Conservation behaviour in action: using fish behaviour to understand and mitigate the impacts of hydropower development

by

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Dirk. A. Algera
Dedication

This thesis is dedicated to all the fish that (un)willingly participated in any of mine and other researcher’s projects. This thesis, or fish-related conservation research for that matter, would not be possible without you.
Abstract

The impacts that hydropower facilities have on non-anadromous downstream migrants and other resident freshwater fish are increasingly being recognized by environmental managers. The overall goal for my thesis was to apply conservation behaviour and risk analysis approaches to inform decision making for avoiding/mitigating common hydropower-related hazards faced by freshwater fish. Specifically, the thesis considers the risks of injury and mortality from entrainment and exposure to supersaturated total dissolved gasses (TDG).

Many studies have quantified entrainment-related mortality and injury, but these studies generated site-specific data. To address this knowledge gap, I conducted a systematic review to quantify the risk associated with common hydropower infrastructure. My results revealed an increased overall injury and mortality risk resulting from entrainment relative to control fish. An increased risk was also revealed for several infrastructure types and fish taxa. To examine the re-entrainment risk of a freshwater resident fish, I tracked the movements of salvaged Kokanee salmon in the forebay area of a large hydropower facility. Telemetry data revealed minimal re-entrainment risk for salvaged Kokanee at the facility. Several studies have examined spatial-temporal movements of diadromous fish relative to TDG levels, but few have examined resident fish species. To examine the TDG exposure risk of resident fish, TDG was modeled in an impounded hydro-affected river system, and I tracked Rainbow Trout and Mountain Whitefish movement and depth use. Telemetry data revealed patterns in MW reach and depth residency that corresponded to spawning, foraging, and refuge behaviour whereas RT exhibited high site fidelity in one area of the system. The risk assessment revealed that Rainbow Trout had a higher TDG risk exposure relative to Mountain Whitefish, and that risk was highest in both species at locations near one of the hydropower facilities.
The results presented in this thesis are novel in that they provide some of the first empirical data to quantify the risk of common hazards associated with hydropower facilities and will, therefore, be useful from a hydropower management perspective. Moreover, this thesis provides an example of how to incorporate fundamental behavioural research into hydropower management regimes and frameworks through the use of risk analysis.
Acknowledgements

I would first and foremost like to thank my advisors Dr. Steven Cooke and Dr. Michael Power for their support and guidance throughout my degree. I have been fortunate to work with several top-notch graduate and undergraduate students, technicians, and managers throughout my graduate degrees in the Fish Ecology and Conservation Physiology Lab and the greater Carleton community. My time here has resulted in many great friendships and collaborations. I have been fortunate to meet so many inspirational people throughout my time in the lab and I look forward to continuing to work with many past and present colleagues in the future. I am especially grateful to T. Ward, J. Bergman, B. Hlina, A Zolderdo, M. Lawrence, N. Lapointe, A. Jeanson, C. Elvidge, E. Tuononen, N. Pliezier, and J. Monoghan, all of whom provided me with support, great discussions, and opportunities to blow off some steam over the years. I could not have completed this degree without you.

Field work always brings some interesting challenges and working in northeastern BC on Williston Reservoir was awe inspiring, but certainly had no shortages of challenges to navigate. I would like to thank R. Zemlak, B. Rowe, P. Morris, I. Hofer, R. Hall, A. Leake, M. MacArthur, and the countless BC Hydro staff members for their advice, logistical assistance, and support. Field work in southeastern BC on the Columbia River was an amazing experience and could not have been done without extensive advice and logistical assistance from J. Crossman, M. Marello, D. Ford, C. King and other staff at Golder, and R. Zavaduk and others in the Castlegar Fly Fishing club for their assistance with angling. A special thank you to L. Masson for help with fish telemetry data collation for the Columbia-Kootenay system.

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grounding me when I was going off the rails. Lastly, a huge shoutout to my dog Duke who has been here with me for my BSc, MSc, and now PhD. I wish you could understand how much you have helped me over these years, such a good boy.
Preface

All research presented in this thesis was conducted following animal care protocols in accordance with the Animal Care Council of Canada guidelines as administered by Carleton University. All animal collection was done under provincial scientific collection permits administered by the British Columbia Ministry of Forests, Lands, and Natural Resource Operations.

Thesis Format and Co-authorship

This thesis consists of five chapters, three of which are written in manuscript format (Chapters 2, 3, and 4). Chapter 1 provides general background information and thesis objectives. Chapter 2 is a systematic review and meta-analysis of the literature on the relative risks and magnitude of mortality and/or injury attributable to hydropower facilities and associated infrastructure. Chapter 3 examines the vulnerability of salvaged Kokanee salmon to entrainment in a large hydropower facility. Chapter 4 examines the reach and depth use of Rainbow Trout and Mountain Whitefish in relation to modelled supersaturated total dissolved gas levels, and assesses the exposure risks associated with these species. Chapter 5 summarizes my general conclusions, the relevance of my research, and proposes future research to address limitations and knowledge gaps resultant from the studies conducted in the present thesis. This thesis is composed of research that is all my own work, but much of it was conducted in collaboration with several other parties who are outlined below.

Chapter 1: General introduction, thesis objectives and scientific contributions.

Chapter 2 (published): What are the relative risks of mortality and injury for fish during downstream passage at hydroelectric dams in temperate regions? A systematic review.

This systematic review was designed by Algera, Rytwinski, Taylor, Smokorowski, and Cooke. Algera collected and processed the data with supplementary contributions from data technicians. Algera and Rytwinski analysed the data and wrote the paper. Bennett, Smokorowski, Harrison, Clarke, Enders, Power, Bevelhimer, and Cooke all contributed to final manuscript preparation.

Chapter 3 (published): Stranded Kokanee salvaged from turbine intake infrastructure are at low risk for re-entrainment: A telemetry study in a hydropower facility forebay.


This study was designed by Algera, Ward, Power, and Cooke. Algera collected and processed the data with significant contributions from Ward and Zemlak. Leake, Crossman, Power, and Cooke provided equipment. Algera analysed the data and wrote the paper. Harrison, Crossman, Power, and Cooke all contributed to final manuscript preparation.

Chapter 4 (unpublished): Exposure risk of fish downstream of a hydropower facility to supersaturated total dissolved gas: An acoustic telemetry study.


This study was designed by Algera, Power, and Cooke. Ward, Kamal, and Crossman contributed to data collection, modeling, and field work support. Crossman, Zhu, Power, and Cooke
provided equipment and logistical support. Algera analyzed the data and wrote the paper, which is currently in preparation for submission to the journal River Research and Applications.

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Chapter 1: General Introduction

In this thesis I examine the role that movement-related behaviours play in mitigating or aggravating the risk of harm to fish in hydropower impounded systems. More specifically, I quantify the risk of harm that hydropower developments have on fish overall, and by examining movements of resident fish, assess the risk of two specific hazards common to hydropower impounded systems: entrainment and elevated total dissolved gasses (TDG). This general introduction provides the broader background information for understanding the development of the ideas, objectives, hypotheses, rationale, and predictions outlined in this thesis. The subsequent chapters provide more context-specific background information. First, I present some background on fish movement, migration, and resident fish, which includes Kokanee (Oncorhynchus nerka), Rainbow Trout (Oncorhynchus mykiss), and Mountain Whitefish (Prosopium williamsoni), the focal study species for two chapters of this thesis (Section 1.1). Next, I provide some context on hydropower developments and their impacts on fish (Section 1.2), using fish behaviour to avoid and/or mitigate these impacts (1.3), and the role of risk management at hydropower facilities (Section 1.4). Lastly, I outline the rationale, objectives, hypotheses, and predictive framework for this thesis (Section 1.5).

1.1 Freshwater fish movement and migration

Fish undertake locomotor-based behaviours to fulfill various requirements for fitness related vital rates (i.e., growth, survival, reproduction). This thesis focuses on hydropower facilities that can affect the movement and/or migration and key locomotor-based behaviours at multiple temporal and spatial scales. Many definitions of movement and migration exist in the literature. For the purposes of this thesis, movement is defined as when individual fish decide to change location or position among or within habitats in their home range (Morais and Daverat...
2016), whereas migration is defined as when individuals or (parts of) populations move between well defined habitats on a temporally predictable basis (Dingle and Drake 2007). Movements typically occur at a smaller spatial scale and commonly include changing positions within home range habitats for foraging or predator avoidance purposes. Migrations typically occur at a larger spatial scale and consist of directed, undistracted, bi-directional movements between different habitats (Lucas and Baras 2008; Tamario et al. 2019). For example, migrations can span long distances between freshwater and oceanic habitats (or vice versa) for feeding and spawning purposes, include movement from littoral to pelagic zones within the same waterbody, or temporary diel shifts in position for foraging and predator avoidance (Chapman et al. 2011, 2012, Bronmark et al. 2013). There is considerable overlap in the locomotor-based behaviours examined in the subsequent chapters of this thesis, and it was not always possible to determine whether the behaviours could be classified as movements or migration per se as defined above, so both terms will occur throughout this thesis.

Fish are often characterized by their migratory behaviour for fisheries management and conservation purposes (Fausch et al. 2002; Homel et al. 2015). Diadromous fish include anadromous (e.g., *Oncorhynchus* spp., Pacific salmon) and catadromous (e.g., *Anguilla* spp., Eels) fish that perform largescale migrations, using freshwater and oceanic ecosystems to complete their lifecycle. Anadromous fish, particularly those of the *Salmonidae*, have historically received most of the freshwater fisheries management focus because they are associated with high economic and social value (Gephard and McMenemy 2004; Williams et al. 2012; Hand et al. 2018). However, it has become clear over the last few decades that management regimes targeted solely to anadromous species are not resulting in the desired freshwater fisheries conservation outcomes (Dettmers et al. 2012; Katopodis and Williams 2012). Upstream fish
passage via fishways remains problematic for most species and fishway designs (Hershey 2021). Mallen-Cooper and Brand (2007) reviewed 50 years of monitoring data for a salmonid-designed fishway intended to pass non-salmonid fishes. The authors found that fish passage was very poor, especially among native species, < 1% of the most abundant species ascended the fishway, and three native species declined by 95-100%. Recognizing the ecological value and importance of non-target species to ecosystem function, fisheries managers are increasingly shifting towards an inclusive fisheries management regime for hydropower impounded systems that specifically considers non-target species such as resident freshwater fish (WWF 2021).

Kokanee (Oncorhynchus nerka), Rainbow Trout (Oncorhynchus mykiss), and Mountain Whitefish (Prosopium williamsoni), the focal study species in two of the chapters of this thesis, are resident fish that occupy freshwater systems for their entire lifecycle. Some resident fish undertake potadromous migrations whereby the fish migrates and completes its lifecycle within different areas of a freshwater system. There are several variants of resident fish, but the key types include stream resident, fluvial, and adfluvial fish. Stream resident fish occupy the same watercourse, usually a tributary or small headwater, throughout their lifecycle. Fluvial and adfluvial fish spawn and spend their juvenile stages in smaller tributaries but migrate to grow and mature in a larger mainstem river or a lake, respectively. Resident and potadromous fish populations are distributed worldwide, and similar to their anadromous counterparts are composed of species that are considered ecologically, socially, and economically valuable (Hutt et al. 2013; Lynch et al. 2016). As with anadromous fishes, many of the activities associated with hydropower production disrupt and affect the movement and migration patterns of resident fish (Cote et al. 2009; Harrison et al. 2019; Schwevers and Adam 2020).
1.2 Impacts of hydropower developments

Hydropower is the biggest source of renewable electricity worldwide by a wide margin (Kosnik 2008; IEA 2016; bp 2020). Although hydroelectric carbon footprints are lower relative to other energy sources (Kosnik 2008), hydropower is not without its issues (reviewed in Botelho et al. 2017). For example, in an aquatic context, development alters the biotic and abiotic dynamics of aquatic systems, impacting fish and other aquatic organisms (McCartney 2009) and threatens freshwater ecosystems in general (Vörösmarty et al. 2010; Liermann et al. 2012). On a system-wide scale, hydropower contributes to fish mortality and declines in fish productivity through a variety of means such as changes in water quality, streamflow and habitat alterations, and habitat fragmentation (Rosenberg et al. 1997; Hall et al. 2012; Harnish et al. 2014; but see Welch et al. 2008). Hydropower developments impede connectivity and disrupts resource availability along watercourses (Hirsch et al. 2017; Barbarossa et al. 2020; Duarte et al. 2021), which can have varying impacts on upstream and downstream aquatic systems and fish.

1.2.1 Large scale impacts

One of the greatest impacts of hydropower development is habitat fragmentation whereby hydropower infrastructure impedes upstream and/or downstream connectivity, preventing or delaying fish migration, ultimately contributing to imperilment and losses in biodiversity (Rosenberg et al. 1997; Junge et al. 2014; Mattocks et al. 2017). Habitat fragmentation is widely regarded as one of the biggest threats to animal biodiversity (Fahrig 2003). The placement of a hydropower facility plays an important role in determining the magnitude of the impacts it has on both resident fish and aquatic systems as a whole. Barriers located in the lower reaches of the system (i.e., river mouth) have a greater impact on diadromous fish whereas barriers located in the centre of a system have a greater impact on potadromous fish (Cote et al. 2009). Owing to
long distance migrations and the serious consequences of blocking upstream migration, impacts of hydropower development on economically valuable diadromous and some potadromous fish are well documented (Gephard and McMenemy 2004; Brown et al. 2013). Consequently, upstream passage structures (e.g., fishways) are typically designed for anadromous species, most often salmonids (Novak et al. 2004; Roscoe and Hinch 2010). However, migration is an important movement behaviour occurring at a variety of spatio-temporal scales and displayed by a variety of freshwater fish (Chapman et al. 2011; 2012, Bronmark et al. 2013). Thus, freshwater resident and potadromous fish can also be impacted by hydropower development (Harrison et al. 2019, Schwevers and Adam 2020), but they receive far less attention and management focus relative to diadromous fish.

Though migration or movement is not always required for population maintenance/persistence, potadromous fish may navigate through hydropower infrastructure for spawning and foraging purposes (Northcote 1997). While these migrations are typically at more local scales relative to diadromous fish (Hilderbrand and Kershner 2000), resident fish nevertheless provide valuable contributions to ecosystem structure and function. For example, in sympatry with anadromous counterparts, resident freshwater fish can make greater reproductive contributions to fish productivity in the upper reaches of lotic environments (Charles et al. 2004). Resident fish also contribute to energy flow, transferring energy and nutrients from the lower trophic levels to apex predators. In lotic systems this nutrient transfer varies along the length of watercourses (Vannote et al. 1980; Wipfli et al. 2003), so hydropower developments blocking upstream/downstream access for resident fish may impede energy flow in a lotic system. Owing to a greater understanding of the importance of system connectivity for all species in the fish community, design considerations are now being incorporated into upstream and downstream
passage infrastructure for a wider variety of species (Katopodis and Williams 2012; Silva et al. 2018; Schwevers and Adam 2020).

1.2.2 Fish injury and mortality

Preventing or minimizing fish interactions with hydropower infrastructure is an issue biologists and hydropower engineers have been addressing for decades (Katopodis and Williams 2012). Entrainment, when animals (non-)volitionally pass through hydropower infrastructure (e.g., turbines, spillways), and impingement, when fish become trapped against infrastructure (e.g., screen), can be significant sources of fish injury and mortality (OTA 1995; Pracheil et al. 2016), especially in lotic systems with multiple hydropower facilities (Budy et al. 2002). Additionally, when no upstream connectivity exists (i.e., no fishway or useable passage infrastructure), fish that survive entrainment events are permanently lost to the upstream population.

The passage route that a fish must navigate through can be an important factor in entrainment outcomes (i.e., survival, injury), as different passage routes may be more dangerous than others in terms of fish injury and mortality. Turbine passage, often the only option for downstream passage when no passage structures or operational alterations are provided, is the greatest source of injury and mortality (Muir et al. 2001). Passage routes through other hydropower infrastructures (e.g., spillways, bypasses) are believed to generate less mortality (Muir et al. 2001), but can be unpopular choices for hydropower operators because of trade-offs with operating efficiencies and lost revenues (e.g., spilling water). Furthermore, spilling water over spillways can produce elevated levels of supersaturated total dissolved gasses (TDGs). This occurs when atmospheric gases mix with the water passing through the gates, air bubbles become entrained, and the bubbles dissolve into the water in the plunge pool at the base of the
spillway. Fish tissues and blood can become supersaturated with TDGs, they can accumulate and come out of solution (i.e., nucleate) under conditions of sudden changes in temperature and pressure, which can result in the development of gas bubble trauma (GBT) (Bouck 1980, Weitkamp and Katz 1980, Pleizier et al. 2020a). As a result of GBT, bubbles can form in the fins, skin, or behind the eyes, whereas more severe injuries such as bubbles forming in the blood or gills can cause mortality. Injury and mortality resulting from GBT depends on the duration and the level of TDG exposure. In Rainbow Trout (*Oncorhynchus mykiss*), mortality rarely occurs from exposure to < 110% TDG, takes roughly 10 days to occur at 110%, and can be as rapid as 2 h at 140% (Pleizier et al. 2020a).

### 1.3 Using fish behaviour to reduce harm

Fish behaviour and correlated traits are important considerations for effectively mitigating hydropower-related impacts on fish (Coutant and Whitney 2000). Fish residing in or frequenting the forebay area of a hydropower facility face increased entrainment risk, which itself is behaviourally influenced by body size and behaviour (Čada and Schweizer 2012; Prach et al. 2016). The downstream passage route chosen by fish may be affected by behavioural traits such as preferential attraction flows, which can differ among species and life stage. During turbine passage large fish have a greater risk of injury and/or mortality relative to small fish (Ferguson et al. 2008). Body size mediates behavioural responses, scaling with physiological processes, swimming kinematics, and life history traits (Blueweiss et al. 1978; Webb et al. 1984; Goolish 1991), and has a significant influence on foraging (Webb 1984; Byström et al. 2006). Foraging behaviour may increase entrainment risk for species whose food resources are proximately abundant around turbine and spillway intakes (Coutant and Whitney 2000). Depth use also contributes to entrainment risk because turbine intakes can be located at
considerable water depths. Thus benthic oriented species (i.e., fish with colder thermal or depth foraging preferences) could be at increased risk of entrainment relative to pelagic species, and visa versa for surface intakes (Kasul and Conley 1992; Maiolie and Elam 1996; Smith 2000; Harrison et al. 2016).

Owing to the costs of retrofits or lost profits from operational changes, infrastructure and operational alterations are typically directed at enhancing upstream and/or downstream passage for a limited set of target species and/or life stages having economic, recreational and/or subsistence fishery value (Gephard and McMenemy 2004; Williams et al. 2012). There are well over 1,100 freshwater fish species in 50 families in North America (Warren Jr. and Burr 2014), many of which would be affected by hydropower developments. No extensive reviews of Canadian fish taxa are available, but existing reviews and compendiums in the United States highlight the focus on a handful of target species for entrainment studies. For example, Winchell et al. (2000) conducted a comprehensive review compiling entrainment data from over 100 hydropower projects in the United States, and the data only encompassed about 30 fish species, most of which were valued for their fisheries importance. Taking behaviour into account for designing fish passage enhancements that encompass a wide variety of species and life stages can prove difficult owing to the among species differences in physical capabilities (swimming, jumping) and hydrological preferences (e.g., attraction flow) (Williams et al. 2012). What is appropriate for salmonids may not be effective for other species (Gephard and McMenemy 2004). Differences among life history stages may further complicate approaches to enhancing passage. For example, most juvenile salmonids exhibit positive rheotactic behaviour prior to smolt development (Enders et al. 2009), a behaviour very different to that of smolts and adults migrating downstream which swim with the current (Thorpe and Morgan 1978).
Advances in fish passage enhancement have often employed a trial and error approach, which can be appropriate when basic knowledge is lacking (Williams et al. 2012). The trial and error approach is time consuming, costly, and passage efficiency gains are often only applicable to a few species (Čada et al. 2006, Williams et al. 2012). Mitigation efforts based on the trial and error approach have been largely unsuccessful (Brown et al. 2013). Conservation behaviour, where conceptual animal behaviour research is used to inform practical decision making and to understand and solve conservation related issues, is being increasingly embraced by conservation managers and resource practitioners (Caro 1998; Festa-Blanchet and Apollonio 2003; Cooke et al. 2014; Brooker et al. 2016). However the complex nature of the analyses, individual level focus, and high variation found within behavioural data in an ecological context makes extrapolation of obtained results to the population level difficult, and can complicate the implementation of analytical conclusions by environmental managers (Caro 1999; 2007; Cooke et al. 2014). Thus, conservation research using fundamental and conceptual animal behaviour (see Berger-Tal et al. 2011) is lacking in developed frameworks for the assessment of hydropower mitigation strategies.

