1.26	1.94	0.46	6.49	0.48	6
Fish		-24.79	0.95	4.28	1.57	0.17	1.98	15		-24.79	0.95	4.28	1.57	0.17	1.98	15
Collector	FITZ	-27.85	1.94	-0.49	1.02	-5.61	1.01	9	ROE	-24.15	0.68	-0.62	1.59	3.07	1.40	9
Scraper		-30.38	1.29	-1.37	0.54	-3.63	6.35	8		-26.92	0.93	-2.49	0.95	2.66	0.88	6
Shredder		-26.32	2.11	-0.56	2.15	-1.43	4.82	29*		-26.95	2.60	-1.11	1.17	1.76	3.46	9
Predator		-27.09	1.54	0.81	0.74	-5.79	0.82	15		-24.95	0.75	0.50	0.64	2.75	0.40	8
Fish		-24.79	0.95	4.28	1.57	0.17	1.98	15		-24.79	0.95	4.28	1.57	0.17	1.98	15
Collector	RUTH	-26.73	1.18	-0.47	0.84	-2.38	1.18	13	PEM	-25.49	0.78	-0.44	0.67	1.15	1.07	12
Scraper		-29.36	1.78	-1.20	1.68	-2.29	0.82	7		-26.74	0.66	-1.58	0.70	1.78	1.64	6
Shredder		-27.15	2.46	-0.15	3.24	-2.63	1.58	3		-26.95	2.60	-1.11	1.17	1.76	3.46	9
Predator		-26.80	1.18	0.43	0.68	-2.69	0.86	10		-25.33	1.17	-0.33	0.83	2.01	0.53	7
Fish		-24.79	0.95	4.28	1.57	0.17	1.98	15		-24.79	0.95	4.28	1.57	0.17	1.98	15
Collector	FIRE	-26.70	1.41	-1.39	1.78	-7.27	1.07	17	SLO	-24.87	2.11	-2.09	1.70	0.38	0.89	6
Scraper		-29.99	1.53	-2.02	1.58	-6.65	2.51	8		-27.99	1.39	-1.73	1.01	2.39	2.30	25*
Shredder		-26.60	2.51	-1.41	2.97	-6.42	1.69	10		-24.71	2.37	-0.39	0.98	0.40	0.35	3
Predator		-26.80	1.53	-0.03	1.82	-5.99	0.55	10		-26.32	0.87	-0.25	2.19	0.48	0.20	6
Fish		-24.79	0.95	4.28	1.57	0.17	1.98	15		-24.79	0.95	4.28	1.57	0.17	1.98	15
Collector	TIP	-27.25	1.55	-1.14	1.76	1.90	2.93	17	OWL	-27.05	0.12	1.36	0.64	0.21	0.42	3
Scraper		-29.82	0.82	-2.28	1.86	1.92	3.30	10		-30.09	0.29	-0.93	0.36	-0.21	0.51	3
Shredder		-26.55	1.85	0.40	0.94	1.20	2.23	6		-28.02	1.01	-0.54	0.43	-1.35	0.43	3
Predator		-26.68	1.45	0.62	1.15	1.11	1.58	10		-28.08	0.23	1.85	0.26	-0.15	0.16	3
Fish		-24.79	0.95	4.28	1.57	0.17	1.98	15		-24.79	0.95	4.28	1.57	0.17	1.98	15
Collector	SOO	-29.56	1.68	0.23	0.38	-0.64	1.23	2								
Scraper		-33.82	2.39	-0.80	0.20	-3.02	0.19	3								
Shredder		-26.32	2.11	-0.56	2.15	-1.43	4.82	29*								
Predator		-30.20	0.46	2.03	0.05	-1.40	0.22	3								

Appendix 35. Summary statistics for the proportion of each prey source to the diet of American Dippers (n=96) at regulated and unregulated streams. Diet proportions were calculated using a Bayesian mixing model in the program MixSIAR using stable isotope values (δ^{13}C, δ^{15}N, δ^{34}S) fom separate invertebrate samples collected at each stream (n=7 regulated and 7 unregulated)