Biotelemetry technologies are used to remotely track fish (Cooke et al. 2013) and provide a means for a mechanistic approach to fundamental and applied behavioural ecology and conservation planning (Cooke et al. 2004; Simpfendorfer et al. 2010; Donaldson et al. 2014). Acoustic telemetry produces high resolution spatial and temporal data, and thus is now commonly used as a tool for observing and analysing fish behaviour around hydropower facilities and infrastructure (e.g., Steig and Holbrook 2012; Martins et al. 2014; Harrison et al. 2019). For these reasons, acoustic telemetry is an effective tool for applying a conservation behaviour approach to hydropower-related management and conservation efforts.
1.4 Risk management at hydropower facilities

Regulatory approaches to reducing environmental impacts, including for hydropower-developments, often follow a mandate that harm should be avoided, and if this is not possible then mitigated, or as a last resort compensated. That is the case in Canada where the federal department of Fisheries and Oceans is responsible for enforcing the fish habitat provisions of the Fisheries Act (see Fisheries and Oceans Canada, 2019). Existing hydropower developments undoubtedly have negative impacts on fish, so the goal of environmental managers and hydropower operators is to avoid or mitigate further harm. The direct and indirect impacts of a facility may not be known, may lack comprehensive empirical data, or the data may have high uncertainty. Thus, existing data may not be reasonably or easily extrapolated (e.g., onto other species) to inform decision-making for a particular impact. In these situations, characterizing the risk that hydropower-related infrastructure and activities pose to fish can be used to aid managers in decision-making and ideally to decrease the probability and impact of hazardous events. Risk can broadly be defined as the probability and severity of a hazardous event occurring (Burgman 2005). More specifically, in the context of this thesis risk describes the probability (likelihood) of an event of a given magnitude occurring. An environmental risk management cycle, which involves problem formulation, hazard assessment, risk analysis, sensitivity analysis, and monitoring, is a tool used by regulators and proponents to guide planning and decision-making to reduce or eliminate the probability and severity of hazards (Burgman 2005; Shaktawat and Vadhera 2021). The underlying philosophy driving a risk management cycle is akin to adaptive management such that it feeds back into itself to permit learning and ideally reduce uncertainties for future decision-making (Burgman 2005). Risk management can be used for decision-making on mitigating or avoiding a variety of hydropower-related environmental and ecological risk
factors including impacts at the whole project level (Tang et al. 2013) and to specific risk factors such as: biodiversity and biomass loss (Ziv et al. 2012), and fish entrainment and/or impingement (Langford et al. 2016; Harrison et al. 2019; van Treeck et al. 2021).

The goals of the problem formulation process are to: 1) define the scope of the problem and the types of solutions, and 2) define the type(s) of risk assessment used. In a hydropower context, problem formulation would define the problem that fish will be impacted by the facility and how they will be affected by decision-making. Following problem formulation, a tiered process of hazard identification and assessment, and risk assessment, analysis, and evaluation (henceforth referred to as risk analysis) is conducted (Burgman 2005; Shaktawat and Vahera 2021). The risk analysis components of the risk management cycle are the most pertinent components to the studies conducted in this thesis. For hydropower developments, an environmental or ecological risk analysis is almost always required and conducted for relicensing existing facilities, retrofits or construction activities, and siting/building of new facilities (Shaktawat and Vahera 2021). Briefly, when using fish entrainment as an example risk factor, hazard identification would list the possible hazards (e.g., entrainment of certain species) without quantifying them. In the hazard assessment process decision-makers would describe the possible consequences of the hazards (e.g., mortality, injury) and the ways in which they may occur (e.g., turbine blade strike). In the risk assessment process decision-makers assign probabilities to quantify the hazards (e.g., through controlled release studies) and assesses the potential of a hazard having an effect (e.g., likelihood or relative likelihood of entrainment affecting fish). Risk can then be analyzed and evaluated through qualitative methods such as risk ranking and logic trees, or through quantitative methods such as Monte Carlo (Burgman 2005).
1.5 Rationale, goals, objectives, hypothesis, challenges, and scientific contributions

1.5.1 Rationale

Hydropower presents a relatively successful example of behavioural research translating to successful management outcomes. There has been uptake of behavioural research in upstream passage, resulting in greater usage and passage efficiency for many species (Silva et al. 2018). Research on harm prevention devices (e.g., screens) and operational regimes (e.g., flow dynamics and approach velocity around infrastructure) have led to reductions or avoidance of turbine entrainment (Schwevers and Adam 2020). Operational regimes have been developed and implemented to reduce TDG to levels that, if adhered to, could reduce the risk of incidences of gas bubble disease in fish in the studied systems (Feng et al. 2018; Witt et al. 2020). Research to develop or enhance behavioural guidance devices (Hansen et al. 2018; Elvidge et al. 2018) and “fish friendly” turbines (Foust et al. 2011; Amaral et al. 2020; Schwevers and Adam 2020) have used fish behaviour to drive infrastructure design and show promise for avoiding harm, but these technologies remain largely experimentally unproven to date. Irrespective of these efforts and successes, improving downstream fish passage and entrainment/impingement related injuries and mortalities (Knott et al. 2019; Cooke et al. 2020; Schwevers and Adam 2020; Zielinski and Freiburger 2020), and reducing the generation of elevated supersaturated TDGs (Ma et al. 2018; Kamal et al. 2019; Yuan et al. 2020) remain as persistent problems for hydropower impounded systems. These hydropower related issues were recently identified as prominent research priorities for fish migration conservation science and policy by leading researchers in the field (Lennox et al. 2019; Reid et al. 2019). Moreover, the behaviour of resident fish and the magnitude of risk associated with downstream passage, entrainment, and TDG exposure are relatively understudied.
1.5.2 Goal, objectives, and hypothesis

The overall goal of my thesis is to apply conservation behaviour and risk analysis approaches to guide decision-making for avoiding or mitigating hydropower-related hazards to freshwater fish. More specifically, my objective for this thesis is twofold: 1) to synthesize the magnitude of risk that hydropower facilities and associated infrastructure have on freshwater fish downstream passage; 2) to examine movement-related behaviours that mitigate or aggravate the risk of harm to freshwater resident fish in systems with hydropower developments. My overarching aim for the thesis is to demonstrate that a conservation behavior approach can be used to determine associated risk levels and inform management decision-making for avoiding or mitigating hydropower-related impacts on resident freshwater fish.

To this end, my thesis includes upstream and facility-level components examining entrainment risk and a downstream component examining supersaturated TDG exposure risk (Figure 1.1). Individual chapters in this thesis are arranged logically in a framework such that I first place the overall risk of hydropower facilities into context by conducting a systematic literature review and meta-analysis to determine the magnitude of mortality and injury risk from entrainment and/or impingement associated with common hydropower infrastructure (i.e., upstream/facility-level component). Next, I examine Kokanee salmon (*Oncorhynchus nerka*) entrainment risk after being salvaged from intake towers at a large hydropower facility (facility-level component). Finally, I assess the exposure risk of resident Rainbow Trout (*Oncorhynchus mykiss*) and Mountain Whitefish (*Prosopium williamsoni*) to supersaturated TDG levels in a system impounded by two hydropower facilities.
1.5.3 Challenges

There were some logistical challenges in completing the studies for this thesis that resulted in changes to the research questions and objectives that I was intending to address. The original study design of Chapter 3 was to examine fine scale behaviour of Kokanee salmon. Despite having an extensive hydrophone array, the equipment could not achieve sufficient spatial resolution for fine scale behavioural analysis. Furthermore, the tagged fish did not remain in the array long enough to evaluate their fine scale behaviour. The Chapter 4 study was originally to be conducted in the same system as Chapter 3 (Williston Lake) to provide a more complete synthesis of the effects of a single hydropower facility (W.A.C. Bennett facility). However, operational and dam maintenance considerations forced the industrial partner to change their operational plans for the facility such that no large-scale release of water for TDG generation could occur, making the study and modelling of TDG effects impossible. Consequently, the TDG study of Chapter 4 was changed to another location (Columbia River), shifting the focus of the study to other species and their habitats.

1.5.4 Scientific contribution

Freshwater fish populations are in rapid decline worldwide (Deinet et al. 2020; WWF 2021). Given the global rapid expansion of hydropower, especially in the developing world where basic biological knowledge is lacking (Anderson et al. 2018; Barbarossa et al. 2020), mechanistic conservation behaviour approaches are needed to help inform decision-makers attempting to avoid or mitigate the potential impacts of hydropower on freshwater fish and other aquatic taxa (Reid et al. 2019). From a hydropower management perspective, a systematic review and meta-analysis can quantify the overall and infrastructure-specific risk levels, which could then be used as proxy baseline data where site-specific data are lacking. Several studies
examine fish movements in relation to TDG levels, but none of these studies have placed their results in context for management purposes by conducting a risk analysis to inform operational decision making regarding TDG risk abatement. Additionally, to my knowledge, no studies exist that examine the entrainment of fish salvaged from turbine infrastructure. This thesis will also contribute to addressing other biological knowledge gaps. Behavioural studies on resident freshwater fish and small fish (i.e., small body size, juvenile) in impounded systems are underrepresented in the literature (Roscoe and Hinch 2010). For example, at a species level, relatively little is known regarding Kokanee and Mountain Whitefish spatial and temporal movements around hydropower facilities.

**Figure 1.1:** Organization and framework outlining specific aspects of impacts associated with hydropower facilities addressed in each data chapter of this thesis.
Chapter 2: What are the relative risks of mortality and injury for fish during downstream passage at hydroelectric dams in temperate regions? A systematic review

2.1 Abstract

**Background.** – Fish injury and mortality resulting from entrainment and/or impingement during downstream passage over/through hydropower infrastructure has the potential to cause negative effects on fish populations. The primary goal of this systematic review was to address two research questions: (1) What are the consequences of hydroelectric dam fish entrainment and impingement on freshwater fish productivity in temperate regions?; (2) To what extent do various factors like site type, intervention type, and life history characteristics influence the consequences of fish entrainment and impingement?

**Methods.** – The review was conducted using guidelines provided by the Collaboration for Environmental Evidence and examined commercially published and grey literature. All articles found using a systematic search were screened using a priori eligibility criteria at two stages (title and abstract, and full-text, respectively), with consistency checks being performed at each stage. The validity of studies was appraised and data were extracted using tools explicitly designed for this review. A narrative synthesis encompassed all relevant studies and a quantitative synthesis (meta-analysis) was conducted where appropriate.

**Review findings.** – A total of 264 studies from 87 articles were included for critical appraisal and narrative synthesis. Studies were primarily conducted in the United States (93%) on genera in the Salmonidae family (86%). The evidence base did not allow for an evaluation of the consequences of entrainment/impingement on fish productivity per se; therefore, the risk of freshwater fish injury and mortality owing to downstream passage through common hydropower
infrastructure was evaluated. The quantitative synthesis suggested an overall increased risk of injury and immediate mortality from passage through/over hydropower infrastructure. Injury and immediate mortality risk varied among infrastructure types. Bypasses resulted in decreased injury risk relative to controls, whereas turbines and spillways were associated with the highest injury risks relative to controls. Within turbine studies, those conducted in a lab setting were associated with higher injury risk than field-based studies, and studies with longer assessment time periods (≥ 24–48 h) were associated with higher risk than shorter duration assessment periods (< 24 h). Turbines and sluiceways were associated with the highest immediate mortality risk relative to controls. Within turbine studies, lab-based studies had higher mortality risk ratios than field-based studies. Within field studies, Francis turbines resulted in a higher immediate mortality risk than Kaplan turbines relative to controls, and wild sourced fish had a higher immediate mortality risk than hatchery sourced fish in Kaplan turbines. No other associations between effect size and moderators were identified. Taxonomic analyses revealed a significant increased injury and immediate mortality risk relative to controls for genera Alosa (river herring) and Oncorhynchus (Pacific salmonids), and delayed mortality risk for Anguilla (freshwater eels).

**Conclusions.** – The synthesis suggests that hydropower infrastructure in temperate regions increased the overall risk of freshwater fish injury and immediate mortality relative to controls. The evidence base confirmed that turbines and spillways increase the risk of injury and/or mortality for downstream passing fish compared to controls. Differences in lab- and field-based studies were evident, highlighting the need for further studies to understand the sources of variation among lab- and field-based studies. I was unable to examine delayed mortality, likely due to the lack of consistency in monitoring for post-passage delayed injury and mortality. The synthesis suggests that bypasses are the most “fish friendly” passage option in terms of reducing
fish injury and mortality. To address knowledge gaps, studies are needed that focus on systems outside of North America, on non-salmonid or non-sportfish target species, and on population-level consequences of fish entrainment/impingement.

2.2 Introduction

Worldwide over 58,000 dams (> 15 m height) have been constructed for various uses including irrigation, flood control, navigation, and hydroelectric power generation (International Commission on Large Dams 2015). As the number of dams continues to increase worldwide, so too have concerns for their effects on fish populations. Dams can act as a barrier to migratory (i.e., anadromous, catadromous, potamodromous) and resident fish (i.e., those that complete their life cycle within a reservoir or section of the river), fragmenting rivers and degrading habitats. The negative impacts of dams on upstream migration of diadromous fish are widely acknowledged, and the installation of various types of fishways to facilitate upstream passage are commonplace (Bunt et al. 2012). However, downstream migration of fish at dams remains a challenge (Buysse et al. 2012; Calles et al. 2012). Depending upon the life history of a given migratory fish, mature adults seeking spawning grounds (catadromous species) or juveniles or post-spawn adults (iteroparous species) seeking rearing and feeding habitats (anadromous species) may all need to move downstream past dams. Resident species may also move considerable distances throughout a riverine system for reproduction, rearing, and foraging (e.g., Kokanee Oncorhynchus nerka; White Sucker Catostomus commersonii; Walleye Sander vitreus) or simply move throughout reservoirs where they may traverse forebay areas.

Injury and mortality resulting from entrainment, when fish (non-)volitionally pass through hydropower infrastructure, or impingement, when fish become trapped against infrastructure, associated with hydroelectric facilities may have serious consequences for fish populations.
Sources of entrainment or impingement-related injury or mortality include the following: (1) fish passage through hydroelectric infrastructure (i.e., turbines, spillways, sluiceways, and other passage routes) during downstream migration for migratory fish; (2) the entrainment of resident fish; and (3) the impingement of adult or large fish (migratory or resident) against screens/trash racks. Some hydropower facilities are equipped with fish collection and bypass systems, primarily for juvenile salmonids, to facilitate downstream passage. Migrating fish will use existing dam structures such as spillways and outlet works, used to release and regulate water flow, for downstream passage. When no bypass is available and there are no spills occurring owing to low reservoir water levels, both resident and facultative migrant fish can be attracted to the turbine intake tunnels, often the only other source of downstream flow present in the forebay area of the dam. Entrainment, occurring when fish travel through a hydro dam to the tailraces, can result in physical injury and mortality from fish passing through turbines and associated components (Čada 1997; EPRI 2011). Injury and mortality can occur through several means from hydroelectric components. Freefall from passing over a spillway, abrasion, scrapes, and mechanical strikes from turbine blades are well known causes of physical injury and mortality (reviewed in Čada 1997; Larinier and Travade 2002; EPRI 2011). Injuries from turbulence and shear owing to water velocity differentials across the body length, occurs when passing over a spillway or through turbine components (Čada 1997; Čada et al. 2006). Water pressure associated injuries and mortality can occur from low pressure, rapid changes in pressure, shear stress, turbulence, cavitation (extremely low water pressures that cause the formation of bubbles which subsequently collapse violently), strikes, or grinding when fish become entrained in turbine components (Čada 2001; Čada et al. 2007; Brown et al. 2014). Injury and mortality can also occur from fish being impinged against screens or trash racks that
are intended to prevent debris, or in some cases fish, from being drawn into water intakes (Barnthouse 2013).

Since downstream migrants are not often observed (e.g., juvenile fish), historically far less consideration has been afforded to downstream passage, such that management strategies and/or structures specifically designed to accommodate downstream passage were not implemented nearly as frequently (Katopodis and Williams 2012). To date, literature on downstream passage largely focuses on juvenile survival, particularly in Pacific salmonids *Oncorhynchus* spp., popular commercial and recreational species in which the adults senesce after spawning. Minimal research exists on downstream passage and entrainment risk of resident fish species (Larinier and Travade 2002). However, research on adult downstream passage in migratory fish is growing in popularity in temperate Europe and North America, particularly for species of conservation interest such as eels *Anguilla* spp. (Jansen et al. 2007; Carr and Whoriskey 2008; Travade et al. 2010; Besson et al. 2016; Eyler et al. 2016; Haro et al. 2016) and sturgeons *Acipenser* spp. (Acolas et al. 2012; McDougal et al. 2013; McDougal et al. 2014). To enhance downstream passage and reduce mortality, management strategies have included selectively timing spills to aid juvenile fish, the installation of “fish friendly” bypass systems and screens directing fish to these systems, and retrofitting dams with low-volume surface flow outlets (Johnson and Dauble 2006) or removable spillway structures designed to minimize fish harm (Adams et al. 2014). The use of light, sound bubble curtains, and electrical currents to act as repellent from harmful paths or potentially an attractant to more desirable (fish friendly) paths have been explored (Popper and Carlson 1998; Ostrand et al. 2009; Zielinski and Sorensen 2015). Given that the timing of downstream migration differs among life stages and is species-dependent (Larinier and Travade 2002), mitigating injury and mortality during downstream
passage in a multispecies system could prove challenging and disruptive to power generation operations. Furthermore, operational strategies can be complicated by environmental regulations such as water quality requirements.

From a fish productivity perspective, minimizing impacts during downstream passage for migratory fish, unintended entrainment of resident species, and/or fish impingement, is an integral part of managing fish productivity. Downstream passage mortality from a single hydropower dam may appear low (i.e., 5-10%), but system-wide cumulative mortalities may be considerable in systems greatly fragmented by multiple dams (Marohn et al. 2014). Adult survival affects population dynamics (e.g., effective population size), and thus fisheries yields (e.g., sustainable yield, maximum sustainable yield). Juvenile survival affects recruitment (i.e., fish reaching an age class considered part of a fishery), ultimately contributing to fisheries productivity. Literature reviews and technical reports compiled to date have primarily focused on how fish injury and mortality occurs, and/or evaluate the effectiveness of various management strategies used to mitigate harm during downstream passage (Čada 1997; Larinier and Travade 2002; EPRI 2011). Given the contributions of migratory and resident adults and juveniles to fish production, a natural extension would be evaluating the impacts of fish injury and mortality from hydropower dam entrainment and impingement on fish productivity. Here, a ‘systematic review’ approach (Pullin and Stewart 2006) was used to evaluate the existing literature base to assess the consequences of hydroelectric dam entrainment and impingement on freshwater fish productivity, and to identify to what extent factors like site type, intervention type, and life history characteristics influence the impact of different hydroelectric infrastructure on fish entrainment and impingement.
2.2.1 Topic identification and stakeholder input

During the formulation of the question for this review, an Advisory Team made up of stakeholders and experts was established and consulted. This team included academics, staff from the Oak Ridge National Laboratory (U.S. Department of Energy) and staff from Fisheries and Oceans Canada (DFO), specifically the Fish and Fish Habitat Protection Program (FFHPP) and Science Branch. The Advisory Team guided the focus of this review to ensure the primary question was both answerable and relevant, and suggested search terms to capture the relevant literature. The Advisory Team was also consulted in the development of the inclusion criteria for article screening and the list of specialist websites for searches.

2.2.2 Objective of the review

The objective of the systematic review was to evaluate the existing literature base to assess the consequences of fish entrainment and impingement associated with hydroelectric dams in freshwater temperate environments.

2.2.3 Primary question

What are the consequences of hydroelectric dam fish entrainment and impingement on freshwater fish productivity in temperate regions? The primary study question can be broken down into the study components:

*Subject (population). – Freshwater fish, including diadromous species, in temperate regions.*

*Intervention. – Infrastructure associated with hydroelectric facilities (i.e., turbines, spillways, sluiceways, outlet works, screens, water bypasses, louvers, penstocks, trash racks, etc.).*

*Comparator. – No intervention or modification to intervention.*
Outcomes. – Change in a component of fish productivity (broadly defined in terms of: mortality, injury, biomass, yield, abundance, diversity, growth, survival, individual performance, migration, reproduction, population sustainability, and population viability).

2.2.4 Secondary question

To what extent do factors such as site type, intervention type, life history characteristics influence the impact of fish entrainment and impingement?

2.3 Methods

The search strategy for this review was structured according to the guidelines provided by the Collaboration for Environmental Evidence (Collaboration for Environmental Evidence 2018) and followed that published in the a priori systematic review protocol (Rytwinski et al. 2017). Note, no deviations were made from the protocol.

2.3.1 Searches

A search string was used to query publication databases, Google Scholar, and specialist websites (see Appendix A). Search terms were limited to English language due to project resource restrictions. The search string was modified depending on the functionality of different databases, specialist websites and search engine (see Appendix A - Additional file 1). Full details on search settings and subscriptions can be found in Appendix A - Additional file 1. To ensure the comprehensiveness of the search, the search results were checked against a benchmark list of relevant papers provided by the Advisory Team. The reference lists of papers were also searched until the number of relevant returns significantly decreased. This increased the likelihood that relevant articles not captured by the literature search were still considered.
I did not undertake an explicit test of the comprehensiveness of the search by checking the search results against a benchmark list of relevant papers. This was largely because most of the evidence base on this topic was presumably going to be considered grey literature sources, making estimation of comprehensiveness challenging. However, as mentioned above, screening was conducted on bibliographies of: (1) a large number of relevant reviews identified at title and abstract (84 reviews) or full-text screening (30 reviews); (2) additional relevant reviews identified from within the bibliographies of the reviews (54 reviews); and (3) included articles. Reference lists of papers were searched until the reviewer deemed that the number of relevant returns had significantly decreased. This increased the likelihood that relevant articles not captured by the literature search were still considered.

All articles generated by publication databases and Google Scholar were exported into separate Zotero databases. After all searches were complete and references found using each different strategy were compiled, the individual databases were exported in to EPPI-reviewer (eppi.ioe.ac.uk/eppireviewer4) as one database. Due to restrictions on exporting search results, the Waves database results were screened in a separate Excel spreadsheet. Prior to screening, duplicates were identified using a function in EPPI Reviewer and then were manually removed by one reviewer (TR). One reviewer manually identified and removed any duplicates in the Waves spreadsheet (TR). All references regardless of their perceived relevance to this systematic review were included in the database.

2.3.2 Article screening and study eligibility criteria

2.3.2.1 Screening process

Articles found by database searches and the search engine were screened in two distinct stages: (1) title and abstract, and (2) full text. Articles or datasets found by other means than
database or search engine searches (i.e., specialist website or other literature searches) were entered at the second stage of this screening process (i.e., full text) but were not included in consistency checks. Prior to screening all articles, a consistency check was done at title and abstract stage where two reviewers (DAA and TR) screened 233/2324 articles (10% of the articles included in EPPI Reviewer which did not include grey literature, other sources of literature, or the articles in the Waves excel spreadsheet). The reviewers agreed on 86.30% of the articles. Any disagreements between screeners were discussed and resolved before moving forward. If there was any further uncertainty, the Review Team discussed those articles as a group to come up with a decision. Attempts were made to locate full-texts of all articles remaining after title and abstract in the Carleton University library and by using interlibrary loans. Reviewers did not screen studies (at title and abstract or full-text) for which they were an author.

A consistency check was done again at full-text screening with 51/500 articles (10% of the articles included in EPPI Reviewer which did not include grey literature, other sources of literature, or the articles in the Waves excel spreadsheet). Reviewers (DAA and TR) agreed on 90.2% of articles. After discussing and resolving inconsistencies, the screening by a single reviewer (DAA) was allowed to proceed. A list of all articles excluded on the basis of full-text assessment is provided in Appendix A - Additional file 2, together with the reasons for exclusion.

2.3.2.2 Eligibility criteria

Each article had to pass each of the following criteria to be included:

*Eligible populations.* – The relevant subjects of this review were any fish species, including diadromous species, in North (23.5°N to 66.5°N) or South (23.5°S to 66.5°S) temperate regions.
Only articles located in freshwater ecosystems, including lakes, rivers, and streams that contain fish species that are associated with a hydroelectric dam system were included.

*Eligible interventions.* – Articles that described infrastructure associated with hydroelectric facilities that may cause fish to be entrained or impinged (i.e., turbines, spillways, sluiceways, outlet works, screens, tailraces, water bypasses, tailwaters, penstocks, trash racks, etc.) were included. Articles that examined “general infrastructure”, where entrainment or impingement was examined but no specific infrastructure component was isolated, were also included for data extraction. See Table 2.1 for definitions of the intervention types considered in the review. Only articles that describe water that moves via gravity were included. Articles were excluded where water was actively pumped for: (1) power generation [e.g., storage ponds (Robbins and Mathur 1976)]; (2) irrigation; or (3) cooling-water in-take structures for thermoelectric power plants. Other studies excluded described infrastructure associated with other operations: (1) nuclear facilities; (2) dams without hydro; (3) hydrokinetic systems (i.e., energy from waves/currents); or (4) general water withdrawal systems (e.g., for municipal drinking, recreation).

*Eligible comparators.* – This review compared outcomes based on articles that used Control-Impact (CI) and Controlled Trials (randomized or not). Before-After (BA) and studies that combined BA and CI designs, Before-After-Control-Impact (BACI), were considered for inclusion but none were found (i.e., there were no studies that collected before intervention data within same waterbody pre-installation/modification). Relevant comparators included: (1) no intervention (e.g., control experiments whereby each phase of a test procedure was examined for sources of mortality/injury other than passage through infrastructure such as upstream introduction and/or downstream recovery apparatus); (2) an unmodified version of the intervention on the same or different study waterbody, or (3) controlled flume study. Studies that
only reported impact (i.e., treatment) data (i.e., no control site data) were excluded from this review. Note, at the request of stakeholders, studies that only reported impact-only data were included through the full-text screening stage but were excluded during the initial data extraction stage to obtain an estimate of the number of studies that used this type of study design in this area of study. Simulation studies, review papers, and policy discussions were also excluded from this review.

**Eligible outcomes.** – Population-level assessments of entrainment and impingement impacts on fish productivity outcomes were considered for inclusion but were rarely conducted. Most metrics used to evaluate consequences of fish entrainment and impingement were related to fish mortality and injury. Any articles that used a metric related to: (1) lethal impact: direct fish mortality or indirect mortality (e.g., fish are disoriented after passage through hydroelectric dam and then predated upon), and (2) sublethal impacts: external and/or internal injury assessments (e.g., signs of scale loss, barotrauma, blade strike, etc.,) – were included. These metrics could include, but were not limited to, reported mortality rate (%), survival rate (%), recovery rate (%), the number of fish impinged or entrained (i.e., used as a measure of risk of impingement/entrainment and not mortality/injury per se), injury rate (% of population) with particular types of injuries (e.g., signs of blade strike), all injury types combined, or numbers of injuries.

Furthermore, linkages between intervention and outcome needed to have been made clear to allow for the effects of fish mortality/injury from entrainment and impingement to be isolated from other potential impacts of hydroelectric power production such as barriers to migration and/or habitat degradation. Studies were excluded where no clear linkage between intervention and outcome were identified (e.g., if fish density was surveyed up-and down-stream of a hydro
dam but any difference or change in fish density could not be clearly attributed to impingement or entrainment in isolation of other effects). Fish passage/guidance efficiency studies that determined the number of fish that passed through a particular hydropower system, typically through a bypass or under differing operating conditions, were excluded if there was no explicit entrainment/impingement or injury/mortality assessment. Studies that investigated passage route deterrence and/or enhanced passage efficiency facilitated via behavioural guidance devices and techniques (e.g., bubble screens, lights, sound; Popper and Carlson 1998) were excluded, except where mortality or injury was assessed.

2.3.2.3 Language

Only English-language literature was included during the screening stage.

2.3.3 Study validity assessment

All studies included on the basis of full-text assessment were critically appraised for internal validity (susceptibility to bias) using a predefined framework (see Table 2.2 for definitions of terms such as study). If a study contained more than one project (i.e., differed with respect to one or more components of critical appraisal; see Table 2.3), each project received an individual validity rating and was labelled in the data extraction table with letters (e.g., “Ruggles and Palmeter 1989 A/B/C” indicating that there are three projects within the Ruggles and Palmeter article). For example, sample size (i.e., the total number of fish released) was an internal validity criterion (Table 2.3). If a study conducted a project with a sample size of > 100 fish it received a different internal validity assessment label than a project that used < 50 fish. The critical appraisal framework (see Table 2.3) developed for this review considered the features recommended by Bilotta et al. (2014) and was adapted to incorporate components specific to the studies that answer the primary question. The framework used to assess study
validity was reviewed by the Advisory Team to ensure that it accurately reflected the characteristics of a well-designed study. The criteria in the critical appraisal framework refer directly to internal validity (methodological quality), whereas external validity (study generalizability) was captured during screening or otherwise noted as a comment in the critical appraisal tool. The framework was based on an evaluation of the following internal validity criteria: study design (controlled trial or gradient of intervention intensity including "zero-control", or CI), replication, measured outcome (quantitative, quantitative approximation, semi-quantitative), outcome metric (a metric related to mortality, injury, productivity, or the number of fish entrained), control matching (how well matched the intervention and comparator sites were in terms of habitat type at site selection and/or study initiation, and sampling), confounding factors [environmental or other factors that differ between intervention and comparator sites and/or times, that occur after site selection and/or study initiation (e.g., flood, drought, unplanned human alteration)], and intra-treatment variation (was there variation within treatment and control samples). Each criterion was scored at a “High”, “Medium”, or “Low” study validity level based on the predefined framework outlined in Table 2.3. The study was given an overall “Low” validity if it scored low for one or more of the criteria. If the study did not score low for any of the criteria, it was assigned an overall “Medium” validity. If the study scored only high for all of the criteria, it was assigned an overall “High” validity. This approach assigns equal weight to each criterion, which was carefully considered during the development of the predefined framework. Reviewers did not critically appraise studies for which they were an author.

Study validity assessments took place at the same time as data extraction and were performed by two reviewers (DAA and W. Twardek). For each study, one reviewer would assess
study validity and extract the meta-data. However, a consistency check was first undertaken on 7.8% (8/104) of articles by three reviewers (DAA, WT, and TR). Validity assessments and meta-data on these studies were extracted by all three reviewers. Before DAA and WT proceeded independently and on their own subsets of the included studies, discrepancies were discussed and, when necessary, refinements to the validity assessment and meta-data extraction sheets were made to improve clarity on coding. Reviewers did not critically appraise studies for which they were an author. No study was excluded based on study validity assessments. However, a sensitivity analysis was carried out to investigate the influence of study validity categories (see Sensitivity analyses below).

2.3.4 Data coding and extraction strategy

2.3.4.1 General data-extraction strategy

All articles included on the basis of full-text assessment, regardless of their study validity category, underwent meta-data extraction. Data extraction was undertaken using a review-specific data extraction form given in Appendix A - Additional file 3. Extracted information followed the general structure of the PICO framework (Population, Intervention, Comparator, Outcome) and included: publication details, study location and details, study summary, population details, intervention and comparator details, outcome variables, etc. The number of fish injured, the number of fish killed, and the number of fish entrained/impinged were treated as continuous outcome variables. The mortality outcome was further subgrouped into immediate mortality (i.e., mortality was assessed ≤1 h after recapture was in the tailrace i.e., immediately below intervention), and delayed mortality [i.e., mortality was (re)assessed >1 h after recapture and/or recapture was beyond the tailrace, i.e., further downstream of intervention]. Immediate mortality was used to capture the direct, lethal impact of the intervention, while delayed
mortality allowed understanding of the potential indirect, lethal impacts (e.g., mortality as a result of infection or disease following injury from intervention some time later). In some cases, post-passage delayed mortality can be indirectly attributed to factors other than the hydropower infrastructure itself (e.g., predation after injury). When explicitly reported, delayed mortality from sources not directly attributed to hydropower infrastructure was excluded at the data extraction stage. Supplementary articles (i.e., articles that reported data that could also be found elsewhere or contained portions of information that could be used in combination with another more complete source) were identified and combined with the most comprehensive article (i.e., primary study source) during data extraction (Appendix A - Additional file 3). Data on potential effect modifiers and other meta-data were extracted from the included primary study source or their supplementary articles whenever available.

In addition, all included articles on the basis of full-text assessment, regardless of their study validity category, underwent quantitative data extraction. Sample size (i.e., total number of fish released) and outcome (number of fish injured, killed, or entrained/impinged), where provided, were extracted as presented from tables or within text. When studies reported outcomes in the form of percentages, this metric was converted into a number of fish killed or injured, when the total number of fish released was provided. For studies that reported survival (e.g., number of fish that successfully passed through intervention) or detection histories from telemetry studies (i.e., number of detections), these were converted into the number of fish killed (assumed mortality) by subtracting the reported response from the total number of fish released. For fish injury, I extracted the total number of fish injured, regardless of injury type [i.e., if data were provided for >1 injury type (e.g., descaled, bruising, eye injuries, etc.) the number of fish with any injury was extracted]. When multiple injuries were reported separately, I extracted the
most comprehensive data available for a single injury type and noted the relative proportions/frequencies in the data extraction form (see Appendix A - Additional file 3). For delayed mortality responses, a cumulative outcome value was computed (i.e., the total number of fish killed from the entire assessment period – immediate time period + delayed time period).

Data from figures were extracted using the data extraction software WebPlotDigitizer (Rohatgi 2015) when necessary.

2.3.4.2 Data extraction considerations

Defining a ‘study’ was challenging in this as there was no clear distinction in the evidence base between studies and experiments (see Table 2.2 for definitions of terms). This was often because a single article could report multiple investigations within a single year [e.g., various changes in operational conditions (alone or in combination), various life stages or sources of released fish for the same or different species], or over multiple years. Often, at any one site, investigations conducted over multiple years could be reported within the same article, within different articles by the same authors, or by different authors in different articles (e.g., results from a technical report for a given time period are included in another publication by different authors conducting a similar updated study at the same site). In such cases, it was not always easy to discern whether the same investigations were repeated across years or whether the investigations were in fact changed (e.g., slight modifications in operational conditions were made). During data extraction, duplicate sources of data were removed when identified (i.e., overlapping data). However, this was an inherently challenging task due to the lack of detail in the study reports. As such, during data extraction there were a number of considerations made in defining the database of information.
Site. – Each hydroelectric facility and research laboratory/testing facility (i.e., where lab studies were conducted), were given a “Site ID”. If a single article reported data separately for different hydroelectric facilities within the same or different waterbodies, I regarded these data as independent and assigned each study a separate “Site ID”.

Study. – If at a given site (i.e., hydroelectric facility or laboratory), evaluations of responses were conducted for different: (1) operational conditions (e.g., turbine discharge, wicket gate opening width, dam height); (2) modifications of a specific intervention (e.g., number of turbine runner blades); or (3) depth at fish release; I considered these separate studies and each were given a “Study ID”. I regarded these as separate studies since independent releases of fish were used i.e., different fish were released in each release trial (if more than one trial conducted) within each study.

If at a given site, evaluations of responses were conducted for different interventions (e.g., mortality at turbines and at spillways), I only considered these separate studies if the fish were released separately for each intervention (i.e., different release points immediately above the intervention under evaluation, within the same or different years). When studies released a group of fish at a single location above all interventions, and the outcomes came from route-specific evaluations, these were considered the same study and received the same Study ID.

Data set. – A single study could report separate relevant comparisons (i.e., multiple non-independent data sets that share the same Site ID) for different species, and/or the same species but responses for different outcomes (i.e., mortality, injury, number of fish entrained/impinged). Furthermore, a single study could report a mortality response for the same species but separately for: (1) immediate mortality [i.e., spatial assessment was conducted just after intervention (in the tailrace) and/or the mortality assessment was conducted ≤1 h after release], and (2) delayed
mortality (i.e., spatial assessment was conducted beyond the tailrace and/or the mortality assessment was conducted >1 h after release) but otherwise the same for all other meta-data. For quantitative synthesis, I treated these comparisons as separate data sets (i.e., separate rows in the database that share the same Site ID).

If authors reported responses for the same species for the same outcome category in a single study but separately for different: (1) life stages (e.g., the mortality of juveniles for species A, and the mortality of adults for species A); and/or (2) sources of fish (i.e., hatchery, wild, stocked sourced) and otherwise the same for all other meta-data, I extracted these as separate data sets for the database. Furthermore, if the same study (e.g., same operating condition) was conducted in multiple years at the same site, meta-data (and quantitative data when available) were extracted separately for each and given the same Study ID. For quantitative analyses, I aggregated these data sets to reduce non-independence and data structure complexity (see Appendix A - Additional file 4: Combining data across subgroups within a study).

2.3.4.3 Potential effect modifiers and reasons for heterogeneity

For all articles included on the basis of full-text assessment, I recorded, when available, the following key sources of potential heterogeneity: site type (laboratory or field-based studies), intervention type [i.e., turbine, spillway, sluiceway, water bypass, dam, general infrastructure, exclusionary/diversionary installations (e.g., screens, louveres, trash racks), and any combination of these interventions; see Table 2.1 for definitions], turbine type (e.g., Kaplan, Francis, S-turbine, Ossberger), hydro dam head height (m), fish taxa (at the genus and species level), life stage [egg (zygotes, developing embryos, larvae), age-0 (fry, young-of-the-year), juvenile (age-1), adult, mixed stages)], fish source [i.e., hatchery (fish raised in a hatchery environment and released into system), wild (fish captured/released that originate from the source waterbody),
stocked (fish captured/released that were from the source waterbody but originated from a hatchery)], sampling method [i.e., telemetry, mark-recapture, net samples, visual, in-lab, passive integrated transponder tags (PIT tags)], and assessment time (h). Potential effect modifiers were selected with consultation with the Advisory Team. After consultation with the Advisory Team, there were effect modifiers that were originally identified in the protocol that were removed from data extraction for this review. Due to limitations in time and resources, I did not search external to the article for life history strategies, fish body size/morphology, or turbine size, as they were often not reported within the primary articles. Also, I did not include study design or comparator type since there was little variation across these variables [(e.g., all studies either used a control trial or CI study design (i.e., there were no BA or BACI study designs]. When sufficient data were reported and sample size allowed, these potential modifiers were used in meta-analyses (see Quantitative synthesis below) to account for differences between data sets via subgroup analyses or meta-regression.

2.3.5 Data synthesis and presentation

2.3.5.1 Descriptive statistics and a narrative synthesis

All relevant studies included on the basis of full-text assessments, were included in a database which provides meta-data on each study. All meta-data were recorded in a MS-Excel database (Appendix A - Additional file 3) and were used to generate descriptive statistics and a narrative synthesis of the evidence, including figures and tables.

2.3.5.2 Quantitative synthesis

Eligibility criteria. – Relevant studies that were included in the database were considered unsuitable for meta-analysis (and were therefore not included in quantitative synthesis) if any of the following applied:
• Quantitative outcome data were not reported for the intervention and/or comparator group(s);
• The total number of fish released was not reported for the intervention and/or comparator group(s);
• For route specific outcomes (i.e., studies that release a single group of fish upstream of hydroelectric infrastructure whereby fish can take different routes through/over such infrastructure), the total number of fish that took a specific route through hydroelectric infrastructure was zero.
• The outcomes for both intervention and control groups were zero resulting in an undefined effect size (see effect size calculation below).
• For both intervention and control groups, all fish released were killed or injured resulting in an estimated sampling variance of zero (i.e., a division of zero in the equation to calculate typical within-study variance – see Effect size calculation below).

Data preparation. – Where zero values for outcomes were encountered (168 of 569 data sets) for either the intervention or control group, data were imputed by adding one to each cell in the 2 x 2 matrix to permit calculation of the risk ratio [i.e., a value of one was added to each of event (number of fish killed or injured) or non-event (number of fish that survived or uninjured) cells in each of the two group] (Lipsey and Wilson 2001). Note, I performed a sensitivity analysis to investigate the influence of the value of the imputation by comparing results using a smaller value of 0.5 (Deeks and Higgins 2010; Deeks et al. 2011) (see Sensitivity analyses below). Exceptions occurred when mortality/injury were both zero for the intervention (A) and control group (C) within a data set (i.e., A = C = 0; risk ratios are undefined) (73 data sets) or when
mortality/injury were 100% for both the intervention and control group within a data set (4 data sets from a single study) (Deeks and Higgins 2010) (see Appendix A - Additional file 5 Quantitative synthesis database).

To reduce multiple effect sizes estimates from the same study – which is problematic because this would give studies with multiple estimates more weight in analyses – data sets were aggregated (see Appendix A - Additional file 4 for full description) in three instances when studies reported: (1) responses from multiple life stages separately within the same outcome and intervention subgroup (e.g., mortality of species A age-0 and juveniles separately) (20 studies); (2) responses from multiple sources for fish released separately within the same outcome and intervention subgroup for the same species (e.g., mortality of species A hatchery reared individuals and wild sourced individuals separately) (8 studies); and (3) when the same study (e.g., same operating condition) was conducted in multiple years at the same site, and all other meta-data were the same (22 studies).

Furthermore, there were a number of instances of multiple group comparisons whereby studies used a single control group and more than one treatment group within a single study or across studies within an article. In such cases, the control group was used to compute more than one effect size, and in consequence, the estimates of these effect sizes are correlated. This lack of independence needed to be accounted for when computing variances (see Appendix A - Additional file 4: Handling dependence from multiple group comparisons, for a full description and the number of cases).

Effect size calculation. – Studies primarily reported outcomes in the form of the number of events (e.g., number of fish killed or injured) and non-events (e.g., number of fish that survived or uninjured). Thus, to conduct a meta-analysis of the quantitative data I used risk ratio (RR) as
an effect size metric (Borenstein et al. 2009):

\[ RR = \frac{A / n_1}{C / n_2} \]  

Risk ratios compare the risk of having an event (i.e., fish mortality or injury) between two groups, A waterbodies or simulated lab settings whereby fish are exposed to infrastructure associated with hydroelectric facilities, and C waterbodies/ simulated settings without this intervention (control group), and n₁ and n₂ were the sample sizes of group A and group C. If an intervention has an identical effect to the control, the risk ratio will be 1. If the chance of an effect is reduced by the intervention, the risk ratio will be <1; if it increases the chance of having the event, the risk ratio will be >1. Therefore, a risk ratio of >1 means that fish are more likely to be killed or injured with passage through/over hydroelectric infrastructure than killed or injured by sources other than contact with hydroelectric infrastructure.

Risk ratios were log transformed to maintain symmetry in the analysis, with variance calculated as (Borenstein et al. 2009):

\[ V_{\text{LogRiskRatio}} = \frac{1}{A} - \frac{1}{n_1} + \frac{1}{C} - \frac{1}{n_2} \]  

I acknowledge that risk can be expressed in both relative terms (e.g., risk ratio) as well as absolute terms [i.e., risk difference (RD)]. Relative risk provides a measure of the strength of the association between an exposure (e.g., fish exposed to infrastructure associated with hydroelectric facilities) and an outcome (e.g., fish injury/mortality) whereas absolute risk provides the actual difference in the observed risk of events between intervention and control groups. A concern with using relative risk ratios is that it may obscure the magnitude of the effect of the intervention (Noordzij et al. 2017), making in some situations, the effect of the
intervention seem worse than it actually is. For instance, the same risk ratio of 1.67 (i.e., the risk of fish mortality was 67% higher in the intervention group compared to the control group) can result from two different scenarios, for example: (1) an increase in mortality from 40% in the control group to 66% in the intervention group (i.e., RD=24%), or (2) an increase from 3% in the control group to 5% in the intervention group (i.e., RD= 2%). From these examples, I can see that absolute risk (i.e., RD) provides insight into the actual size of a risk, and can, in some situations provide additional context for hydropower managers and regulators to help inform their decisions. Therefore, I chose to base the quantitative synthesis on pooled estimates using risk ratio as the effect size measure; however, to provide additional insight on the magnitude of risk to help inform decision making, I also calculated the absolute risk difference for individual comparisons, carried out in raw units (Borenstein et al. 2009):

\[ RD = \frac{A}{n_1} - \frac{C}{n_2} \]  

(3)

With variance calculated as (Borenstein et al. 2009):

\[ V_{RiskDifference} = \frac{AB}{n_1^3} + \frac{CD}{n_2^3} \]  

(4)

Where \( B \) and \( D \) are the number of non-events (e.g., number of fish that survived or uninjured) for the intervention and control groups, respectively. Note, only those studies that were considered suitable for meta-analysis using risk ratio were used to calculate summary effects using the risk difference. However, where zero values for outcomes were encountered for either the intervention or control group (as described under Quantitative synthesis — data preparation above), data were not imputed by adding a value of one (or 0.5) since this was not necessary for risk difference calculations.
Meta-analysis. – To determine whether fish passing through/over infrastructure associated with hydroelectric facilities increased, on average, the risk of mortality or injury compared to controls, I first conducted random-effects meta-analyses using restricted maximum-likelihood (REML) to compute weighted average risk ratios for each outcome separately [i.e., injury (k=104 effect sizes), immediate mortality (k = 162), and delayed mortality (k = 256)]. In each model, data from all intervention types and all temperate freshwater fish were combined. To further account for multiple data sets from the same study site (i.e., different studies or species), Study ID nested within Site ID was considered a random factor in each analysis. All summary effects (and associated 95% confidence intervals) were converted back to, and reported as, risk ratios [i.e., RR = exp(LogRiskRatio)]. Heterogeneity in effects was calculated using the $Q$ statistic, which was compared against the $\chi^2$ distribution, to test whether the total variation in observed effect sizes ($Q_T$) was significantly greater than that expected from sampling error ($Q_E$) (Hedges and Olkin 1985). A larger $Q$ indicates greater heterogeneity in effects sizes (i.e., individual effect sizes do not estimate a common population mean), suggesting there are differences among effect sizes that have some cause other than sampling error. I also produced forest plots to visualize mean effect sizes and 95% confidence intervals from individual comparisons. Mean effect sizes were considered statistically significant if their confidence intervals did not include an RR = 1. I also analyzed the impacts of fish entrainment and impingement associated with hydroelectric dams separately on outcomes for the select few taxonomic groups (at the genus and species level) when there were sufficient sample size to do so.