		Regulated							Unregulated							
Source	**Stream**	**Mean**	**S.D.**	**5%**	**25%**	**50%**	**75%**	**95%**	**Stream**	**Mean**	**S.D.**	**5%**	**25%**	**50%**	**75%**	**95%**
Collector	Brandy	0.18	0.089	0.051	0.11	0.17	0.23	0.34	Mad	0.12	0.101	0.015	0.048	0.094	0.17	0.32
Fish		0.23	0.056	0.14	0.19	0.23	0.27	0.33		0.36	0.076	0.23	0.308	0.36	0.41	0.48
Predator		0.30	0.12	0.11	0.22	0.3	0.38	0.49		0.16	0.114	0.028	0.078	0.14	0.23	0.37
Salmon		0.014	0.009	0.002	0.007	0.013	0.019	0.031		0.008	0.008	0.001	0.003	0.006	0.011	0.025
Scraper		0.078	0.054	0.01	0.036	0.069	0.11	0.18		0.13	0.125	0.004	0.027	0.091	0.21	0.38
Shredder		0.20	0.07	0.096	0.15	0.2	0.25	0.32		0.22	0.115	0.038	0.125	0.22	0.30	0.41
Collector	Fitz	0.12	0.16	0.007	0.023	0.052	0.12	0.55	Roe	0.21	0.144	0.018	0.088	0.187	0.3	0.47
Fish		0.15	0.099	0.02	0.068	0.14	0.22	0.33		0.088	0.056	0.018	0.046	0.077	0.12	0.19
Predator		0.39	0.32	0.025	0.1	0.27	0.74	0.9		0.5	0.203	0.122	0.366	0.52	0.65	0.81
Salmon		0.011	0.014	0	0.002	0.006	0.015	0.04		0.01	0.01	0.001	0.003	0.006	0.013	0.029
Scraper		0.033	0.037	0.002	0.009	0.021	0.043	0.1		0.075	0.071	0.004	0.021	0.053	0.112	0.22
Shredder		0.30	0.22	0.01	0.048	0.34	0.49	0.61		0.12	0.08	0.02	0.055	0.11	0.17	0.26
Collector	Ruth	0.15	0.14	0.017	0.052	0.11	0.2	0.43	Pemb	0.28	0.227	0.018	0.081	0.22	0.45	0.71
Fish		0.22	0.13	0.039	0.11	0.2	0.31	0.45		0.16	0.065	0.051	0.112	0.16	0.20	0.27
Predator		0.15	0.11	0.023	0.068	0.12	0.2	0.34		0.34	0.221	0.035	0.146	0.31	0.51	0.72
Salmon		0.053	0.042	0.001	0.011	0.05	0.087	0.13		0.011	0.011	0.001	0.003	0.007	0.015	0.035
Scraper		0.057	0.061	0.004	0.017	0.037	0.076	0.17		0.059	0.065	0.003	0.015	0.035	0.08	0.20
Shredder		0.37	0.12	0.17	0.3	0.37	0.45	0.57		0.15	0.111	0.018	0.058	0.13	0.22	0.36
Collector	Soo	0.13	0.1	0.016	0.048	0.097	0.18	0.33	Owl	0.11	0.097	0.012	0.038	0.079	0.15	0.29
Fish		0.31	0.13	0.089	0.22	0.31	0.39	0.52		0.59	0.13	0.375	0.51	0.59	0.68	0.79
Predator		0.38	0.18	0.07	0.25	0.40	0.52	0.66		0.16	0.106	0.025	0.073	0.14	0.22	0.36
Salmon		0.031	0.034	0.001	0.005	0.017	0.049	0.1		0.021	0.028	0.001	0.003	0.009	0.028	0.084
Scraper		0.061	0.061	0.004	0.018	0.040	0.083	0.19		0.044	0.043	0.003	0.013	0.03	0.062	0.13
Shredder		0.096	0.071	0.017	0.045	0.078	0.13	0.23		0.083	0.06	0.014	0.037	0.068	0.11	0.20
Collector	Doug	0.17	0.11	0.023	0.074	0.15	0.24	0.37	Gow	0.18	0.131	0.018	0.07	0.16	0.27	0.43
Fish		0.26	0.08	0.13	0.21	0.27	0.31	0.39		0.21	0.092	0.056	0.142	0.211	0.28	0.36
Predator		0.28	0.15	0.051	0.16	0.27	0.39	0.56		0.41	0.21	0.074	0.23	0.4	0.57	0.75
Salmon		0.016	0.016	0.001	0.004	0.010	0.024	0.05		0.012	0.011	0.001	0.003	0.008	0.016	0.036
Scraper		0.079	0.072	0.004	0.024	0.057	0.12	0.22		0.062	0.06	0.004	0.017	0.042	0.088	0.19
Shredder		0.20	0.12	0.038	0.11	0.18	0.27	0.41		0.13	0.08	0.023	0.068	0.12	0.18	0.28
Collector	Fire	0.20	0.14	0.025	0.084	0.17	0.28	0.46	Slo	0.19	0.138	0.015	0.067	0.173	0.29	0.43
Fish		0.22	0.084	0.071	0.16	0.22	0.27	0.35		0.39	0.096	0.223	0.339	0.40	0.45	0.53
Predator		0.29	0.17	0.053	0.16	0.27	0.40	0.60		0.18	0.149	0.022	0.075	0.14	0.25	0.48
Salmon		0.016	0.018	0.001	0.004	0.010	0.023	0.055		0.007	0.007	0.001	0.002	0.005	0.01	0.022
Scraper		0.14	0.12	0.005	0.041	0.12	0.23	0.36		0.06	0.067	0.003	0.015	0.036	0.078	0.2
Shredder		0.14	0.095	0.026	0.069	0.12	0.2	0.32		0.17	0.137	0.021	0.064	0.13	0.24	0.45
Collector	**Tip**	**0.18**	**0.13**	**0.018**	**0.074**	**0.15**	**0.26**	**0.42**								
Fish		0.21	0.11	0.05	0.13	0.20	0.29	0.41								
Predator		0.32	0.2	0.047	0.16	0.29	0.45	0.68								
Salmon		0.012	0.013	0.001	0.003	0.007	0.016	0.037								
Scraper		0.09	0.086	0.004	0.023	0.062	0.13	0.27								
Shredder		0.19	0.14	0.029	0.08	0.15	0.26	0.48								