As risk ratios may not be easily interpretable, I also calculated the percent relative effect (i.e., the percent change in the treatment group), whereby the control group was regarded as having a 100% baseline risk and the treatment group was expressed relative to the control: %
increase (when RR > 1) = (RR - 1) x 100. For example, fish passing through turbines had a 320%
increase in risk of mortality versus the risk of mortality in control fish released downstream of
any hydroelectric infrastructure (100%). Also, as noted above, to provide additional context on
the magnitude of risk, I report weighted average absolute risk differences, estimated following
the same methods outlined in the paragraph immediately above as for estimating weighted
average risk ratios. Because complex analyses beyond estimating summary effects using the risk
difference are not recommended (i.e., investigating heterogeneity with moderators e.g., meta-
regression) (Lipsey and Wilson 2001), I accompany pooled risk ratios with pooled absolute risk
differences and 95% confidence intervals for main summary effects only (i.e., for each outcome,
intervention type, and genus separately).

I examined the robustness of the models by analyzing for publication biases in two ways.
First, I used visual assessments of funnel plots (i.e., scatter plots of the effect sizes of the
included studies versus a measure of their precision e.g., sample size, standard error, or sampling
variance) (Light and Pillemer 1984). Here, I produced funnel plots using 1/standard error. In the
absence of publication bias, the funnel plot should resemble an inverted funnel. In the presence
of publication bias, some smaller (less precise) studies with smaller effect sizes will be absent
resulting in an asymmetrical funnel plot (Sterne et al. 2001). Second, I used Egger’s regression
test to provide more quantitative examinations of funnel plot asymmetry (Egger et al. 1997).

To test for associations between effect size and moderators, I used mixed-effects models
for categorical moderators and meta-regression for continuous moderators, estimating
heterogeneity using REML. I first evaluated the influence of intervention type on each outcome
subgroup separately. Then, I tested for associations between other moderators (i.e., turbine type,
hydro dam head height, site type, life stage, fish source, sampling method, assessment time) and
effect sizes within intervention type subsets. I tested for associations within intervention subsets for two reasons. First, many moderators of interest were related to specific intervention types (e.g., turbine type, hydro dam head height). To reduce potential confounding effect of intervention type, associations between other moderators and effect sizes were evaluated separately for different interventions. Second, since information on all moderators was not always provided in articles (e.g., assessment time was not reported in all studies) and the distribution of moderators varied substantially between intervention types, I removed effect sizes with missing information and tested for associations within intervention type subsets.

Before examining the influence of moderators within intervention subsets, I made the following modifications to the coding to reduce the number of studies I needed to exclude. First, since there was only a single case where juveniles and adult life stages were used together, I added this category to the mixed life stage category (applicable for the immediate mortality analysis only). Second, I combined studies that used mark-recapture sampling gear and methods (e.g., fin clips, balloon tags, or PIT tags for identification only, with or without netting) with netting alone methods (e.g., a known number of unmarked fish were released and recaptured in netting downstream of intervention(s)) into a single category (i.e., recapture). For studies that used telemetry (radio, acoustic, or PIT tags for remote tracking) either alone or in combination with any other category, I combined them into a single category (i.e., telemetry). Third, assessment time was categorized into three time periods: (1) <24 h; (2) ≥24-48 h; and (3) >48 h. Fourth, I included data sets that evaluated impacts of turbines+trash racks into the turbine intervention category (for immediate fish mortality only).

I conducted $\chi^2$ tests to assess independence of moderators for each intervention separately. When moderators within an intervention subset were confounded, and/or the distribution
between moderator categories was uneven, I avoided these problems by constructing independent subsets of data in a hierarchical approach. For example, within the immediate mortality outcome subgroup, there were no wild sourced fish used in studies conducted in a lab setting; therefore, the influence of fish source on effect size was investigated within the subset of field-based studies only.

Where there was sufficient sample size within each of the subsets to include a moderator, I included the moderator into the model individually, and in combination when possible. I restricted the number of fitted parameters \( j \) in any model such that the ratio \( k/j \), where \( k \) is the number of effect sizes, was \( >5 \), which is sufficient in principle to ensure reasonable model stability and sufficient precision of coefficients (Vittinghoff et al. 2005). Selection between the models (including the null model, i.e., a random-effects model with no moderator) was evaluated using sample-size-corrected Akaike Information Criterion (AICc) (i.e., based on whether the mixed-effects model(s) had a lower AICc than the null model) and accompanied by corresponding \( Q_E \) (test statistic of residual heterogeneity) and \( Q_M \) (heterogeneity explained by the model). The statistical significance of \( Q_M \) and \( Q_E \) were tested against a \( \chi^2 \) distribution. I only performed analyses on categorical moderators where there were sufficient combinable data sets (i.e., \( >2 \) data sets from \( \geq 2 \) sites). Thus, in some cases, I either combined similar categories to increase the sample size (detailed in results below) or deleted the categories that did not meet the sample size criteria. The single continuous moderator variable, hydro dam head height, was log-transformed to meet test assumptions.

Sensitivity analyses. – Sensitivity analyses were carried out to investigate the influence of: (1) study validity categories; (2) imputing data (i.e., a value of one) to each cell in the matrix to permit calculation of the risk ratio where zero values for outcomes were encountered; (3)
imputing a different value (i.e., 0.5) to each cell in the matrix to permit calculation of the risk ratio where zero values for outcomes were encountered; (4) multiple group comparisons where a single control group was compared to more than one intervention type within the same study and outcome subgroup, and (5) converting studies that reported survival (e.g., number of fish that successfully passed through intervention) or detection histories from telemetry studies (i.e., number of detections) into the number of fish killed (assumed mortality). First, models were fit using just those studies assessed as being “Medium” or “High” validity. Given that there were only two criteria for which a “Medium” score could be applied, and the relatively small differences between a “Medium” and “High” score for these criteria, I merged these two categories for the sensitivity analysis i.e., I assigned an overall “Medium/High” category all studies that did not score low for any criteria. Second, separate models were fit using only those studies that did not require computational adjustments during initial data preparation. Third, separate models were fit using all data sets calculated from imputing a value of 0.5 rather than one for risk ratios where zero values for outcomes were encountered. Fourth, separate models were fit using data sets that did not include multiple group comparisons. Lastly, models were fit using only those studies that did not require a conversion from fish survival or detection to assumed mortality by subtracting the reported response from the total number of fish released (only applicable for immediate and delayed mortality outcomes). In all five sets of analyses, the results were compared to the overall model fit to examine differences in pooled effect sizes. All meta-analyses were conducted in R 3.4.3 (R Development Core Team 2017) using the “rma.mv” function in the metafor package (Viechtbauer 2010).
2.4 Results

2.4.1 Review descriptive statistics

2.4.1.1 Literature searches and screening

Searching five databases and Google Scholar resulted in finding 3,121 individual records, of which 2,418 articles remained after duplicate removal (Figure 2.1). Title and abstract screening removed 1,861 articles, leaving 557 articles for full-text screening. Full-text screening removed 418 articles, and 32 articles were unobtainable due to either insufficient citation information provided within the search hit, or they could not be located through internet, library, or inter-library loan sources. Unobtainable articles and articles excluded at full-text screening are listed with an exclusion decision in Appendix A - Additional file 2. A total of 107 articles were included for data extraction from database and Google Scholar searches. Screening bibliographies of relevant reviews identified at title and abstract or full-text screening resulted in an additional 99 articles included (~85% of which were grey literature sources that were not picked up by the database searches e.g., government reports, and theses). Full-text screening of grey literature sources from website searches and submissions via social media/email resulted in no additional articles for data extraction.

A total of 206 articles were initially included for data extraction. During data extraction, one article was excluded for an irrelevant intervention and 89 articles were excluded for having an impact-only study design (i.e., treatment-only, no comparator; Figure 2.1 and Appendix A - Additional file 2). Further, 29 articles were identified as having overlapping data and/or projects (listed as Supplementary Articles in Appendix A - Additional file 3), resulting in a total of 87 articles with 264 studies included in the narrative synthesis. Of these, 75 articles with 222 studies were included in quantitative synthesis.
2.4.1.2 Sources of articles used for data extraction

A total of 60 grey literature (i.e., government/consultant reports, conference proceedings, book chapters) and 27 commercially published articles published throughout 1952-2016 were included for data extraction and quality assessment (Figure 2.2). Grey literature accounted for a higher frequency of included articles in all decades with the exception of the current decade. Grey and commercially published literature published between 2000-2009 represented the greatest proportion of articles (29%), followed by those published in the 1990s (23%) and the 1980s (16%).

2.4.1.3 Study validity assessment

Validity assessments were conducted for 128 individual projects identified from the 264 studies included (Appendix A - Additional file 6). Over half of the projects were assigned an overall “Low” validity (53%), whereas projects assigned overall “High” and “Medium” validity accounted for 30% and 17%, respectively. All projects critically appraised employed a CI design. Most projects (93%) reported quantitative data on fish mortality/injury relative to an appropriate control (98%) and satisfied the various performance bias criteria (Table 2.4). However, many projects were assigned a “High” ranking in one (or several) categories, but many of these projects received a “Low” ranking for confounding sampling, habitat, and environmental factors, consequently resulting in the increased proportion of overall “Low” ranked projects (see Table 2.4; Appendix A - Additional file 6). For example, a project assessed as meeting the criteria for a “High” ranking with exception of receiving a “Low” ranking in performance and sample bias because there was heterogeneity within treatment and control samples (e.g., environmental conditions or operating conditions varied during turbine releases).
The frequencies of overall “High”, “Medium”, and “Low” ranked studies varied over time (Figure 2.3). The 1960s, 1990s, and 2000-2009 decades produced the most “High” and “Medium” ranked studies, and “High” and “Medium” ranked studies accounted for most of the studies conducted in these decades (77%, 75%, and 62%, respectively). The 1980s, 2000-2009, and 2010-2016 decades produced the most overall “Low” ranked studies. Within the 1970s, 1980s and 2010-2016, “Low” ranked studies accounted for most of the studies conducted in these decades (75%, 71%, and 75%, respectively).

2.4.2 Narrative synthesis

The narrative synthesis was based on 264 studies from 87 articles. Descriptive meta-data, coding, and quantitative data extracted from these studies can be found in Appendix A - Additional file 3.

2.4.2.1 Study location

Studies included in the narrative were conducted in five countries in the north temperate zone and two countries in the south temperate zone. The vast majority of studies were conducted in North America (97%), with the United States (93%) and Canada (4%) accounting for the highest and second highest number of studies. The remaining 3% of studies were conducted in European (France, Germany, Sweden) and Oceania (Australia and New Zealand) regions. Most studies were field based (75%), conducted at 46 sites (i.e., dams), with most sites located in the United States (78%; Table 2.5). Lab studies, conducted at four research centers based in the United States, accounted for 24% of the studies.

2.4.2.2 Population

Mortality/injury from entrainment/impingement was investigated in 35 species spanning 24 genera and 15 families (Figure 2.4). The majority of studies were conducted on the Salmonidae
family from genera *Oncorhynchus* (259 studies), *Salmo* (6 studies), and *Salvelinus* (6 studies). Anadromous fish represented just under 30% of the species included in the narrative but accounted for the bulk of the studies. Numerous resident (47% of species studied) and other migratory species (e.g., catadromous, potamodromous, 26% of species studied) were included but contributed far fewer studies. The most frequently studied species were Pacific salmonids (*Oncorhynchus* spp.) including Chinook Salmon (*O. tshawytscha*, 142 studies), Rainbow Trout/steelhead (*O. mykiss*, 76 studies), and Coho Salmon (*O. kisutch*, 42 studies). The most common non-salmonid species studied were American Shad (*Alosa sapidissima*, 11 studies), Pacific Lamprey (*Entosphenus tridentatus*, 10 studies), Bluegill (*Lepomis macrochirus*, 9 studies) American Eel (*Anguilla rostrata*, 6 studies), and Blueback Herring (*Alosa aestivalis*, 5 studies). Most species (25 species) contributed <5 studies.

Most studies were conducted on juvenile fish (e.g., yearlings, smolts, 224 studies; Figure 2.5). Hatchery and wild juvenile fish (179 and 34 studies, respectively) were the most commonly studied. Wild fish accounted for most studies of adult fish (8 of 10 studies), and very few studies were conducted on larval stages (3 studies).

### 2.4.2.3 Intervention

Fish entrainment/impingement was studied for a variety of hydropower intervention types including turbines, spillways, bypasses, and exclusionary/diversionary installations (e.g., screens, louvers, trash racks). The most common intervention type studied was turbines (173 studies), followed by spillways (34 studies; Figure 2.6). The “general” intervention type (i.e., where specific infrastructure was not isolated but entrainment/impingement was attributable to hydropower infrastructure) accounted for 33 studies. Intervention types included in the narrative but not commonly studied in isolation were exclusionary/diversionary installations, the dam, fish
ladders, and outlet works. Some studies applied an intervention in combination with one or more other interventions. A combination of interventions (e.g., turbine and trash rack, spillway and removable weir) was used in six turbine studies, eight spillway studies, and seven bypass studies.

Several turbine types were studied, with Kaplan turbines being the most common (81 studies) followed by Francis turbines (41 studies) (Figure 2.7). Other turbines [Advanced Hydro Turbine System (AHTS), bulb, S-turbine, and Ossberger] were used in six studies. Very low head (VLH) hydraulic and rim-drive turbines were only used in a single study each. Pressure chambers that simulate passage through Kaplan or Francis turbines were used in 14 studies.

2.4.2.4 Study design and comparator

All 264 studies from the 87 articles included in the narrative used a CI design. Impact-only articles (i.e., those with no comparator; I-only) were included at full text screening but excluded during data extraction (89 articles; see Appendix A - Additional file 3). Some articles included both CI and I-only datasets; I-only datasets were removed during data extraction.

Comparator types included fish released downstream of an intervention (e.g., tailrace releases), and handling/holding (e.g., fish handled and placed into a holding tank). Downstream comparators, the most frequently used comparators, were most commonly used in field-based studies (194 studies). Only 15 field studies used handling/holding comparators, whereas all lab-based studies used handling/holding comparators (70 studies).

2.4.2.5 Outcomes

The most frequently reported measured outcome was mortality (252 studies). Injury was reported in 128 studies, and number of fish entrained/impinged was reported in 3 studies. Delayed mortality (210 studies) was more frequently reported than immediate mortality
(assessed <1 h after recapture; 159 studies). Mark-recapture sampling gear and methods (e.g., nets, fin clips) were the most frequently used for assessing mortality (114 studies) and injury (44 studies) compared to tagging gear (e.g., telemetry) which was used in 21 and 15 studies for mortality and injury assessment, respectively. The most common injury type reported was descaling. When not specified, injuries were reported as mechanical, pressure, shear, major or minor. Lab studies most frequently investigated barotrauma injuries. For relative proportions of injury types reported in the studies see Appendix A - Additional file 3. Delayed mortality assessment time varied from 2 h to several days. Delayed mortality was most frequently assessed between 24 and 48 h (91 studies) or greater than 48 h (66 studies; Figure 2.8). Injury assessment time also varied but was typically assessed within 48 h.

2.4.3 Quantitative synthesis

2.4.3.1 Description of the data

Of the 264 studies (from 87 articles) included in the narrative synthesis, 222 studies (from 75 articles) with 522 data sets after aggregation were included in developing the quantitative synthesis database (Appendix A - Additional file 5).

Of the 522 data sets used in Global meta-analyses below, 55% were assessed as having ‘High’ overall validity, 12% as having ‘Medium’ overall validity, and 33% as ‘Low’ overall validity.

Data sets included in the quantitative synthesis were largely from North America (494), predominately from USA (475 of 494 data sets), followed by some from Oceania (18) and Europe (10). The majority of studies were field-based studies in rivers (72% of data sets), and the remaining were lab-based studies conducted in research facilities (28%).
Among the 522 data sets, 104 data sets reported fish injuries, 162 data sets reported immediate fish mortality, and 256 reported delayed fish mortality (Table 2.6). The majority of studies on the impacts of fish entrainment and impingement were evaluations of turbines (67% of data sets), followed by general infrastructure, spillways, and turbines with trash racks (9%, 7%, and 6% of data sets respectively; Table 2.6). For all other interventions, impacts on fish responses were evaluated in ≤5% of data sets (Table 2.6).

Within the quantitative synthesis database, 31 species from 22 genera and 14 families were evaluated for impacts of fish entrainment and impingement. The most commonly evaluated species were from the Salmonidae family and included Chinook Salmon (203 data sets), Rainbow Trout/steelhead (133), and Coho Salmon (52).

Studies reporting outcomes using juveniles (age 1 to smolt) as the life stage made up the largest portion (82.3% of data sets), whereas all other life stages were evaluated less frequently (eggs, age 0, age 0+juveniles, juveniles+adults, adults, and mixed life stages, made up 3%, 4%, 2%, 0.2%, 3%, and 6% of data sets, respectively).

Fish used in study evaluations of intervention impacts were primarily sourced from hatcheries (77% of data sets), followed by wild, mixed (i.e., a mixture of wild and hatchery), and stocked sourced fish (16%, 4%, and 2% of data sets, respectively).

Information on the type of turbine used in evaluations was reported in 89% of turbine data sets, with the majority being Kaplan (43% of data sets) and Francis (37% of data sets) turbines. Hydro dam head height was reported in 54% of data sets involving spillways and ranged from 15.2-91.4 m.
Various sampling methods were used to evaluate fish responses to interventions. All lab-based studies used visual methods (134 data sets), though some included mark-recapture methods (e.g., use of PIT tags for fish identification only; 13 data sets). For field-based studies, the majority used mark-recapture sampling gear and methods (e.g., fin clips, balloon tags, or PIT tags for identification only, with or without netting; 224 data sets) or telemetry methods (e.g., acoustic, radio, or PIT tags used for remote tracking; 115 data sets). Netting alone was also used but less frequently (36 data sets).

Information on the assessment time for evaluating fish responses was reported in 84% of the data sets. Most data sets were short-term evaluations of the impacts of fish entrainment and impingement on fish responses, with 46% of the available data sets reporting assessment times \(<24\) h after fish were released. I found data sets reporting longer-term evaluations, with 32% of the available data sets reporting fish responses within \(\geq24\)–\(48\) h after fish were released, and 22% of data sets reported data more than \(48\) h after fish were released.

2.4.3.2 Global meta-analyses

Fish injury. – The pooled risk ratio for fish injury was 3.17 (95% CI: 1.74, 5.78; Figure 2.9, Table 2.7A, and Figure 1 in Appendix A - Additional file 7) indicating an overall increase in risk of fish injuries with passage through/over hydroelectric infrastructure relative to controls (i.e., 217% increase in risk over and above the risk in the control group). The forest plot for this meta-analysis suggested that a large number of cases (85 of 104 data sets) showed increased chances of fish injury relative to controls (i.e., 82% of studies had RRs > 1), with many of these individual comparisons being statistically significant (53 out of 85 cases had confidence intervals that did not include 1; Figure 1 in Appendix A - Additional file 7). The \(Q\) test for heterogeneity suggested that there was substantial variation in effect sizes (\(Q = 2796.31, p < 0.0001\)). There
was no obvious pattern of publication bias in either the funnel plot of asymmetry, or the Egger’s regression test ($z = 0.31, p = 0.741$; Figure 2 in Appendix A - Additional file 7).

The sensitivity analysis for medium/high validity studies indicated a higher pooled risk ratio compared to the overall meta-analysis [$RR = 4.15$ (95% CI: 2.42, 7.11), $k = 72, p < 0.0001$], suggesting that this result may not be robust to differences in study validity as assessed by critical appraisal, i.e., higher validity studies may result in higher risk ratio estimates (Figure 3 in Appendix A - Additional file 7). Studies that did not require zero cell adjustments, as well as studies that did not include multiple group comparisons had similar results to the overall meta-analysis; [$RR = 2.61$ (95% CI: 1.57, 4.33), $k = 71, p = 0.0002$; $RR = 3.68$ (95% CI: 2.12, 6.39), $k = 102, p < 0.0001$, respectively]. Furthermore, using a value of 0.5 for zero cell adjustments yielded similar results to the overall meta-analysis using a data imputation of one [$RR = 3.31$ (95% CI: 1.83, 5.99), $k = 104, p < 0.0001$]. These sensitivity analyses suggested that this result may be robust to computational adjustments made in initial data preparation, and the inclusion of a single study that compared two intervention types with a single control group (Figure 4-6 in Appendix A - Additional file 7).