Appendix 36. Model selection results testing for differences in the mean proportion of **salmon** (arcsine square-root transformed) in the American Dipper diet between regulated and unregulated streams. A linear mixed-effects model was run in R with stream type, elevation, salmon, and interactions between type*elevation included as fixed effects. Watershed was included as a random effect. Models with weight>0 and the null (intercept-only) are presented for comparison.

Response	**Model Structure**	**AICc**[1]	**Δ AICc**	**Deviance**[2]	**Model Weight**	**df**
Salmon diet proportion	**null**	**-31.8**	**0**	-40.44	**0.97**	**3**
	Type	**-24.6**	**7.16**	-37.62	**0.027**	**4**

[1] Akaike's Information Criterion, corrected for small sample sizes

[2] -2 (Log Likelihood)

Appendix 37. Model selection results testing for differences in the mean proportion of **shredders** (arcsine square-root transformed) in the American Dipper diet between regulated and unregulated streams. A general linear model was run in R with stream type, elevation, salmon, and interactions between type*elevation included as fixed effects. Models with weight>0 and the null (intercept-only) are presented for comparison.

Response	**Model Structure**	**AICc**[1]	**Δ AICc**	**Deviance**[2]	**Model Weight**	**df**
Shredder diet proportion	**Elevation**	**-18.7**	**0**	**-27.40**	**0.37**	**3**
	null	**-18.4**	**0.32**	**-23.62**	**0.32**	**2**
	Type	**-17.7**	**1.05**	**-26.36**	**0.22**	**3**
	Type+Elevation	-15.7	3.01	-28.73	0.082	4
	Type*Elevation	-11.5	7.28	-30.02	0.010	5

[1] Akaike's Information Criterion, corrected for small sample sizes

[2] -2 (Log Likelihood)

Appendix 38. Model selection results testing for differences in the mean proportion of **resident fish** (arcsine square-root transformed) in the American Dipper diet between regulated and unregulated streams. A general linear model was run in R with stream type, elevation, salmon, and interactions between type*elevation included as fixed effects. Models with weight>0 and the null (intercept-only) are presented for comparison.

Response	**Model Structure**	**AICc**[1]	**Δ AICc**	**Deviance**[2]	**Model Weight**	**df**
Resident fish diet proportion	**null**	**-9.3**	**0**	-14.476	**0.63**	**2**
	Salmon	**-8.0**	**1.31**	-16.632	**0.33**	**3**
	Type+Salmon	-3.7	5.58	-16.69	0.039	4
	Type+Salmon+ Elevation	1.8	11.13	-16.72	0.0020	5

[1] Akaike's Information Criterion, corrected for small sample sizes

[2] -2 (Log Likelihood)

Appendix 39. Model selection results testing for differences in the mean proportion of **scrapers** (arcsine square-root transformed) in the American Dipper diet between regulated and unregulated streams. A linear mixed-effects model was run in R with stream type, elevation, salmon, and interactions between type*elevation included as fixed effects. Watershed was included as a random effect. Models with weight>0 and the null (intercept-only) are presented for comparison.

Response	**Model Structure**	**AICc**[1]	**Δ AICc**	**Deviance**[2]	**Model Weight**	**df**
Scraper diet proportion	**null**	**-23.4**	**0**	-32.06	**0.99**	**3**
	Type	-14.1	9.30	-27.09	0.0090	4

[1] Akaike's Information Criterion, corrected for small sample sizes

[2] -2 (Log Likelihood)

Appendix 40. Model selection results testing for differences in the mean proportion of **collector-gatherers** (arcsine square-root transformed) in the American Dipper diet between regulated and unregulated streams. A general linear model was run in R with stream type, elevation, salmon, and interactions between type*elevation included as fixed effects. Models with weight>0 and the null (intercept-only) are presented for comparison.

Response	**Model Structure**	**AICc**[1]	**Δ AICc**	**Deviance**[2]	**Model Weight**	**df**
Collector-Gatherer diet proportion	**null**	**-31.1**	**0**	**-36.27**	**0.50**	**2**
	Elevation	**-30.8**	**0.26**	**-39.48**	**0.44**	**3**
	Elevation+Salmon	-26.6	4.49	-39.58	0.053	4

[1] Akaike's Information Criterion, corrected for small sample sizes

[2] -2 (Log Likelihood)

Appendix 41. Model selection results testing for differences in the proportion of **predatory invertebrates** (arcsine square-root transformed) in the American Dipper diet between regulated and unregulated streams. A general linear model was run in R with stream type, elevation, salmon, and interactions between type*elevation included as fixed effects. Models with weight>0 and the null (intercept-only) are presented for comparison.

Response	**Model Structure**	**AICc**[1]	**Δ AICc**	**Deviance**[2]	**Model Weight**	**df**
Predator diet proportion	**null**	**-13.3**	**0**	-18.536	**0.81**	**2**
	Salmon	-10.2	3.12	-18.88	0.17	3
	Type+Salmon	-5.9	7.39	-18.95	0.020	4
	Type+Salmon+ Elevation	-0.5	12.85	-19.06	0.0010	5

[1] Akaike's Information Criterion, corrected for small sample sizes

[2] -2 (Log Likelihood)

Appendix 42. Summary of American Dipper whole blood (n = 92) and feather (n = 97) Hg (mean ± S.E.) at regulated and unregulated streams. Mercury was measured as THg, but can be interpreted as 100% MeHg in dipper blood and feathers.

Stream	Type	n Blood	n Feather	Mean Blood Hg (ng/g ww)	S.E. Blood Hg (ww)	Mean Blood Hg (ng/g dw)	S.E. Blood Hg (dw)	Mean Blood % Moisture	S.E. Blood Moisture	Mean Feather Hg (ng/g dw)	S.E. Feather Hg
Douglas	Regulated	12	12	987.8	167.2	1106.5	182.7	11.1	1.2	3338.6	819.0
Soo	Regulated	2	2	473.1	19.6	525.9	23.6	10.0	0.3	1379.9	616.9
Tipella	Regulated	2	3	452.1	193.0	504.0	223.1	9.5	1.8	914.7	411.2
Madeley	Unregulated	4	3	402.3	129.9	454.9	155.0	10.2	1.5	2311.1	802.6
Sloquet	Unregulated	9	8	354.5	82.9	397.6	98.5	8.9	1.0	986.1	95.7
Gowan	Unregulated	10	10	339.5	38.14	380.5	44.6	10.9	0.8	1086.8	172.1
Rutherford	Regulated	9	10	301.8	17.76	347.6	23.4	12.6	1.7	792.3	78.7
Owl	Unregulated	2	2	294.9	118.5	337.3	135.4	12.6	0.1	942.3	262.6
Roe	Unregulated	7	8	282.8	42.6	312.3	44.6	10.2	1.7	950.6	117.0
Fire	Regulated	5	6	253.8	37.2	290.2	41.6	12.8	2.4	612.9	94.2
Pemberton	Unregulated	7	7	197.4	9.3	225.5	13.5	12.0	1.5	684.0	132.3
Fitzsimmons	Regulated	10	11	158.9	24.7	178.9	27.4	11.4	1.0	504.0	35.9
Brandywine	Regulated	13	15	125.9	21.5	141.9	23.6	11.6	0.7	561.7	131.5
Regulated		53	59	417.6	74.1	466.0	81.3	11.6	0.5	1564.6	367.2
Unregulated		39	38	340.7	42.7	382.6	50.4	10.5	0.5	1149.0	152.1