Immediate fish mortality. – The pooled risk ratio for immediate mortality was 3.35 (95% CI: 2.38, 4.69; Figure 2.9 and Table 2.7A), indicating an overall increase in risk of fish mortality immediately following passage through/over hydroelectric infrastructure relative to controls (i.e., 235% increase in risk over and above the risk in the control group). The forest plot for this meta-analysis suggested that 90% of studies (145 of 162) showed increased chances of fish mortality relative to controls (i.e., $RRs > 1$), with many of these studies having significant effect sizes (106 out of 145 cases) (Figure 7 in Appendix A - Additional file 7). However, the $Q$ test for heterogeneity suggested that there was significant heterogeneity between effect sizes ($Q =$
11684.88, \( p < 0.0001 \)). Funnel plots of asymmetry suggested possible evidence of publication bias towards studies showing increased chances of fish mortality relative to controls (Figure 8 and 9 in Appendix A - Additional file 7). Egger’s regression test further supported this assessment (\( z = 4.58, \ p < 0.0001 \)). Removing two outliers did not improve bias estimates (\( z = 4.51, \ p < 0.0001 \)). Interestingly, when separating commercially published studies from grey literature studies, evidence of publication bias was only present in the latter (\( z = 0.74, \ p = 0.458, \ k = 18, \) and \( z = 4.65, \ p < 0.0001, \ k = 144, \) respectively).

The meta-analysis based only on medium/high validity studies had a similar result to the overall meta-analysis [\( RR = 3.26 \) (95% CI: 2.25, 4.73); \( k = 123, \ p < 0.0001 \)], suggesting that this result may be robust to differences in study validity (Figure 10 in Appendix A - Additional file 7). Furthermore, no evidence of bias was apparent from sensitivity analysis of studies that did not require computational adjustments in initial data preparation [\( RR = 3.03 \) (95% CI: 2.08, 4.40); \( k = 108, \ p < 0.0001 \)], as well as studies that did not include multiple group comparisons [\( RR = 3.01 \) (95% CI: 2.17, 4.16); \( k = 155, \ p < 0.0001 \); Figures 11, 12 in Appendix A - Additional file 7]. I could not obtain a pooled risk ratio using a value of 0.5 for zero cell adjustments due to instability of model results, because the ratio of the largest to smallest sampling variance was very large. The analysis based on studies that did not require a conversion from fish survival or detection to assumed mortality showed a higher pooled risk ratio compared to the overall meta-analysis [\( RR = 4.52 \) (95% CI: 3.08, 6.63), \( k = 119, \ p < 0.0001 \)]. Thus, this result may not be robust to conversions made to outcome metrics i.e., studies that measure actual fish mortality, instead of inferred mortality from survival estimates or detection histories, may result in higher risk ratio estimates (Figure 13 in Appendix A - Additional file 7).
Delayed fish mortality. – A pooled risk ratio for delayed fish mortality was not obtained due to instability of model results, because the ratio of the largest to smallest sampling variance was very large. Model instability also precluded the ability to test for associations between pooled risk ratios for delayed fish mortality and moderators.

2.4.3.3 Effects of moderators on fish injury

To address the question, to what extent does intervention type influence the impact of fish entrainment and impingement, there were only sufficient sample sizes (i.e., >2 data sets from ≥2 sites) to include the following interventions for fish injury: (1) Turbines; (2) General infrastructure; (3) Bypasses; and (4) Spillways (Figure 2.9).

Intervention type was associated with pooled risk ratios (Table 2.8A), with spillways and turbines associated with higher risk ratios than general infrastructure and water bypasses for fish injury (792% and 406% increase vs. 250% increase and 82% decrease, respectively; Figure 2.9 and 2.10, and Table 2.7B).

Turbines. – There were only sufficient sample sizes and variation to permit meaningful tests of the influence of the following moderators: (1) Site type; (2) Fish source; (3) Assessment time. None of the factors were found to be confounded (Table 1A in Appendix A - Additional file 8).

Site type was associated with average risk ratios (Table 2.8B), with studies conducted in a lab setting associated with higher risk ratios than field-based studies relative to controls (718% vs 182% increase, respectively; Figure 2.9 and 2.11). Assessment time was marginally associated with average risk ratios (Table 2.8B), with longer assessment time periods (≥24-48 h) associated with higher risk ratios than shorter duration assessment periods (<24 h) (890% vs 268% increase, respectively; Figure 2.9 and 2.11). No detectable association was found between fish source and
average effect sizes. The model including both site type and assessment time was more informative than any univariate model (Table 2.8B). However, there was still significant heterogeneity remaining in all moderated models (Table 2.8B).

*General infrastructure.* – For the quantitative synthesis, “general infrastructure” primarily included studies that simulated the effects of shear pressure during fish passage through turbines, spillways, and other infrastructure in a lab setting (e.g., Deng et al. 2005; Boys et al. 2016). There was only sufficient sample size within life stage (eggs or juveniles) and assessment time (≥24-48 or >48 h) to investigate the influence of modifiers on the impact of general infrastructure for fish injury. I only found a detectable association with average effect sizes and life stage (Table 2.8C), with the juvenile life stage associated with higher risk ratios than the egg life stage relative to controls (312% vs 9% increase, respectively; Figure 2.9 and 2.12).

*Bypasses.* – The influence of factors was not investigated owing to inadequate sample sizes (Figure 2.9).

*Spillways.* – The influence of factors was not investigated owing to inadequate sample sizes (Figure 2.9). The majority of spillway studies included chute and freefall designs and tended to focus on enumerating mortality rather than injury.

### 2.4.3.4 Effects of moderators on immediate fish mortality

To address the question, to what extent does intervention type influence the impact of fish entrainment and impingement, there were only sufficient sample sizes (i.e., >2 data sets from ≥2 sites) to include the following interventions for immediate mortality: (1) Turbines; (2) General infrastructure; (3) Bypasses; (4) Spillways, and (5) Sluiceways (Figure 2.9).
Intervention type was associated with pooled risk ratios for immediate fish mortality (Table 2.9A), with general infrastructure, turbines, and sluiceways associated with higher risk ratios than spillways and water bypasses (371%, 283%, and 261% increase vs. 101 and 11% increase, respectively) (Figure 2.9 and 2.13, and Table 2.7B).

_Turbines._ – There were only sufficient sample sizes to permit meaningful tests of the influence of the following factors: (1) Site type; (2) Source; (3) Life stage; and (4) Sampling method. Due to uneven distributions between fish source and sampling method categories, the influence of fish source and sampling method on effect size was investigated within the subset of field-based studies only (see below).

Site type was associated with average risk ratios (Table 2.9B), with lab-based studies having higher risk ratios than to field-based studies (1776% vs 247% increase, respectively) (Figure 2.9 and 2.14). No detectable association was found between life stage and average risk ratios (Table 2.9B). There was still significant heterogeneity remaining in all moderated models (Table 2.9B).

Within the subset of field-based turbine studies, there were adequate sample sizes to evaluate the influence of turbine type, sampling method, and fish source. Due to uneven distributions within sampling methods and fish source for different turbine types (i.e., there was no telemetry sampling methods or wild sourced fish used with Francis turbines) (Table 2B in Appendix A - Additional file 8), the influence of sampling method and fish source was evaluated within Kaplan turbines only (below). However, within the field-based subset, there was a detectable association between turbine type and average risk ratios (Table 2.9C), with Francis turbines having higher risk ratios than Kaplan turbines (522 vs 144% increase, respectively; Figure 2.9 and 2.15A).
For the subset of Kaplan turbine studies, the magnitude of immediate mortality responses to turbines relative to controls varied with fish source (Table 2.9D), with wild sourced fish having higher risk ratios than hatchery sourced fish (Figure 2.9; Figure 2.15B). No detectable association was found between sampling method and average risk ratios (Table 2.9B). A model including fish source and sampling method was only slightly more informative than the univariate model including fish source (Table 2.9D).

*General infrastructure.* – The influence of factors was not investigated owing to inadequate sample sizes (Figure 2.9).

*Bypasses.* – The influence of factors was not investigated owing to inadequate sample sizes (Figure 2.9).

*Sluiceways.* – The influence of factors was not investigated owing to inadequate sample sizes (Figure 2.9).

*Spillways.* – The influence of factors was not investigated owing to inadequate sample sizes (Figure 2.9). Although small sample sizes precluded testing potential reasons for variation in fish mortality from spillways, other variables not tested in the analyses such as spillway height and design, use of energy dissipators, downstream water depth, and presence of rock outcrops at the base of the spillway outflow are known to be important for spillway related mortality (Bell et al. 1972; Ruggles and Murray 1983).

### 2.4.3.5 Taxonomic analyses

There were only sufficient sample sizes to investigate impacts of hydroelectric infrastructure on outcomes of five temperate freshwater fish genera: (1) *Alosa* (river herring; injury, immediate and delayed mortality outcomes); (2) *Anguilla* (freshwater eels; delayed
mortality only); (3) *Lepomis* (sunfish; injury only); (4) *Salmo* (Atlantic Salmon *Salmo salar*; delayed mortality only); and (5) *Oncorhynchus* (Pacific salmon and trout; injury, immediate and delayed mortality outcomes). Forest plots for all analyses are presented in Appendix A - Additional file 9.

*Alosa.* – Overall, there was a similar increase in risk of injury and immediate mortality following passage through/over hydroelectric infrastructure relative to controls for river herrings (127% and 144% increase in risk over and above the risk in the control group, respectively) (Figure 2.16A and B, and Table 2.7C). In contrast, there was no statistically significant effect of delayed mortality for this group (Figure 2.16C and Table 2.7C). In all outcomes, either all or the majority of the data sets were from turbine studies (i.e., injury: all data sets; immediate mortality: 11 of 12; delay mortality: 7 of 9). Sample sizes were too small to evaluate the influence of moderator variables within outcome subsets for this genus.

*Anguilla.* – For freshwater eels, the overall risk of delayed mortality following passage through/over hydroelectric infrastructure was high relative to controls (1275% increase in risk over and above the risk in the control group; Figure 2.16C and Table 2.7C). Two species of freshwater eels were represented, European (*Anguilla anguilla*) and American (*Anguilla rostrata*) eels, with 80% of the individual comparisons using adult eels and focusing on turbine impacts. Sample sizes were too small in this group as well to evaluate the influence of moderator variables within outcome subsets for this genus.

*Lepomis.* – For sunfish, there was sufficient data available to evaluate the impact of turbines on injury. There was no statistically significant effect of turbines on sunfish injury as a whole (Figure 2.16A, and Table 2.7C).
Salmo. – There was adequate data available to evaluate the impact of turbines on delayed mortality with all comparisons representing a single species, the Atlantic Salmon. I found no overall significant effect of turbines on Atlantic Salmon mortality (Figure 2.16C and Table 2.7C), with evident variation in delayed mortality responses (i.e., large upper confidence interval).

Oncorhynchus. – Within the Pacific salmon and trout group, there was a similar overall increase in risk of injury and immediate mortality following passage through/over hydroelectric infrastructure relative to controls (323% and 237% increase in risk over and above the risk in the control group, respectively; Figure 2.16A and B, and Table 2.7C). A pooled risk ratio for delayed mortality was not obtained for this group of fish due to instability of model results.

Intervention type was associated with pooled risk ratios for both injury and immediate mortality outcomes ($Q_M = 40.66, p < 0.0001, k = 43$; $Q_M = 10881, p < 0.0001, k = 125$, respectively). Spillways and turbines were associated with higher risk ratios than water bypasses for injury (1241% and 613% increase vs. 80% decrease, respectively; Figure 2.16D), and immediate mortality (260% and 261% increase vs. 225% increase, respectively; Figure 2.16E). However, there was still significant heterogeneity remaining in moderated models ($Q_E = 1869.55, p < 0.0001, k = 43$; $Q_E = 214.69, p < 0.0001, k = 125$, respectively). Furthermore, although pooled risk ratios for both spillways and turbines were significant (i.e., 95% CIs did not overlap with 1) in both outcome subsets, upper confidence intervals were large for injury responses, indicating substantial variation in the magnitude of negative injury responses among individual comparisons. To further explore reasons for heterogeneity in responses, I tested the influence of species type on effect sizes within the turbine subset of studies for all outcome subsets (i.e., the intervention with the largest sample size to permit meaningful analyses). No
detectable association was found between species [i.e., Rainbow Trout and Chinook Salmon] and average risk ratios for Pacific salmon and trout injury ($Q_M = 1.63, p = 0.201, k = 33$). However, species was associated with average risk ratios for immediate mortality ($Q_M = 89.93, p < 0.0001, k = 97$), with studies on Rainbow Trout associated with higher risk ratios than either Coho or Chinook salmon to controls (539% vs 279%, and 246% increase in risk over and above the risk in the control group, respectively; Figure 2.17A).

Within Pacific salmon and trout species subsets for immediate mortality responses to turbines, there were sufficient samples sizes to investigate the influence of the following moderators: (1) turbine type within field studies for both Coho and Chinook salmon; (2) sampling method within Kaplan turbine types for Chinook Salmon; and (3) site type for Rainbow Trout.

*Coho Salmon.* – Within the field-based subset, a detectable association was found between turbine type and average risk ratios ($Q_M = 4.14, p = 0.042, k = 10$), with Francis turbines having a much higher pooled risk ratio than Kaplan turbines relative to controls (1658 vs 285% increase, respectively; Figure 2.17B). There was little variation among data sets with respect to other moderators, i.e., all data sets used hatchery sourced fish, telemetry sampling methods, and juvenile fish.

*Chinook Salmon.* – Within the field-based subset, no detectable association was found between turbine type and average risk ratios ($Q_M = 0.54, p = 0.461, k = 38$). Within Kaplan turbines, no detectable association was found between sampling method (recapture vs. telemetry) and average risk ratios ($Q_M = 0.17, p = 0.684, k = 25$). Here as well, there was little variation among data sets with respect to other moderators i.e., all field-based data sets used juvenile fish and mostly hatchery sourced fish.
Rainbow Trout. – There was no detectable association between site type and average risk ratios ($Q_M = 0.64, p = 0.425, k = 45$). Otherwise, there was little variation among data sets with respect to other moderators i.e., all data sets used hatchery sourced fish (or not reported), recapture sampling methods, and juvenile fish, and 26 of 27 field-based studies evaluated Francis turbines.

2.4.3.6 Review limitations

Addressing fish productivity. – Although the research question pertains to fish productivity, owing to how the studies were conducted and the data typically reported in the commercially published and grey literature, it was not feasible to evaluate the consequences of entrainment/impingement on fish productivity per se as a measure of the elaboration of fish flesh per unit area per unit time. Rather, I evaluated the risk of freshwater fish injury and mortality owing to downstream passage through common hydropower infrastructure. Productivity is a broad term often represented more practically by various components of productivity (e.g., growth, survival, individual performance, migration, reproduction), which if negatively affected by human activities, would have a negative effect on productivity (Bradford et al. 2014). In terms of the consequences of entrainment to fish productivity in the upstream reservoir, all entrained fish are no longer contributing regardless of the outcome of their passage success (i.e., survival or mortality) if no upstream passage is possible. In the case of mortality, fish are permanently removed from the whole river system and thus cannot contribute to reproduction/recruitment. To estimate the impact of entrainment consequences to fish productivity, knowledge is required of the fish mortality in the context of population vital rates. Both of these metrics are extremely difficult and costly to measure in the field and are thus rarely quantified. However, since injury and mortality would directly impact components of fish productivity, I contend that evaluating
injury and mortality contribute to addressing the impacts of entrainment and/or impingement on fish productivity.

Poor data reporting. – In total, 166 data sets from 96 studies were excluded from quantitative synthesis, largely (53% of these data sets) for two main reasons: (1) quantitative outcome data (e.g., number of fish injured or killed) were not reported for the intervention and/or comparator group(s); or (2) the total number of fish released was either not reported at all for the intervention and/or comparator group(s), or only an approximate number of fish released were reported. Both cases did not allow for an effect size to be calculated, excluding studies from the meta-analysis. I did not attempt to contact authors for the missing data due to time constraints. Data availability through online data depositories and open source databases have improved dramatically over the years. Reporting fish outcomes as well as the total fish released for both treatment and control groups in publications (or through supplementary material) would benefit future (systematic) reviews.

Potential biases. – I attempted to limit any potential biases throughout the systematic review process. The collaborative systematic review team encompassed a diversity of stakeholders, minimizing familiarity bias. There was no apparent evidence of publication bias for fish injury studies (Figure 2 in Appendix A - Additional file 7), but there was possible evidence of publication bias towards studies showing increased chances of fish mortality relative to controls (Figure 8 and 9 in Appendix A - Additional file 7). Interestingly, when separating commercially published studies from grey literature studies (i.e., reports and conference proceedings), evidence of publication bias was only present in the latter, of which represented 87% of the immediate mortality data sets. A possible explanation for this observation could be that these technical reports are often commissioned by hydropower operators to quantify known injury and mortality.
issues at their facilities. The commercially published literature in this evidence base was
typically more question-driven and exploratory in design, whereas the technical reports were
largely driven by specific objectives (i.e., typically placing empirical value on fish mortality
known to occur at a given facility). This also highlights another important finding from the
review that nearly 70% (i.e., 60/87 articles) of the evidence base was grey literature sources.
Again, while I made every effort to systematically search for sources of evidence, I received
limited response from the calls for evidence targeting sources of grey literature through relevant
mailing lists, social media, and communication with the broader stakeholder community. As
such, I believe there is still relevant grey literature that could have been included if it would have
been more broadly available from those conducting the research (i.e., consultant groups or
industry rendering reports easily accessible, or at least not proprietary).

Geographical and taxonomic biases were evident in the quantitative synthesis – the
majority of included studies were from the United States (91%) and a large percentage (81%)
evaluated salmonid responses to hydroelectric infrastructure, potentially limiting interpretation of
review results to other geographic regions and taxa. These biases were previously noted by other
hydropower-related reviews (e.g., Prachéil et al. 2016). To limit availability bias, extensive
efforts were made obtain all relevant materials through my resource networks; however, there
were several reports/publications (n = 32) that were unobtainable. A number of unpublished
reports, older (e.g., pre-1950’s) preliminary/progress reports, and other unofficial documents
were cited in the literature but were unavailable because they were not published. This review
was limited to English language, presenting a language bias. Other countries such as France,
Germany, and China have hydropower developments and research the impacts on temperate fish
species, but the relevant hydropower literature base (32 reports/articles) was excluded at full text screening due to language.

2.4.3.7 Reasons for heterogeneity

Several moderators were tested in the quantitative synthesis; however, considerable residual heterogeneity remained in the observed effects of hydropower infrastructure on fish injury and immediate mortality. In some cases, meta-data was extracted from studies within the evidence base but was not included in quantitative analyses owing to small sample sizes. Four main factors were noted as contributing to heterogeneity in fish injury and mortality.

First, a top priority of hydropower operators is to identify trade-offs in facility operations and fish passage, attempting to balance fish passage requirements while maximizing power generation. Variation in geomorphology and hydrology among hydropower sites results in site-specific conditions, thus site-specific studies across a variety of operating conditions are required to determine the most favourable conditions for fish passage while maintaining power generation output. The facility or intervention characteristics (e.g., dam height, water levels, turbine model, etc.,) are a major factor in the resulting operating conditions of a hydropower facility at a given time. Some site characteristics would have direct implications for fish injury and mortality. For example, spillways with a freefall drop exceeding 50 m are known to result in higher injury and/or mortality compared to spillways with a shorter drop (Bell et al. 1972). The present quantitative synthesis encompassed 42 field sites, resulting in considerable variability in site characteristics and operating conditions of the facilities or interventions (e.g., turbine wicket gate opening, spillway gate opening), which would have a measurable impact on injury and mortality. Owing to this variability, I was unable to achieve sufficient sample sizes to effectively include site-specific characteristics or operating conditions as effect modifiers.
Second, environmental factors that affect migration/emigration and physiological processes that could have a measurable impact on fish injury and mortality. Water temperature affects locomotor activity and fatigue time (Brett 1967; Bernatchez and Dodson 1985; Claireaux et al. 2006), and thus may affect a fish’s ability to avoid or navigate through infrastructure. Since fish are unable to regulate their body temperature, water temperature also affects many important physiological processes that are implicated in post-passage injury and/or mortality such as body condition and wound healing (Anderson and Roberts 1975; Clarke and Johnston 1999). For example, within the salmonid family there is variability in the emigration time of juveniles, even within the same species (Bennett et al. 2011), such that there are numerous emigration events throughout the year. Juveniles emigrating during the summer may be more susceptible to injury and mortality owing to higher water temperatures at the time of emigration relative to emigrants in other seasons. Owing to the variability in environmental conditions during passage, it is unlikely that I would have been able to achieve sufficient sample sizes to effectively include environmental factors as effect modifiers.

Third, behaviour is recognized as paramount to fish passage (Coutant and Whitney 2000; Pracheil et al. 2016), which would have a measurable effect on injury and/or mortality. Throughout the screening process many studies that had a fish behaviour component were excluded from the evidence base because there was no relevant injury and/or mortality outcome. The majority of these excluded studies examined various mechanisms to attract fish towards or deter fish from entering certain infrastructure (e.g., lights to attract to bypasses, strobe lights to deter from entering turbine intakes) (see Popper and Carlson 1998; Enders 2012) or focused on fish passage efficiency and route choice under various environmental conditions (e.g., flow regimes). Behaviour is difficult to incorporate into conservation science because there is high
variation in behavioural data and behaviour studies have an individual-level focus, which often proves difficult to scale up to the population level (Caro 1999; Cooke et al. 2014). For example, fish have species-specific swimming behaviours that influence positional approaches to infrastructure (e.g., rheotaxis in juvenile salmonids) (Enders et al. 2009), which may lead to increased entrainment risk. Behavioural commonalities do exist within and among species, so some behaviour-related heterogeneity was likely accounted for when species was included in the analyses. However, owing to the small sample size of behavioural studies within the evidence base with injury and/or mortality outcomes, I was unable to explicitly include any specific behavioural factors as a moderator in the analyses.