Appendix 43. Estimates of *post-hoc* Tukey contrasts comparing mean American Dipper blood Hg (ng/g ww) (n=92) between individual regulated and unregulated streams. Significant differences are bolded.

Linear Hypothesis	Estimate	S.E.	z value	Pr(>|z|)	Linear Hypothesis	Estimate	S.E.	z value	Pr(>|z|)
DOUG-BRANDY=0	0.88	0.08	10.88	**<0.01**	**SLO-FITZ=0**	0.32	0.09	3.55	**0.02**
FIRE-BRANDY=0	0.35	0.11	3.26	0.05	**SOO-FITZ=0**	0.51	0.16	3.27	**0.05**
FITZ-BRANDY=0	0.13	0.09	1.48	0.96	**TIP-FITZ=0**	0.45	0.16	2.87	0.16
GOW-BRANDY=0	0.47	0.08	5.64	**<0.01**	**MAD-GOW=0**	0.04	0.12	0.33	1.00
MAD-BRANDY=0	0.51	0.12	4.39	**<0.01**	**OWL-GOW=0**	-0.07	0.16	-0.47	1.00
OWL-BRANDY=0	0.39	0.15	2.57	0.31	**PEMB-GOW=0**	-0.21	0.10	-2.17	0.59
PEMB-BRANDY=0	0.26	0.09	2.70	0.23	**ROE-GOW=0**	-0.09	0.09	-0.97	1.00
ROE-BRANDY=0	0.38	0.09	4.14	**<0.01**	**RUTH-GOW=0**	-0.03	0.09	-0.34	1.00
RUTH-BRANDY=0	0.44	0.09	4.98	**<0.01**	**SLO-GOW=0**	-0.02	0.09	-0.24	1.00
SLO-BRANDY=0	0.45	0.09	5.24	**<0.01**	**SOO-GOW=0**	0.17	0.16	1.09	1.00
SOO-BRANDY=0	0.64	0.15	4.15	**<0.01**	**TIP-GOW=0**	0.11	0.16	0.69	1.00
TIP-BRANDY=0	0.58	0.15	3.74	**0.01**	**OWL-MAD=0**	-0.11	0.18	-0.64	1.00
FIRE-DOUG=0	-0.53	0.11	-4.96	**<0.01**	**PEMB-MAD=0**	-0.25	0.13	-1.98	0.72
FITZ-DOUG=0	-0.76	0.09	-8.73	**<0.01**	**ROE-MAD=0**	-0.13	0.12	-1.06	1.00
GOW-DOUG=0	-0.41	0.08	-4.90	**<0.01**	**RUTH-MAD=0**	-0.07	0.12	-0.58	1.00
MAD-DOUG=0	-0.37	0.12	-3.20	**0.06**	**SLO-MAD=0**	-0.06	0.12	-0.51	1.00
OWL-DOUG=0	-0.49	0.15	-3.15	**0.07**	**SOO-MAD=0**	0.13	0.18	0.75	1.00
PEMB-DOUG=0	-0.63	0.10	-6.50	**<0.01**	**TIP-MAD=0**	0.07	0.18	0.39	1.00
ROE-DOUG=0	-0.51	0.09	-5.47	**<0.01**	**PEMB-OWL=0**	-0.14	0.16	-0.86	1.00
RUTH-DOUG=0	-0.44	0.09	-4.98	**<0.01**	**ROE-OWL=0**	-0.02	0.16	-0.12	1.00
SLO-DOUG=0	-0.44	0.09	-5.02	**<0.01**	**RUTH-OWL=0**	0.04	0.16	0.27	1.00
SOO-DOUG=0	-0.24	0.15	-1.58	0.93	**SLO-OWL=0**	0.05	0.16	0.33	1.00
TIP-DOUG=0	-0.31	0.15	-1.98	0.72	**SOO-OWL=0**	0.24	0.20	1.20	0.99
FITZ-FIRE=0	-0.22	0.11	-2.00	0.71	**TIP-OWL=0**	0.18	0.20	0.89	1.00