Finally, fish passage issues are complex, so the studies in the evidence base employed a wide variety of assessment methodologies depending on research objectives, site characteristics, and target species. Combining data from studies that use different methodologies to assess fish injury and mortality can be problematic for meta-analyses because the data provided is not necessarily comparable among studies. The evidence base encompasses several decades of fish passage research (1950 to 2016; Figure 2.3) and vast improvements in fish tracking technology, experimental design, and statistical analyses have occurred over that timeframe. Early fish passage research employed rudimentary methodologies and lacked standardization compared to modern research, which could lead to measurable differences among older and more recent studies in the evidence base. Some tracking/marking techniques are more invasive than others, which could ultimately influence fish behaviour during downstream passage events. For example, surgically implanting an acoustic telemetry transmitter typically involves sedation and the implanted transmitter can produce an immune response, both of which may impair fish behaviour (Semple et al. 2018). Conversely, PIT tags typically do not require sedation and are
minimally invasive to implant in the fish. Furthermore, assessing mortality among the different fish identification techniques (physical marking, PIT tags, telemetry) requires varying levels of extrapolation. Injury and mortality can be directly observed and enumerated in studies that pass fish through a turbine and recapture occurs at the downstream turbine outlet. Releasing fish implanted with a transmitter relies on subsequent detection of the animal to determine the outcome, and the fate of the fish is inferred from these detections, not directly observed. Several factors can affect fish detection such as noisy environments (e.g., turbine generation, spilling water), technical issues related with different tracking infrastructure (e.g., multipath, signal collisions), and water conditions (e.g., turbidity) (Kessel et al. 2014). A sensitivity analysis revealed that studies inferring fish mortality from detections histories (or survival estimates) produced lower risk ratio estimates than studies that directly measured mortality (e.g., release upstream - recapture downstream with net), suggesting disparities in mortality estimates between these two methods.

2.5 Review conclusions

Entrainment and impingement can occur during downstream passage at hydropower operations, causing fish injury and mortality, and these hydropower-related fish losses have the potential to contribute to decreased fish productivity (Rosenberg et al. 1997; Hall et al. 2012). Even if fish survive an entrainment event, they are moved from one reach to another, influencing reach-specific productivity. Hydropower facilities differ dramatically in their infrastructure configuration and operations and each type of infrastructure presents different risks regarding fish injury and/or mortality (Muir et al. 2001). Quantifying injury and mortality across hydropower projects and intervention types is fundamental for characterizing and either mitigating or off-setting the impact of hydropower operations on fish productivity.
Here, I present what I believe to be the first comprehensive review that systematically evaluated the quality and quantity of the existing evidence base on the topic of the consequences of entrainment and impingement associated with hydroelectric dams for fish. I was unable to specifically address productivity per se in the present systematic review, rather the focus was on injury and mortality from entrainment/impingement during downstream passage (see Review Limitations section above). With an exhaustive search effort, I assembled an extensive database encompassing various intervention types (i.e., infrastructure types), locations (lab, field studies), species, life stages (e.g., juveniles, adults), and sources (e.g., hatchery, wild). I identified 264 relevant studies (from 87 articles), 222 of which were eligible for quantitative analysis.

2.6 Implications for policy/management

The synthesis of available evidence suggests that hydropower infrastructure entrainment increased the overall risk of freshwater fish injury and immediate mortality in temperate regions, and that injury and immediate mortality risk varied among intervention types. The overall impact of hydroelectric infrastructure on delayed mortality was not evaluated due to model instability, likely because sampling variances of individual effect sizes were extremely large. Owing to variation among study designs encompassed within the overall analysis, uncertainty may be high, and thus there may be high uncertainty associated with the injury and immediate mortality risk estimates revealed in the analysis. Regardless of the wide range of studies included in the analyses contributing to high variability and the use of two different effective size metrics, the conclusions are consistent: downstream passage via hydropower infrastructure results in a greater risk of injury and mortality to fish than controls (i.e., non-intervention downstream releases).
Bypasses were found to be the safest fish passage intervention, resulting in decreased fish injury and little difference in risk of immediate mortality relative to controls, a somewhat expected result given that bypasses are specifically designed as a safe alternative to spillway and turbine passage (Mighetto and Ebel 1994; Katopodis and Williams 2012). In agreement with findings highlighted in earlier non-systematic reviews (i.e., Federal Energy Regulatory Commission 1995; OTA 1995; Coutant and Whitney 2000; Schilt 2007), spillway and turbine passage resulted in the highest injury and immediate mortality risk on average, and that Francis turbines had a higher mortality risk relative to controls compared to Kaplan turbines (Electric Power Research Institute 1992; Larinier 2001; Pracheil et al 2016; but see Eicher Associates 1987). General infrastructure posed an increased risk of injury; however, this category encompassed testing on a diversity of hydropower infrastructure types (turbines, spillways, outlets) and thus is of limited use in addressing the secondary research question. Lab based turbine studies resulted in a higher risk of injury than field-based studies, suggesting that field trials may be underestimating fish injury from turbines.

Taxonomic analyses for three economically important fish genera revealed that hydropower infrastructure increased injury and immediate mortality risk relative to controls for *Alosa* (river herring) and Pacific salmonids (salmon and trout), and delayed mortality risk for *Anguilla* (freshwater eels). Owing to small sample sizes within the evidence base, I was unable to include resident (and other underrepresented) species in the taxonomic analyses. However, I stress that the absence of these species within the evidence base and analysis does not suggest that injury and mortality risk is lower for these species, just that there is insufficient information to quantify such impacts. Furthermore, a lack of a statistically significant overall effect of injury or mortality from hydropower infrastructure for the two other genera that had ‘sufficient’
samples sizes for inclusion in the analyses (i.e., *Lepomis* and *Salmo*), does not imply they are not affected by hydropower infrastructure, only that I was not able to detect an effect (i.e., there could be an effect but I did not detect it, possibly due to low power).

My analyses also demonstrate that the relative magnitude of hydropower infrastructure impacts on fish appears to be influenced by study validity and the type of mortality metric used in studies. Higher risk ratios were estimated for analyses based on studies with lower susceptibility to bias and those that measured actual fish mortality, rather than inferred mortality from survival estimates or detection histories. Overall, placing an empirical value (whether relative or absolute) on the overall injury and mortality risk to fish is valuable to hydropower regulators with the caveat that my analyses encompass a broad range of hydrological variables (e.g., flow), operating conditions, and biological variables.

### 2.7 Implications for research

The evidence base of this review encompasses a small fraction of temperate freshwater fish, particularly biased towards economically valuable species such as salmonids in the Pacific Northwest of North America. As previously noted by others (Roscoe and Hinch 2010; Pracheil et al. 2016), research on the impacts of hydropower infrastructure on resident fish and/or fish with no perceived economic value is underrepresented in the commercially published and grey literature. Several imperiled fishes also occupy systems with hydropower development although they have rarely been studied in the context of entrainment (Limburg and Waldman 2009). Therefore, studies that focus on systems outside of North America, on non-salmonid or non-sportfish target species, and on population-level consequences of fish entrainment/impingement are needed to address knowledge gaps.
Aside from immediate (direct) mortality outcomes, which are more easily defined and measured using recapture-release methods (Burnham et al. 1987), no clear guidelines or standardized metrics for assessing injuries and delayed mortality outcomes (e.g., temporal and/or spatial measurement) were overtly evident in the literature searches and screening. Consistency in monitoring and measuring fish injury and immediate mortality has been reached to some degree, but monitoring fish post-passage for delayed injury and mortality is lacking in general (Federal Energy Regulatory Commission 1995; Roscoe and Hinch 2010). The “gold standard” of examining the impacts of hydropower on fish should presumably include delayed mortality, which I was unable to assess in the present review. Drawing from issues I encountered during quantitative synthesis and commonalities among studies in the evidence base, some clear recommendations for standards pertaining to delayed mortality outcomes and general data analysis include: (1) assessing delayed mortality between 24 to 48 h; (2) using a paired control group (downstream release) for each treatment group (e.g., instead of a common control comparator among several treatment release groups); (3) using quantitative outcomes (instead of qualitative descriptors e.g., of the 50 fish released, most survived); (4) to the extent possible, use similar sampling methods and sampling distances between release and recapture (or survey) among treatment and control groups.
Table 2.1: Intervention, fish injury/impact, and general hydropower terms and definitions used in the systematic review. Most of the hydropower terms are adapted from OTA 1995, ASCE 1995, and Čada et al. 1997, see these publications for a comprehensive list of definitions and hydropower related terms.

<table>
<thead>
<tr>
<th>Term</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Interventions</strong></td>
<td></td>
</tr>
<tr>
<td>Bypass</td>
<td>A structure that collects fish upstream and deposits fish downstream of the facility. Typically used for juveniles. Several bypass types, but surface and turbine bypasses are most common.</td>
</tr>
<tr>
<td>Dam</td>
<td>Structure for impounding water. Dam height generates head pressure for the turbines.</td>
</tr>
<tr>
<td>Draft tube</td>
<td>A column (structure) from the turbine outlet to the tailrace that water flows through.</td>
</tr>
<tr>
<td>Exclusionary device</td>
<td>Structure(s) to prevent or divert fish entrance/passage. Often used to divert fish from turbines into bypasses. Common structures include various screens.</td>
</tr>
<tr>
<td>General infrastructure</td>
<td>Category used to capture studies that evaluated entrainment or impingement through &gt;1 components of a hydroelectric facility. Within the meta-analysis, this category encompassed lab studies that simulate conditions fish may experience (e.g., shear forces) through various infrastructure.</td>
</tr>
<tr>
<td>Louver</td>
<td>A structure of set angled bars or slats that can be used to divert/guide fish towards bypasses or sluices. These structures do not exclude fish like screens, rather alter hydraulic flow patterns and/or streamflow to guide fish.</td>
</tr>
<tr>
<td>Outlet works</td>
<td>A combination of structures designed to control reservoir water levels and/or water release for hydropower facility operations. Structures can include intake towers, outlet tunnels and/or conduits, control gates, and discharge channels. Intake structures can have trash racks or other purposefully designed fish intakes.</td>
</tr>
<tr>
<td>Penstock</td>
<td>An intake structure (channel, pipe) that leads into the turbines.</td>
</tr>
<tr>
<td>Screen</td>
<td>An exclusionary device to prevent fish from entering a structure (e.g., turbine) or divert fish towards a bypass.</td>
</tr>
<tr>
<td>Spillway</td>
<td>An outlet or channel in a dam or reservoir that discharges surplus water downstream of a dam. Spillways can vary by design (e.g., channel type, height).</td>
</tr>
<tr>
<td>Sluiceways</td>
<td>A surface channel extending from the forebay to the tailrace designed to allow ice and debris to pass.</td>
</tr>
<tr>
<td>Surface bypasses</td>
<td>Structures that spill minimal amounts of water to facilitate passage over a dam. Several types exist (see [23]). Fish are collected and pass through a series channels that discharges downstream of the facility into the tailrace. Typically used for juvenile salmonids, taking advantage of their surface-oriented swimming behaviour.</td>
</tr>
<tr>
<td>Trash rack</td>
<td>A type of exclusionary device designed to keep debris out of turbine intakes, but can be used to guide fish to “safer” passage routes such as bypasses and sluices.</td>
</tr>
<tr>
<td>Term</td>
<td>Definition</td>
</tr>
<tr>
<td>-----------------------------</td>
<td>-------------------------------------------------------------------------------------------------------------------------------------------</td>
</tr>
<tr>
<td>Turbine (hydraulic)</td>
<td>A structure that converts the energy of flowing water into mechanical energy. There are several turbine types with different configurations, the most common are Francis and Kaplan (see definitions below).</td>
</tr>
<tr>
<td>Kaplan turbine</td>
<td>An “axial”, vertical, propeller-like turbine used for lower pressure heads (less than 100 m). Smaller in overall size (relative to Francis), typically has 4 to 8 adjustable blades and a specific running speed ranging 250 to 250 rpm.</td>
</tr>
<tr>
<td>Francis turbine</td>
<td>A “radial” turbine used for higher pressure heads (100 to 500 m). Larger in overall size (relative to Kaplan), typically has 16 to 24 fixed blades and a specific running speed of 50 to 250 rpm.</td>
</tr>
<tr>
<td>Turbine bypass</td>
<td>A structure that fish can enter from the gatewell, bypasses the turbines and powerhouse through a series of channels, and discharges downstream into the tailrace. Typically used for juvenile salmonids.</td>
</tr>
<tr>
<td>Fish injuries/impacts</td>
<td></td>
</tr>
<tr>
<td>Abrasion</td>
<td>Damage to skin and/or scales.</td>
</tr>
<tr>
<td>Blade strike</td>
<td>Turbine blade striking a fish. Can result in injuries/mortality from grinding (depending on blade spacing, small fish more prone to this), bruising, and cuts of varying severity (superficial, mortal wounding).</td>
</tr>
<tr>
<td>Barotrauma</td>
<td>Damage caused from exposure to rapid changes in barometric pressure, typically during turbine passage. The most common injuries/mortalities are related to swim bladder ruptures. In the presence of high total dissolved gasses, rapid pressure changes can cause gas embolisms in tissues/organs and other symptoms of gas bubble disease.</td>
</tr>
<tr>
<td>Descaling</td>
<td>Scale loss. Often expressed as a percentage of the scale loss on the whole fish (e.g., 20% scale loss).</td>
</tr>
<tr>
<td>Entrainment</td>
<td>When fish (non-) volitionally pass through hydropower infrastructure.</td>
</tr>
<tr>
<td>Hemorrhage</td>
<td>Bleeding, blood loss.</td>
</tr>
<tr>
<td>Impingement</td>
<td>When a fish becomes pinned/trapped against an infrastructure.</td>
</tr>
<tr>
<td>Cavitation</td>
<td>Formation of gas bubbles in water, which when collapsed generate a pressure wave that can cause ill effects for fish in close proximity.</td>
</tr>
<tr>
<td>Mechanical effects</td>
<td>Damage (injury/mortality) caused from fish physically interacting with structures (e.g., blade strike).</td>
</tr>
<tr>
<td>Pressure effects</td>
<td>Rapid changes in pressure (perpendicular to surface, dorsoventral) during passage that can cause fish damage.</td>
</tr>
<tr>
<td>Shear effects</td>
<td>Rapid changes in pressure (parallel to surface, anteroposterior) during passage that can cause fish damage.</td>
</tr>
<tr>
<td>Turbulence effects</td>
<td>Damage (injury/mortality) to fish caused by turbulent water (irregular movement of water).</td>
</tr>
<tr>
<td>General terms</td>
<td></td>
</tr>
<tr>
<td>Forebay</td>
<td>Impoundment area directly above a hydropower facility.</td>
</tr>
<tr>
<td>Head</td>
<td>Difference in elevation between two water levels (e.g., reservoir water level and tailrace). There are various operational head definitions (see [34]).</td>
</tr>
<tr>
<td>Passive Integrated Transponder (PIT) tag</td>
<td>A small tag implanted into a fish that transmits a unique code when activated. Can be used to track fish passage and survival through specific routes and river systems.</td>
</tr>
<tr>
<td>Tailrace</td>
<td>A channel downstream of turbine outlets discharged water flows away from the facility.</td>
</tr>
<tr>
<td>Telemetry</td>
<td>A system for tracking fish movements through specific routes at a facility as well as along watercourses. Common methods are acoustic, radio, and passive integrated transponder (PIT) tag telemetry.</td>
</tr>
</tbody>
</table>
Table 2.2: Definitions of terms used throughout the systematic review.

<table>
<thead>
<tr>
<th>Term</th>
<th>Definitions</th>
</tr>
</thead>
<tbody>
<tr>
<td>Article</td>
<td>An independent publication (i.e., the primary source of relevant information). Used throughout the review.</td>
</tr>
<tr>
<td>Site</td>
<td>A specific hydroelectric facility (i.e., hydro dam) or research laboratory/testing facility (lab) where experiment(s) or observation(s) were undertaken and reported from the same or different article. Used throughout the review.</td>
</tr>
<tr>
<td>Study</td>
<td>If at a given site, evaluations of responses were conducted for different: (1) operational conditions (e.g., turbine discharge, wicket gate opening width, dam height); (2) modifications of a specific intervention (e.g., number of turbine runner blades); or (3) depth at fish release; I considered these separate studies and each were given a “Study ID”. If at a given site, evaluations of responses were conducted for different interventions (e.g., mortality at turbines and at spillways), I only considered these separate studies if the fish were released separately for each intervention (i.e., different release points immediately above the intervention under evaluation, within the same or different years). When studies released a group of fish at a single location above all interventions, and the outcomes came from route-specific evaluations, these were considered the same study and received the same Study ID. Used throughout the review.</td>
</tr>
<tr>
<td>Project</td>
<td>Individual investigations within a study that differed with respect to ≥1 aspects of the study validity criteria (e.g., study design). Used in Review descriptive statistics and narrative synthesis.</td>
</tr>
<tr>
<td>Data set</td>
<td>(1) A single study from a single article; or (2) when a single study reported separate comparisons for different: (a) species, and/or (b) the same species but responses for different: (i) outcome subgroup categories (i.e., injury, immediate mortality, delayed mortality, number of fish entrained); (ii) life stages for the same outcome subgroup; and/or (iii) sources of fish for the same outcome subgroup. The number of datasets was only considered for quantitative analyses.</td>
</tr>
</tbody>
</table>
Table 2.3: Critical appraisal tool for study validity assessment. Reviewers provided a rating of High, Medium, or Low for each of the specific data quality features.

<table>
<thead>
<tr>
<th>Category</th>
<th>Bias and generic data quality features</th>
<th>Specific data quality features</th>
<th>Validity</th>
<th>Design of assessed study</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Selection and performance bias: study design</td>
<td>Design (i.e., well-controlled)</td>
<td>High</td>
<td>Controlled trial (randomized or not) or Gradient of intervention intensity including &quot;zero-control&quot;</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>High</td>
<td>CI</td>
</tr>
<tr>
<td>2</td>
<td>Assessment bias: measurement of outcome</td>
<td>Replication (level of total fish released/surveyed)</td>
<td>High</td>
<td>Large sample size (n&gt;100 fish)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Medium</td>
<td>Moderate sample size (n = 50-100 fish)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Low</td>
<td>Low sample size (n&lt;50 fish), or unclear/not indicated</td>
</tr>
<tr>
<td></td>
<td>Measured outcome</td>
<td></td>
<td>High</td>
<td>Quantitative</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Medium</td>
<td>Quantitative approximations (estimates)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Low</td>
<td>Semi-quantitative, or no extractable results</td>
</tr>
<tr>
<td></td>
<td>Outcome metric</td>
<td></td>
<td>High</td>
<td>The change in a metric related to fish mortality, injury, or productivity relative to an appropriate control</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Low</td>
<td>A metric related to risk of impingement/entrapment (i.e., number of fish entrained) and not mortality/injury/productivity per se</td>
</tr>
<tr>
<td>3</td>
<td>Selection and performance bias: baseline comparison (heterogeneity between intervention and comparator with respect to defined confounding factors before treatment)</td>
<td>Habitat type</td>
<td>High</td>
<td>Control and treatment samples homogenous</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Low</td>
<td>Control and treatment samples not comparable with respect to confounding factors OR insufficient information</td>
</tr>
<tr>
<td></td>
<td>Sampling</td>
<td></td>
<td>High</td>
<td>Treatment and control samples homogenous with respect to sampling distance</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Low</td>
<td>Control and treatment samples not comparable with respect to confounding factors OR insufficient information</td>
</tr>
<tr>
<td></td>
<td>Other confounding environmental factors</td>
<td></td>
<td>High</td>
<td>Intervention and comparator sites homogenous</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Low</td>
<td>Intervention and comparator sites not comparable with respect to confounding factors OR insufficient information</td>
</tr>
<tr>
<td>4</td>
<td>Selection and performance bias: Intra treatment variation [heterogeneity within both treatment and control samples (i.e., releases or surveys) with respect to confounding factors]</td>
<td>Intervention type</td>
<td>High</td>
<td>No heterogeneity within treatment and control samples</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Low</td>
<td>Samples within treatment and control arms not comparable OR insufficient information</td>
</tr>
<tr>
<td></td>
<td>Sampling</td>
<td></td>
<td>High</td>
<td>No heterogeneity within treatment and control samples</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Low</td>
<td>Samples within treatment and control arms not comparable OR insufficient information</td>
</tr>
</tbody>
</table>
**Table 2.4:** Results of study validity assessment using the critical appraisal tool (see Table 2.3).

Numbers indicates the number of projects that received the critical appraisal score for each criterion.

<table>
<thead>
<tr>
<th>Category</th>
<th>Reason</th>
<th>Projects (#)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Low</strong></td>
<td>Replication: less than 50 fish released or not indicated</td>
<td>28</td>
</tr>
<tr>
<td></td>
<td>Measured Outcome: semi-quantitative</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Outcome metric: risk of entrainment/impingement, not mortality/injury <em>per se</em></td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>Intervention and Comparator Bias: habitat type confounding</td>
<td>19</td>
</tr>
<tr>
<td></td>
<td>Intervention and Comparator Bias: confounding sampling factors</td>
<td>39</td>
</tr>
<tr>
<td></td>
<td>Intervention and Comparator Bias: confounding environmental factors</td>
<td>15</td>
</tr>
<tr>
<td></td>
<td>Intra-treatment Performance Bias: variation within treatment/control samples (intervention type)</td>
<td>12</td>
</tr>
<tr>
<td></td>
<td>Intra-treatment Performance Bias: variation within treatment/controls samples (sampling)</td>
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<td><strong>Medium</strong></td>
<td>Sample size: between 50 and 100 fish</td>
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<td>Measured Outcome: quantitative approximations (estimates)</td>
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<tr>
<td><strong>High</strong></td>
<td>Control-impact or randomized controlled trial design</td>
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<tr>
<td></td>
<td>Sample size: greater than 100 fish</td>
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<td></td>
<td>Measured Outcome: quantitative</td>
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<td>Outcome metric: related to fish mortality, injury, or productivity relative to control</td>
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<td>Intervention and Comparator Bias: habitat type homogenous</td>
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<tr>
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<td>Intervention and Comparator Bias: homogeneity in sampling distance/time</td>
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<td>Intervention and Comparator Bias: homogeneity, environmental factors</td>
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<td></td>
<td>Intra-treatment Performance Bias: No heterogeneity within treatment and control samples (intervention type)</td>
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<td>Intra-treatment Performance Bias: no sampling heterogeneity within treatment/control samples</td>
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**Table 2.5:** Site name, location, setting, and number of included studies.

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<td><strong>TOTAL</strong></td>
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Figure 2.1: ROSES flow diagram (Haddaway et al. 2017) showing literature sources and inclusion/exclusion process.
Figure 2.2: Frequency of grey and commercially published literature included for data extraction and critical assessment in each decade.

Figure 2.3: Frequency of studies within a given time-period in relation to study validity. Critical assessment criteria are outlined in Table 2.4.
Figure 2.4: Frequency of studies contributed by 11 families and 15 genera.
Figure 2.5: The frequency of studies in relation to the life history stage and source of fish used.

Fish used in the studies were wild-type (Wild), originated from a hatchery (Hatchery), or were from the source waterbody but originated from a hatchery (Stocked). Age-0: less than 1 year old; Juvenile: greater than 1 year old or when specified as juveniles; Larval: egg and larval development stages; Mixed: a mixture of life history stages.
Figure 2.6: Frequency of intervention types used in studies. Combination: when a study assessed entrainment/impingement using additional intervention types (e.g., screen, sluice, trash rack) in combination with the single intervention type.
Figure 2.7: Frequency of turbine type. Simulated: pressure chamber simulating turbine passage through a Kaplan or Francis turbine; AHTS: Advanced Hydro Turbine System. Note: some studies with turbine as the intervention type did not specify the turbine type used (34 studies).

Figure 2.8: Study frequency for immediate mortality, delayed mortality, and injury in relation to common post-recapture assessment times.
**Figure 2.9**: Summary flow chart of meta-analyses and results addressing the two main research questions and appropriate subsets (dashed boxes). Boxes indicate potential effect modifiers or subset categories under consideration. Grayed effect modifiers were associated with fish injury or mortality responses. Underlined value indicates statistically significant effect. Subset categories in red indicate an overall average increase in risk of fish injury or mortality with passage through/over hydroelectric infrastructure relative to controls; green indicates an overall average decrease in risk of fish injury or mortality with passage through/over hydroelectric infrastructure relative to controls. k: number of data sets (i.e., effect sizes); RR: mean effect size; CI: 95% confidence interval.
Figure 2.10: Weighted pooled risk ratios by interventions for fish injury responses. Values in parentheses are the number of effect size estimates. Error bars indicate 95% confidence intervals. A mean RR value > 1 (right of the dashed line) indicates an overall increase in risk of fish injury with passage through/over hydroelectric infrastructure relative to controls. 95% confidence intervals that do not overlap with the dashed line indicate a significant effect. General: general infrastructure associated with more than one component of a hydroelectric facility.
Figure 2.11: Weighted pooled risk ratios for fish injury for different site types and assessment times for studies involving turbines. See Figure 2.10 for explanations.

Figure 2.12: Weighted pooled risk ratios for fish injury for different life stages for studies involving general infrastructure. See Figure 2.10 for explanations.
Figure 2.13: Weighted pooled risk ratios by interventions for immediate fish mortality responses. See Figure 2.10 for explanations. General: general infrastructure associated with more than one component of a hydroelectric facility.
Figure 2.14: Weighted pooled risk ratios for immediate fish mortality for different site types for studies involving turbines. See Figure 2.10 for explanations.
Figure 2.15: Weighted pooled risk ratios for immediate fish mortality for studies conducted in the field using different (A) turbine types and (B) sources of fish for Kaplan turbines. See Figure 2.10 for explanations.
**Figure 2.16:** Weighted pooled risk ratios by fish genera (A-C) and interventions within *Oncorhynchus* fish (D and E) for responses to hydroelectric infrastructure. See Figure 2.13 for explanations. General: general infrastructure associated with more than one component of a hydroelectric facility.
Figure 2.17: Weighted pooled risk ratios by (A) fish species for immediate mortality of *Oncorhynchus* fish from turbines, and (B) turbine type for immediate mortality of Coho Salmon (*O. kisutch*) from field-based studies. See Figure 2.13 for explanations.
Chapter 3: Stranded Kokanee salvaged from turbine intake infrastructure are at low risk for re-entrainment: A telemetry study in a hydropower facility forebay.

3.1 Abstract

Entrainment at hydropower facilities, where fish (non-) volitionally enter hydropower infrastructure such as intake towers, can lead to fish becoming stranded for considerable periods of time rather than being flushed to downstream areas. To reduce fish injury and/or mortality from entrainment stranding events, hydropower operators will salvage stranded fish and release them back into the upstream reservoir. I documented the post-release movements of salvaged fish to determine their vulnerability to re-entrainment at a large hydropower facility. Kokanee Oncorhynchus nerka (lacustrine Sockeye Salmon) were collected from the turbine intake towers at the W.A.C. Bennett Dam in northeastern British Columbia, surgically implanted with small acoustic transmitters, and released in the forebay area of the hydropower facility. Fish movements were tracked using an array of hydrophones in the forebay area. While the depths and hydraulics of the forebay resulted in low detection efficiency of the receiver array, detection data for 25 fish revealed that 72% (n = 18) of fish were last detected at hydrophones located > 1000 m from the turbine intakes (considered low risk to re-stranding/re-entrainment), 24% (n = 6) of fish were last detected at hydrophones < 500 m to the turbine intakes (considered vulnerable to re-stranding), and one re-entrainment event (n = 1; 4% maximal entrainment rate) was observed. These results indicate there is a low risk associated with Kokanee re-entrainment events at this large hydropower facility and that manual salvage appears to be a reasonable approach to mitigate fish loss.
3.2 Introduction

Entrainment at hydropower facilities, where fish (non-)volitionally enter hydropower infrastructure such as intake towers, can lead to fish stranding. There are multiple downstream passage routes for fish at hydropower facilities including turbines, spillways, and a variety of bypasses (OTA 1995; Katopodis and Williams 2012). In facilities lacking passage infrastructure, fish passage through turbines is common and can result in mortality and/or injury (Coutant and Whitney 2000; Pracheil et al. 2016; Algera et al. 2020). Turbine intake towers, designed to retain water for safety and maintenance purposes, provide no purpose-built fish passage (aside from being flushed through turbines) and can strand entrained fish for considerable periods of time. Fish entering and remaining in the intake towers via the surge tower avoid turbine passage, which is one of the most hazardous fish passage routes in terms of mortality and injury (Algera et al. 2020). However, it is unknown if fish can navigate out of the intake towers and return to the reservoir. Owing to their design and operation, repurposing or retrofitting turbine intake towers for fish passage is typically not feasible. The environment in the intake towers is noisy (i.e., from turbine generation), lacks a natural diel photoperiod and presumably has no or diminished food resources, so stranding for lengthy time periods typically results in injuries (e.g., scrapes, scale loss), infections, decreased body condition (Supplementary Material), and presumably mortality. In addition, if generating units are under maintenance (1 to 6 months) and there is no flowing water, the oxygen in the water in the surge towers can deplete over time, causing additional stress to the fish present. Manual removal during turbine shut-downs and other maintenance operations is one of the most common mitigation methods used to salvage (i.e., capture and release) trapped fish (Nagrodski et al. 2012), though the effectiveness of these activities is uncertain.
Owing to the breadth of movements within a system for spawning and foraging, migratory (diadromous, potadromous) and resident pelagic fish species are known to be vulnerable to entrainment (Crew et al. 2017; Harrison et al. 2019). Migratory and resident pelagic fish that are salvaged and released back into the reservoir are at risk of re-entrainment because they may be attracted back towards the turbine intake areas by responding to the cues that resulted in prior entrainment. Despite facilities employing opportunistic fish salvage efforts, little is known about the post-release behaviour of salvaged fish or whether fish that are released are vulnerable to becoming re-entrained. Knowledge of the post-release behaviour of salvaged fish would be beneficial in assessing the effectiveness of fish salvage efforts and understanding population level impacts resulting from entrainment.

Williston Lake supports a diverse fish community (21 species) including Kokanee *Oncorhynchus nerka* (lacustrine Sockeye Salmon), Bull Trout *Salvelinus confluentus*, Lake Trout *Salvelinus namaycush*, Rainbow Trout *Oncorhynchus mykiss*, Lake Whitefish *Coregonus clupeaformis*, Mountain Whitefish *Prosopium williamsoni*, and Arctic Grayling *Thymallus arcticus* (Langston and Blackman 1993; Plate et al. 2012). Kokanee were a native species, albeit in low abundance, to some areas of the Williston Lake watershed (Langston and Murphy 2008). To establish a recreational fishery and provide a prey base for other salmonids (e.g., Lake and Bull Trout), Kokanee were stocked into Williston Lake from 1990 to 1997 (Blackman et al. 1990; Sebastian et al. 2003; Langston and Murphy 2008). These stocking efforts appear to have been successful because Kokanee are now one of the dominant pelagic species found in the Peace Reach of Williston Lake and the forebay area of the Bennett Dam forebay area (Sebastian et al. 2008; Plate et al. 2012). Since Kokanee is an important prey base and valued in the recreational fishery, they are regularly assessed within BC Hydro’s Fish Entrainment Strategy.
and were determined to be a medium level entrainment risk using the risk management framework. Harrison et al. (2020) found Bull and Lake Trout entrainment rates were low at a large hydropower facility on Williston Lake, but stranding and entrainment rates of Kokanee are unknown. Manual fish salvage has been conducted in the past at the facility (R. Zemlak, BC Hydro, pers. comm.) but the risk of re-stranding and re-entrainment of Kokanee is also unknown.

Here I assessed the vulnerability of Kokanee, salvaged from turbine intake towers, to re-entrainment at a large hydropower dam. Specifically, I tracked post-release movements of Kokanee following salvage activities to enumerate re-entrainment into the facility. To my knowledge this is the first study to examine fish movements following release from salvage activities and thus has the potential to inform ongoing mitigation at the W.A.C. Bennett Dam and other facilities where fish become stranded within hydropower infrastructure.

3.3 Methods

3.3.1 Study site

The study was conducted from August 2016 to August 2017 at W.A.C. Bennett Dam (hereafter the Bennett Dam), a large hydroelectric facility (> 13,000 GWh annual capacity) owned and operated by BC Hydro, located near Hudson’s Hope, British Columbia (Figure 3.1). By damming the Peace River, The Bennett Dam created Williston Lake (56°01’00”N 122°12’02”W), a large (1,761 km2 surface area) and deep (mean depth 41.7 m, max depth 166 m), ultra-oligotrophic reservoir (Stockner et al. 2005). The Bennett Dam is a 183 m high earthen-filled dam with an 850 m ungated spillway and 10 turbine intakes in the forebay area. The powerhouse consists of 10 Francis turbines (5 x 275 MW, 3 x 310 MW and 2 x 306 MW). The intake towers at the Bennett Dam are semi-cylindrical (diameter of all intakes ~ 5.2 m) concrete structures (Appendix B). Turbine intakes depths for intake tower units 1 to 3 are located at 61–78
m and the total height of each structure is 85 m (bottom of penstock to car deck). Turbine intake depths for units 4 to 10 are located at 27–44 m and the total height of each structure is 51 m. Total depth in each of the intake tower units depends on reservoir elevation, which varies by 7 m between low and high pool in the reservoir. Fish entering the turbine intakes are presented with two options – move into the penstock and down through to the turbines or move up into the surge towers. Fish passed through the Bennett Dam powerhouse turbines are released into Dinosaur Reservoir, a 20.5 km, 805 ha reservoir that is impounded on the downstream end by Peace Canyon Dam, another BC Hydro facility (Hammond 1984).

### 3.3.2 Fish capture and tagging

Stranded Kokanee were captured via angling and netting (Appendix B) from the surge towers of turbine units 7 and 9 during August 2016 (surface water temperatures of 15 to 17°C). To maximize potential for successful tag application and survival, only healthy fish in good body condition (visual assessment) with minimal injuries (i.e., no fungal infections, no scrapes/cuts/hemorrhages, and minimal scale loss) were selected for inclusion in the study. Captured fish were anaesthetized by immersion into a 40 mg/L clove oil solution (1 part clove oil: 9 parts 95% ethanol). After loss of equilibrium, fish were measured for body length [total length (TL), nearest mm] and surgically implanted with a Juvenile Salmon Acoustic Telemetry System (JSATS) acoustic transmitter (Lotek Wireless, Newmarket, Ontario, Canada). I elected to use JSATS technology because they are the smallest commercially-available acoustic telemetry tags, are regarded as being robust to noise around hydropower facilities, and have settings that allow tags to transmit relatively rapidly (i.e., at 20 sec intervals), yet do not suffer from code collisions (McMichael et al. 2010).
Two types of JSATS transmitters were used (L-AMT-5.1B, 5 x 7 x 13 mm, 0.6 g dry weight, 20 s burst rate, expected battery life 327 days; L-AMT-5.2, 7 x 7 x 13 mm, 1.1 g dry weight, 20 s burst rate, expected battery life 568 days) with both types using 416.7 kHz transmitter frequency and transmitter power of 158 dB. Transmitters and surgical gear were disinfected with Betadine prior to surgery and between each fish. Small (~10 mm) incisions were made along the midline, just anterior to the pelvic girdle. Incisions were closed using 2 simple-interrupted absorbable sutures (3/0 monofilament PDSII, Ethicon Inc., Somerville, New Jersey). Recirculating lake water was applied to the gills throughout the entire procedure, which took <5 min for each fish. Body lengths ranged from 112 to 255 mm TL. Weights were not taken to limit air exposure and handling time, but published Kokanee length-weight relationships (Hyatt and Hubert 2000) indicate that fish weights ranged from ~14 to 173 g. The larger 1.1 g JSATS transmitters (n = 46) were implanted into fish in the 158 to 249 mm TL range, which equates to a weight range of ~40 to 161 g and a maximal tag weight of 2.7% of the fish’s body weight. The smaller 0.6 g JSATS transmitters (n = 42) were implanted into fish in the 112 to 255 mm TL range, which equates to a weight range of ~14 to 173 g and a maximal tag weight of 4.2% of the fish’s body weight. Tag weight did not exceed 5% of the body weight, suggesting that tag burden would not impede swimming behaviour (Brown et al. 1999).

Short-term monitoring of fish in coolers after surgery indicated that fish exhibited normal swimming behavior following recovery from the anesthesia. Post-surgery, fish were transported at low density (i.e., < 10 kg-1m3) by truck in a large cooler supplied with ambient lake water and released back into the forebay area at the Elizabeth Creek boat launch (56°01'28.5"N 122°13'24.4"W), approximately 2 km from the turbine intakes. Any tagged fish that exhibited
burdened swimming behaviour (i.e., from surgical transmitter implantation or the holding period) were recovered, humanely sacrificed, and were not included in the study.

### 3.3.3 Telemetry array

In August 2016, an array of fifteen omni-directional hydrophone acoustic telemetry receivers (WHS4520, Lotek Wireless, Newmarket, Ontario, Canada) were deployed in the Bennett Dam forebay area and an additional five receivers were deployed downstream of the dam in the Dinosaur Reservoir and the Peace River (Figure 3.1). The Bennett Dam forebay receivers were anchored ~ 800 m apart in a grid-like pattern except for the three receivers located close to the turbine intakes which were anchored ~ 400 m apart. The telemetry array was active from deployment through to January 2018 and from May to October 2018, with the intervening period equating to the time where a battery change was not possible owing to logistics and safety considerations (e.g., high turbine generation resulting in heavy winter draw down ice conditions).

Two separate range and detection efficiency tests were conducted – one above and one below the dam. Testing was conducted post-hoc in June 2019 because this was when equipment and the appropriate access was available. The same hydrophone receiver model (WHS4520) and the 1.1g JSATS transmitters were used as those in the study. The 0.6g JSATS transmitters were not tested, but this model uses the same frequency and transmitter power as the 1.1g model, therefore range and detection efficiencies were expected to be similar. For the range and detection efficiency array above the dam, three receivers anchored ~400 m apart that were active for 46 h, were deployed in the forebay area of the Bennett Dam in Williston Lake (Supplementary Material). Three transmitters were used, one anchored at 0 m (on the same anchor line as a hydrophone), and at 50 m and 200 m from the 0 m-line receiver. This configuration allowed determination of detection range and efficiency at a variety of distances
from 0 to 800 m. For the range and detection efficiency array below the dam, two hydrophones that were active for 167 h, were deployed in Dinosaur Reservoir at locations that were part of the telemetry study and considered critical to determine entrainment events: 100 m downstream of the Bennett Dam in the tailrace and in front of Gething Creek. The Bennett Dam tailrace is a noisy and high turbulence environment and represents a worst-case scenario from a detection range and efficiency standpoint. Three transmitters were used, one at 0 m on the same anchor line as the Bennett Dam tailrace receiver and two at Gething Creek anchored at 120 and 240 m from the Gething Creek receiver.

3.3.4 Data analysis

Telemetry data, statistical analyses, and maps were processed in R Studio (version 1.2.5042) using R (version 3.6.3. https://cran.r-project.org/bin/windows/base/). By comparing transmitter ID detections against known deployed transmitter IDs, false negative detections (i.e., transmitter IDs that were not implanted into fish in the system) were identified and removed prior to data analysis. False positive detections (i.e., erroneous existing transmitter IDs) were identified and removed from the dataset in two stages by first applying an “interval method” (Lotek Wireless, pers. comm) and then applying a minimum lag method. The interval method utilizes the JSATS burst rate (i.e., regular 20 s interval for tags in the present study) to identify false positive detections. The first transmitter ID detection was considered as a “true” detection and all subsequent detections outside of a 20 s interval were removed from the dataset. The minimum lag method uses an a priori determined, biologically relevant minimum number of detections within a specified time interval window to identify false positive detections (Pincock 2012). In the present study a minimum of two detections within a one-hour period were considered “true” detections. Individual fish abacus plots were visually inspected to verify that
detection timestamps made sense. Maximum detection range was determined by examining post-hoc range testing data. Detection efficiency percentage was calculated at each distance interval as the quotient of the number of observed detections divided by the number of possible detections while the receivers were active. The resulting detection ranges and efficiencies were not further applied to telemetry data analysis, but are presented to provide the level of certainty with interpretation of the telemetry observations.

Entrainment can lead to fish passing through a facility or becoming stranded within the facility. A salvaged fish that was detected at a receiver in the forebay array and then subsequently detected at a receiver in the downstream array below the Bennett Dam (Figure 3.1) was considered as being vulnerable to re-entrainment. A fish was considered as being vulnerable to re-stranding when the last observed detection was at a receiver located < 500 m from the turbine intakes. A fish was considered as having a low vulnerability to re-stranding/re-entrainment when the fish’s last detection was at a receiver > 1000 m from the turbine intakes.

Fish body length data met the assumptions of equal variance and normality, so Welch two sample t-tests were used to determine if there were any statistically significant differences in body length between transmitter types (0.6 g, 1.1 g). A Pearson’s Chi-square test with Yate’s continuity correction was used to determine if there was a difference in the relative proportions of transmitter types that were detected in the array. Time spent in the array of individual fish was calculated by summing the number of seconds between the first and last detections. Fish detection data did not meet the assumption of normality, so a generalized linear mixed model (GLMM) was used to test for any effects among time spent in the array, body length (continuous variable, TL, standardized by subtracting the mean and dividing by the SD), and transmitter type (categorical variable). Because there were multiple observations from each individual fish, a
a random intercept of individual fish (fish ID) was included in the GLMM. A Poisson error distribution was used for the GLMM, which was modeled using the glmer function in the lme4 package (Bates et al. 2020) and verified by plotting the residuals against the fitted values for all the factors.

3.4 Results

A total of 108 Kokanee were tagged, 20 of these tagged fish were affected by the tagging/holding procedure and were humanely sacrificed and excluded from the study, resulting in a total of 88 fish that were tagged and released. After removing false negative and positive detections, a total of 25 of the 88 tagged salvaged Kokanee were detected in the hydrophone array, resulting in 1,671 detections. The body length of the 25 detected fish ranged from 125 to 242 mm TL. The two transmitter sizes were detected equally in the array (0.6 g = 12 fish, 1.1 g = 13 fish), with the proportion of each tag size detected being statistically equivalent ($\chi^2 < 0.001$, df = 1, $P = 1$).

The post-release duration that salvaged fish were detected within the hydrophone array ranged between 3 min and ~16 days. The GLMM revealed that there was no pattern evident among time spent in the array and body length ($Z = -1.651$, df = 21, $P = 0.099$) or transmitter type ($Z = 0.006$, df = 21, $P = 0.995$).

For the Bennett Dam forebay area hydrophones, maximum detection range was $> 50$ m but less than 200 m, with detection efficiency markedly reduced beyond 50 m from the hydrophone (Table 3.1). For the receivers downstream of the Bennett Dam deployed in Dinosaur Reservoir, maximum detection range was between 120 and 240 m and detection efficiency was $< 1\%$ for all of the hydrophones.
3.4.1 Re-stranding and re-entrainment vulnerability

Of the 25 salvaged fish detected in the forebay array (Figure 3.1), 18 (72%) were last (or only) detected on a forebay receiver > 1000 m from the turbine intakes and thus were considered at low risk for re-stranding/re-entrainment. Of those low vulnerability fish, time spent in the array ranged from 3 min to 20 h except one fish which spent ~16 days in the array. Six salvaged fish (24%) were last detected on a forebay receiver < 500 m from the turbine intakes and were thus deemed as being vulnerable to re-stranding. One fish was re-entrained, with detections near the spillway receivers and then subsequent detections in Dinosaur Reservoir downstream of the Bennett Dam. The single re-entrainment event represents a 4% entrainment rate of the 25 fish detected in the forebay array or ~1% entrainment rate for all 88 released fish.