GOW-FIRE=0	0.12	0.11	1.11	1.00	**ROE-PEMB=0**	0.12	0.10	1.15	0.99
MAD-FIRE=0	0.16	0.14	1.18	0.99	**RUTH-PEMB=0**	0.18	0.10	1.78	0.85
OWL-FIRE=0	0.05	0.17	0.28	1.00	**SLO-PEMB=0**	0.19	0.10	1.91	0.77
PEMB-FIRE=0	-0.09	0.12	-0.77	1.00	**SOO-PEMB=0**	0.38	0.16	2.36	0.45
ROE-FIRE=0	0.03	0.12	0.25	1.00	**TIP-PEMB=0**	0.32	0.16	1.97	0.73
RUTH-FIRE=0	0.09	0.11	0.79	1.00	**RUTH-ROE=0**	0.06	0.10	0.61	1.00
SLO-FIRE=0	0.10	0.11	0.90	1.00	**SLO-ROE=0**	0.07	0.10	0.73	1.00
SOO-FIRE=0	0.29	0.17	1.72	0.87	**SOO-ROE=0**	0.26	0.16	1.63	0.91
TIP-FIRE=0	0.23	0.17	1.35	0.98	**TIP-ROE=0**	0.20	0.16	1.24	0.99
GOW-FITZ=0	0.34	0.09	3.87	**<0.01**	**SLO-RUTH=0**	0.01	0.09	0.10	1.00
MAD-FITZ=0	0.38	0.12	3.19	0.06	**SOO-RUTH=0**	0.20	0.16	1.27	0.99
OWL-FITZ=0	0.27	0.16	1.72	0.87	**TIP-RUTH=0**	0.14	0.16	0.87	1.00
PEMB-FITZ=0	0.13	0.10	1.31	0.98	**SOO-SLO=0**	0.19	0.16	1.22	0.99
ROE-FITZ=0	0.25	0.10	2.62	0.28	**TIP-SLO=0**	0.13	0.16	0.82	1.00
RUTH-FITZ=0	0.31	0.09	3.35	**0.04**	**TIP-SOO=0**	-0.06	0.20	-0.31	1.00

Appendix 44. Estimates of *post-hoc* Tukey contrasts comparing mean American Dipper feather Hg (ng/g dw) (n=97) between individial regulated and unregulated streams. Significant differences are bolded.

Linear Hypothesis	**Estimate**	**S.E.**	**z value**	**Pr(>|z|)**	**Linear Hypothesis**	**Estimate**	**S.E.**	**z value**	**Pr(>|z|)**
DOUG-BRANDY=0	0.88	0.08	10.88	**<0.01**	**SLO-FITZ=0**	0.32	0.09	3.55	**0.02**
FIRE-BRANDY=0	0.35	0.11	3.26	**0.05**	**SOO-FITZ=0**	0.51	0.16	3.27	**0.05**
FITZ-BRANDY=0	0.13	0.09	1.48	0.96	**TIP-FITZ=0**	0.45	0.16	2.87	0.16
GOW-BRANDY=0	0.47	0.08	5.64	**<0.01**	**MAD-GOW=0**	0.04	0.12	0.33	1.00
MAD-BRANDY=0	0.51	0.12	4.39	**<0.01**	**OWL-GOW=0**	-0.07	0.16	-0.47	1.00

OWL-BRANDY=0	0.39	0.15	2.57	0.31	**PEMB-GOW=0**	-0.21	0.10	-2.17	0.59
PEMB-BRANDY=0	0.26	0.09	2.70	0.23	**ROE-GOW=0**	-0.09	0.09	-0.97	1.00
ROE-BRANDY=0	0.38	0.09	4.14	**<0.01**	**RUTH-GOW=0**	-0.03	0.09	-0.34	1.00
RUTH-BRANDY=0	0.44	0.09	4.98	**<0.01**	**SLO-GOW=0**	-0.02	0.09	-0.24	1.00
SLO-BRANDY=0	0.45	0.09	5.24	**<0.01**	**SOO-GOW=0**	0.17	0.16	1.09	1.00
SOO-BRANDY=0	0.64	0.15	4.15	**<0.01**	**TIP-GOW=0**	0.11	0.16	0.69	1.00
TIP-BRANDY=0	0.58	0.15	3.74	**<0.01**	**OWL-MAD=0**	-0.11	0.18	-0.64	1.00
FIRE-DOUG=0	-0.53	0.11	-4.96	**<0.01**	**PEMB-MAD=0**	-0.25	0.13	-1.98	0.72
FITZ-DOUG=0	-0.76	0.09	-8.73	**<0.01**	**ROE-MAD=0**	-0.13	0.12	-1.06	1.00
GOW-DOUG=0	-0.41	0.08	-4.90	**<0.01**	**RUTH-MAD=0**	-0.07	0.12	-0.58	1.00
MAD-DOUG=0	-0.37	0.12	-3.20	**0.06**	**SLO-MAD=0**	-0.06	0.12	-0.51	1.00
OWL-DOUG=0	-0.49	0.15	-3.15	**0.07**	**SOO-MAD=0**	0.13	0.18	0.75	1.00
PEMB-DOUG=0	-0.63	0.10	-6.50	**<0.01**	**TIP-MAD=0**	0.07	0.18	0.39	1.00
ROE-DOUG=0	-0.51	0.09	-5.47	**<0.01**	**PEMB-0WL=0**	-0.14	0.16	-0.86	1.00
RUTH-DOUG=0	-0.44	0.09	-4.98	**<0.01**	**ROE-0WL=0**	-0.02	0.16	-0.12	1.00
SLO-DOUG=0	-0.44	0.09	-5.02	**<0.01**	**RUTH-0WL=0**	0.04	0.16	0.27	1.00
SOO-DOUG=0	-0.24	0.15	-1.58	0.93	**SLO-0WL=0**	0.05	0.16	0.33	1.00
TIP-DOUG=0	-0.31	0.15	-1.98	0.72	**SOO-0WL=0**	0.24	0.20	1.20	0.99
FITZ-	-0.22	0.11	-2.00	0.71	**TIP-0WL=0**	0.18	0.20	0.89	1.00

FIRE=0									
GOW-FIRE=0	0.12	0.11	1.11	1.00	**ROE-PEMB=0**	0.12	0.10	1.15	0.99
MAD-FIRE=0	0.16	0.14	1.18	0.99	**RUTH-PEMB=0**	0.18	0.10	1.78	0.85
OWL-FIRE=0	0.05	0.17	0.28	1.00	**SLO-PEMB=0**	0.19	0.10	1.91	0.77
PEMB-FIRE=0	-0.09	0.12	-0.77	1.00	**SOO-PEMB=0**	0.38	0.16	2.36	0.45
ROE-FIRE=0	0.03	0.12	0.25	1.00	**TIP-PEMB=0**	0.32	0.16	1.97	0.73
RUTH-FIRE=0	0.09	0.11	0.79	1.00	**RUTH-ROE=0**	0.06	0.10	0.61	1.00
SLO-FIRE=0	0.10	0.11	0.90	1.00	**SLO-ROE=0**	0.07	0.10	0.73	1.00
SOO-FIRE=0	0.29	0.17	1.72	0.87	**SOO-ROE=0**	0.26	0.16	1.63	0.91
TIP-FIRE=0	0.23	0.17	1.35	0.98	**TIP-ROE=0**	0.20	0.16	1.24	0.99
GOW-FITZ=0	0.34	0.09	3.87	**<0.01**	**SLO-RUTH=0**	0.01	0.09	0.10	1.00
MAD-FITZ=0	0.38	0.12	3.19	**0.06**	**SOO-RUTH=0**	0.20	0.16	1.27	0.99
OWL-FITZ=0	0.27	0.16	1.72	0.87	**TIP-RUTH=0**	0.14	0.16	0.87	1.00
PEMB-FITZ=0	0.13	0.10	1.31	0.98	**SOO-SLO=0**	0.19	0.16	1.22	0.99
ROE-FITZ=0	0.25	0.10	2.62	0.28	**TIP-SLO=0**	0.13	0.16	0.82	1.00
RUTH-FITZ=0	0.31	0.09	3.35	**0.04**	**TIP-SOO=0**	-0.06	0.20	-0.31	1.00