3.5 Discussion

Much research has been conducted on stranding and entrapment in riverine habitats resulting from hydropower operations such as hydropeaking and ramping (McMichael et al. 2006; Young et al. 2011; Nagrodska et al. 2012; Irvine et al. 2015) but almost nothing is known about the type of stranding (i.e., in intake towers) studied here. In the present study, salvaged fish appear to have a low risk for being re-entrained, which to my knowledge is the first study to track and observe movements of salvaged fish that were stranded inside hydropower infrastructure. The relatively high number of fish that were last detected > 1000 m from the turbine intakes and the low re-entrainment proportion suggest that fish salvage efforts for Kokanee at this facility could be effective for mitigating fish losses.

The limited range and low detection efficiency of the forebay and downstream receiver arrays should be given consideration when interpreting the results. Although the smaller JSATS tags allow tagging of relatively small fish, tagging of multiple fish in close proximity with
limited tag collisions, and are frequently used for hydropower studies involving small salmonids (McMichael et al. 2010; Deng et al. 2011), there are trade-offs with detection range and efficiency. Here low detection range and efficiency of the receiver arrays were likely affected by the noisy and turbulent environment in the forebay (Kessel et al. 2014). The results indicate that some fish may have been vulnerable to being re-stranded in the facility and/or the intake towers, but there is high uncertainty associated with this categorization because logistical and site access constraints prevented installation of monitoring equipment within facility structures to confirm re-stranding, and thus the actual fate of fish is unknown. Additionally, I was unable to detect 72% of the 88 fish released in the study and are unsure of their fate. Factors like increased mortality from tag burden, delayed wound-healing, and poor body condition (Wargo Rub et al. 2020) or predation by Bull Trout, Lake Trout, and/or birds in the forebay (Harrison et al. 2020) may have removed these fish from the study. Alternatively, the receivers in the forebay were spaced ~800 m apart, those used to detect potential re-stranding and re-entrainment events were ~400 m from the turbines, and the downstream array had very low detection efficiency. It is possible that fish entered and/or passed through the array and/or facility undetected, and therefore my results of re-entrainment and/or re-stranding risk should be considered as conservative estimates when accounting for range/detection efficiency.

Although fish entering the intake towers are avoiding the turbines and thus the associated direct mortality attributed to turbine passage (Pracheil et al. 2016; Algera et al. 2020), stranding in the surge towers is also potentially hazardous. Anecdotally, during the study dead fish (of various species including Rainbow Trout and Lake Whitefish) were observed and a considerable number of free-swimming fish had fungal infections (Supplemental Material). Furthermore, many fish that were captured during sampling were excluded from the study based on their poor
condition (i.e., emaciated) and I had no way of knowing whether condition is correlated with subsequent re-entrainment. Additionally, there was no way to determine how long the salvaged Kokanee had been stranded in the surge towers. It is currently unknown if fish navigate out of the surge towers or if they become permanently stranded. It is presumed that if the turbines are running, fish located within the surge tower can only escape through the penstock and turbines. The rate at which stranding results in mortality is also unknown, but based on the general poor condition of the fish present in the intake towers and the assumption that fish do not exit the towers once stranded, fish mortality is probable unless fish are salvaged. If no exclusion structures (e.g., screens) can be installed on the structures like trash racks at the turbine intakes because of design constraints or the high flow rates required during generation (USFWS 2017), manual salvage efforts may be required to fulfill any regulatory requirements to mitigate fish losses.

The only re-entrained salvaged fish in this study appeared to survive turbine passage and was last detected over 20 km downstream in Dinosaur Reservoir in the Peace Canyon facility forebay area, which may be desirable because entrained fish are likely the main source of Kokanee for the downstream Dinosaur Reservoir (Murphy and Blackman 2004). Regardless, the Kokanee population in Williston Reservoir has continued to expand since the stocking programs ceased, suggesting that stranding and entrainment are likely not affecting recruitment at this time.

3.6 Management implications

My study reveals that if fisheries managers intend to use manual fish salvage in surge towers as a means of fish loss mitigation, salvaging fish should happen on a frequent basis to increase the number of healthy fish being released. Importantly, future work identifying the
seasonal variations in stranding could help improve the effectiveness of salvage activities. Though not explicitly tested here, fish condition is presumably negatively correlated with time spent in the surge towers. However, an alternative explanation is that fish in poor condition are more likely to be stranded. Nonetheless, this study suggests that fish with a higher body condition could increase the chances of survival after salvage efforts. About 80% (88 of 108) of the healthy fish selected for inclusion showed no signs of impairment after tag implantation, and tagging is inherently more intrusive and stressful than just being captured and released with proper handling and holding procedures in place. Additionally, surge tower fish with fungal infections and poor body condition died rapidly after capture. Thus, limiting the time spent in the towers by conducting frequent salvage efforts could increase survival upon release.

Anecdotally, I found Kokanee to be sensitive to netting and handling, which agrees with another study tracking Kokanee movement in the Williston Lake system that found Kokanee to be sensitive to netting (Fielden 1992). Kokanee’s sensitivity to netting and handling might be somewhat problematic for salvage efforts, but salvage efforts should be viewed as worthwhile attempts to mitigate fish loss because these fish are lost to the system while stranded. From another perspective, Kokanee’s relative sensitivity could also be encouraging for fisheries managers because this species likely represents a worst-case scenario for salvage. Species such as Rainbow Trout that are more resilient to netting, handling, and holding would presumably fare much better if targeted for manual salvage.

It is currently unknown what behaviour leads to stranding in structures like intake towers and why some fish choose to enter the intake towers rather than the turbine intakes. Although my receiver array had low detection efficiency and many fish were not detected in the array, my results offer a preliminary assessment that indicates that manually salvaged fish do not appear be
a high entrainment risk after release. The Bennett Dam is a large facility that has no fish passage enhancement infrastructure such as fishways or bypasses, so downstream passage currently occurs either through turbines or on rare occasions, the spillway. The results of this study can aid decision-making for operators of other large hydropower facilities lacking fish passage options that are looking to undertake manual fish salvage efforts to mitigate fish losses at their facility.

Given the current use of manual salvage efforts and limitations of the present study, additional research is needed on post-release behaviour to evaluate the effectiveness of these efforts. Other species were stranded in the Bennett Dam surge towers including Rainbow Trout and Lake Whitefish, which could be studied to determine if they exhibit similar re-entrainment results when salvaged. Future fish salvage research should track fish depth use and identify proximate reasons for fish habitat use in the forebay area of hydropower facilities. Coupling fish movement data with modeled forebay hydrodynamics (e.g., via computational fluid dynamics) could help determine (re-)entrainment and/or (re-)stranding risk associated with various species and turbine operational regimes.
Table 3.1: Detection range and efficiency of receivers in Williston Lake (Bennett Dam forebay area) and Dinosaur Reservoir (downstream of Bennett Dam facility).

<table>
<thead>
<tr>
<th>Waterbody</th>
<th>Distance (m)</th>
<th>Efficiency (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Williston</td>
<td>0</td>
<td>82.9</td>
</tr>
<tr>
<td></td>
<td>50</td>
<td>22.8</td>
</tr>
<tr>
<td></td>
<td>200</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>350</td>
<td>0.01</td>
</tr>
<tr>
<td></td>
<td>400</td>
<td>0</td>
</tr>
<tr>
<td>Dinosaur</td>
<td>0</td>
<td>0.04</td>
</tr>
<tr>
<td></td>
<td>120</td>
<td>0.38</td>
</tr>
<tr>
<td></td>
<td>240</td>
<td>0</td>
</tr>
</tbody>
</table>
Figure 3.1: Frequency of Kokanee detections and the number of fish detected on each hydrophone receiver in Williston Lake, Dinosaur Reservoir and Peace River. Hydropower facilities (W.A.C. Bennett and Peace Canyon dams) are indicated with dark gray fill colour. Filled circles denote hydrophone receivers; the black open square denotes the release point of salvaged fish; hashed black circle indicates the location of receivers < 500 m from intake towers used to determine vulnerability to re-stranding.
Chapter 4: Exposure risk of fish downstream of a hydropower facility to supersaturated total dissolved gas: An acoustic telemetry study.

4.1 Abstract

Fish exposed to supersaturated TDG levels can develop gas bubble trauma (GBT) which can lead to sublethal effects or mortality. However, hydrostatic (depth) compensation minimizes/mitigates exposure risk and GBT occurrence. My goal for this study was to examine resident fish reach and depth use, and assess exposure risk to elevated supersaturated TDG levels. TDG levels were modeled for three operational scenarios, and I used acoustic telemetry to track resident Rainbow Trout *Oncorhynchus mykiss* (RT) and Mountain Whitefish *Prosopium williamsoni* (MW) movements in the hydropower impounded Columbia-Kootenay system near Castlegar, British Columbia. Telemetry data revealed trends in MW reach and depth residency that corresponded to spawning, foraging, and refuge behaviour whereas RT exhibited a high affinity to areas upstream of the Kootenay Confluence. No significant differences were found in reach residency according to body length, species, or season. Fish did not exhibit any depth preference, and species and body length had no effect on depth residency, but depth residency was found to be significantly different among the seasons and locations. A risk assessment using spring telemetry and TDG data revealed that RT had a significantly higher risk for TDG exposure relative to MW and that exposure risk was highest at locations at the Kootenay Confluence or downstream thereof for both species. The telemetry and risk assessment results can be used by decision-makers to develop operational regimes and TDG risk abatement strategies at hydropower facilities.
4.2 Introduction

Spilling water at dams, where water is passed over/through spillways and related infrastructure rather than through turbines for power generation, is carried out during seasonal high flow events. Spilling can be for operational and/or safety purposes when the water capacity exceeds the load capacity of the hydropower facility, or for meeting conservation requirements such as maintaining minimum flows to mitigate stranding events and/or enhance fish passage (Trevithick et al. 1995; Nagrodski et al. 2012). Spilling water to mitigate fish losses can be beneficial from a conservation standpoint, but the process of spilling water can also generate supersaturated total dissolved gases (TDG) levels in the spilling basin. Aerated flows, created by water passing over hydropower infrastructure such as spillways, entrains bubbles containing atmospheric gases (i.e., nitrogen, oxygen, and other trace gases) which can dissolve in water. Dissolved gas supersaturation, a function of pressure and temperature, occurs when the partial pressures of atmospheric gases in solution exceed their respective partial pressures in the atmosphere. When the sum of the partial pressures of all the dissolved gases (total gas pressure) exceeds atmospheric pressure, gas bubbles can develop in the water and in aquatic organisms inhabiting the water. This means that when water passes over the spillway of a hydropower facility and plunges into the spill basin below, the atmospheric gases can dissolve into the water at depth and supersaturate the water to levels exceeding 100% saturation. Exposure to supersaturated TDG levels can be hazardous to fish occupying habitats downstream because it is known to cause gas bubble trauma (GBT) (Weitkamp and Katz 1980; Pleizier et al. 2020a).

Exposure to TDG supersaturation >125% is known to produce GBT related fish mortality, though sensitivity varies among species and developmental stage (Weitkamp and Katz 1980; Wang et al. 2015; Cao et al. 2019; Ji et al. 2019; Deng et al. 2020). Exposure at low to
moderate TDG levels (i.e., 105-120% supersaturation) can have sub-lethal effects (Pleizier et al. 2020a; 2020b), with fitness related implications (i.e., survival and reproduction) for fishes residing below large hydro dams (McGrath et al. 2006). Since TDG supersaturation is a function of pressure (depth), hydrostatic compensation is possible such that a 1 m increase in depth roughly compensates for 10% TDG supersaturation (Bouck 1980; Pleizier et al. 2020a; 2020b). Thus, a fish positioned at 1 m depth is compensated at 110% TDG supersaturation. Through full and partial hydrostatic (depth) compensation, fish can endure increased TDG levels with no ill effects or GBT occurrence (Dawley et al. 1976), however, symptoms of GBT can manifest with loss of depth compensation.

Generation of TDG is contingent on a hydropower facility’s operational conditions. Spillage is the main factor such that increased spillage results in increased supersaturation levels (Qu et al. 2011). The residency of TDG in waters downstream of the spillway depends on the system hydrology and flow dynamics in the tailwaters (Urban et al. 2008). Dissipation of TDG occurs via air-water contact, so turbulent waters dissipate TDG quicker than flat, standing tailwaters where TDG can remain elevated and travel considerable distances from the dam (Qu et al. 2011). Consequently, fish downstream of the dam are at greatest risk of exposure to higher TDG levels, with exposure risk diminishing as distance from the dam increases (Qu et al. 2011). Mitigating supersaturated TDG levels that are harmful to fish involves preventing production of TDG by avoiding water spillage, or rapidly increasing downstream dissipation through operational modifications or infrastructure installations that increase tailwater turbulence. Passing water through turbines for power generation can minimize TDG supersaturation, but is not always an option under high flow scenarios. Effective implementation of TDG mitigation strategies has not occurred to date and, consequently, TDG remain a persistent problem in some
river systems (McGrath et al. 2006; Ma et al. 2018). In highly impounded systems with multiple hydropower facilities, such as the Columbia River system, TDG levels are already elevated in the receiving waters for facilities sited in the lower reaches of the system. A situation making lower reach TDG management objectives and targets difficult to achieve.

Salmonids are focal species for management and conservation actions in North American aquatic systems where high TDG levels occur because of hydropower operations (Backman and Evans 2002). Fish behaviour may mitigate TDG exposure. Wang et al. (2020) found that resident Cyprinid and Catostomid fish in the Yangtze River system exhibited strong detection and avoidance abilities when TDG is very high (i.e., 145%). Some salmonids appear able to detect high TDG levels and will exhibit lateral movement avoidance behaviours (Stevens et al. 1980). However, salmonid depth compensation responses are varied (Dawley et al. 1976; Lund and Heggberget 1985) and this topic remains largely understudied. Habitat use and residency may increase exposure risk to elevated TDG levels. Mature fish that are spawning may spend more time in certain areas of a watercourse during the spawning season. Furthermore, many salmonids are territorial (Bachman 1984; Gunnarsson and Steingrimsson 2011), with large individuals typically occupying higher quality habitats having higher resource abundance, and site fidelity can be high (Bridcut and Giller 1993; Pert and Erman 1994). If preferred habitats (territorial, spawning) are in areas with frequently elevated TDG levels, there will be an increased exposure risk and probability of developing GBT.

Although studies tracking individual fish movements in relation to elevated TDG levels and hydrostatic compensation have been completed (Weitkamp et al. 2003; Johnson et al. 2005; 2010), knowledge of TDG exposure risk in relation to behavioural traits such as site residency is limited. Most studies have examined migratory salmon and trout, with few having focused on
resident salmonid fishes that would have increased TDG exposure potential year-round.

Furthermore, to my knowledge no studies in the scientific literature have conducted a risk analysis connecting TDG exposure to fish movement behaviour. In this study, three TDG profiles were developed based on operational scenarios for two hydropower facilities located on the Columbia River Basin. Fish movements (location, depth) of two resident species, Rainbow Trout \textit{Oncorhynchus mykiss} and Mountain Whitefish \textit{Prosopium williamsoni}, were then tracked with respect to the dams using acoustic biotelemetry. The purpose of the study was to determine whether fish movement behaviour mitigates or aggravates exposure risk to elevated TDG levels under different hydropower operational scenarios. More specifically, my goal was to examine relationships between seasonal residency and depth use of Mountain Whitefish and Rainbow Trout, and assess their exposure risk to elevated supersaturated TDG levels under high-flow operational scenarios. I hypothesized that: 1) reach and depth residency would vary by body length, species, and season; 2) exposure risk would differ by species and location within the system. I predicted that: 1a) smaller Mountain Whitefish and Rainbow Trout reach residency would be more widespread in the system than for larger conspecifics; 1b) Mountain Whitefish and Rainbow Trout seasonal reach residency would correspond to their species-specific pre-, post- and spawning areas; 1c) Mountain Whitefish and Rainbow Trout would occupy deeper habitats in fall and spring, and shallower habitats in winter; 2a) benthic oriented Mountain Whitefish would be fully depth compensated more frequently than predominantly drift-feeding Rainbow Trout; and 2b) species-specific elevated TDG exposure risk would be highest at locations closer to dams.
4.3 Methods

4.3.1 Study site

The study comprised two field work components, a TDG modeling and an acoustic telemetry component, which were collectively conducted from July 2016 to October 2017 on the Columbia River and Kootenay River systems located near Castlegar, British Columbia (Figure 4.1). The Columbia River segment included the ~56 km stretch downstream of Hugh L. Keenleyside Dam (HLK; 49°20’30”N 117°46’25”W) to Waneta Dam (WAN) at the Pend d’Oreille River confluence (49°00’15”N 117°37’12”W) near the Canada-United States border. The HLK facility, which impounds the Arrow Lakes Reservoir, consists of a 52 m dam, eight low-level outlet gates on either side of a four-bay spillway, and a 185 MW generating station (2 x low head Kaplan turbines) on the left bank. The HLK dam, which was constructed as part of the Columbia River Treaty for water regulation purposes, is owned and operated by BC Hydro, whereas the powerhouse (Arrow Lakes Generating Station) is owned and operated by the provincially owned Columbia Power Corporation. The Kootenay River segment includes the ~2.8 km stretch downstream of Brilliant Dam (BRD; 49°19’29”N 117°37’13”W) to the confluence with the Columbia River. The BRD facility, also owned and operated by Columbia Power Corporation, is a run-of-the-river facility with a 140 MW generating station (4 x vertical Francis turbines) on the right bank, an eight-bay gated spillway, and a 120 MW capacity generating station (1 x Kaplan turbine) 150 m downstream on the left bank.

4.3.2 Fish capture and tagging

Rainbow Trout (RT) and Mountain Whitefish (MW) were captured in October 2016 and October 2017 (surface water temperatures of 8 to 11°C). The 2016 fish were captured via angling (n = 31) or electrofishing (n = 42). Angled fish were captured in the Columbia River ~7 to ~18
km downstream of HLK. Fish caught by electrofishing at night received a passive integrated transponder (PIT) tag prior to surgery. The 2017 fish (n = 19) were all captured via angling ~7 to 8 km downstream of HLK.

Fish were immobilized for surgery using electric fish handling gloves (EFHG) or anesthetized using clove oil. Immobilization with EFHG (Smith Root, Inc., Vancouver, Washington) was achieved using the lowest power settings (i.e., 4 or 6.3 mA) that induced immobilization. Fish that were anesthetized by clove oil were immersed in a 40 mg L\(^{-1}\) clove oil solution (1 part clove oil: 9 parts 95% ethanol) until loss of equilibrium was achieved. Once immobilized or anesthetized, fish were measured for body length [total length (TL), nearest mm], and surgically implanted with an acoustic transmitter (Thelma Biotel, Trondheim, Norway). Betadine was used to disinfect transmitters and surgery equipment prior to surgery and between each fish. Small (~15 mm) incisions were made along the midline, just anterior to the pelvic girdle and closed using 3 simple-interrupted absorbable sutures (3/0 monofilament PDSII, Ethicon Inc., Somerville, New Jersey). During surgery, fish were held in a 100 L cooler containing ambient temperature river water, and the entire surgery procedure took <5 min for each fish. Body lengths for RT ranged from 307 to 504 mm TL and for MW from 310 to 499 mm TL. Weights were not taken to limit air exposure and handling time, but published length-weight relationships suggest that estimated weights for RT ranged from ~315 to 1737 g (Simpkins and Hubert 1996) and for MW ranged from ~300 to 1275 g (Rogers et al. 1996).

Two types of transmitters were used (ADT LP-9-LONG, 9 x 38.5 mm, 6.8 g dry weight, 30 to 90 s duty cycle, 143 dB power output, expected battery life 30 months; ADT LP-7.3-LONG, 7.3 x 27 mm, 2.9 g dry weight, 90 to 120 s duty cycle, 139 dB power output, expected battery life 12 months). Both transmitter types were outfitted with depth sensors and transmitted
using 69 kHz transmitter frequency. The larger 6.8 g LP-9 transmitters (n = 73) were implanted into fish in the 307 to 540 mm TL range. This body length range equates to a weight range of ~315 to 1737 g and a maximal tag weight of 2% of the fish’s body weight. The smaller 2.9 g LP-7.3 transmitters (n = 19) were implanted into fish in the 310 to 506 mm TL range, which equates to a weight range of ~300 to 1427 g and a maximal tag weight of 1% of the fish’s body weight. Transmitter weight did not exceed 2% of the fish body weight, suggesting that tag burden would not impede swimming behaviour (Brown et al., 1999). The LP-9 tags accounted for 79% of the tags in the study and were implanted into fish in October 2016, whereas the LP-7.3 tags accounted for 21% of the tags in the study and were implanted in October 2017. Surgeries were performed as close to the capture location as feasible and fish were released after recovery at the surgery location. During recovery, fish were held at a low density (i.e., < 10 kg m$^{-3}$) in a 100 L cooler containing ambient river water and released once they gained equilibrium.

4.3.3 Telemetry array

An array of 27 omni-directional hydrophone acoustic telemetry receivers (VR2W, Vemco/Innovasea, Halifax, Nova Scotia, Canada) deployed downstream of HLK and BRD was used to track fish movements (Figure 4.1). The telemetry array was active from October 2016 through to April 2019. Thirteen receivers were deployed in October 2016 and the remainder were part of a long-term BC Hydro monitoring program. Receivers were secured to a nylon rope anchor line at ~1 m depth under a large surface buoy and were oriented such that the hydrophone pointed towards the substrate.

Range and detection efficiency testing were conducted in July 2018 using an array of three VR2W receivers and the LP-7.3 acoustic transmitter model. The LP-9 transmitters were not tested, however, the LP-7.3 model has a longer duty cycle and a lower power output than the LP-
9 model. Therefore, the resulting range and detection efficiencies of the LP-9 model was expected to be similar or exceed the LP-7.3 model. For testing, the LP-7.3 transmitter was anchored at a location ~300 m downstream of the HLK dam face and receivers were anchored 50, 100, and 150 m from the transmitter. The receivers remained anchored for the duration of the range and detection efficiency testing. Since the transmitter depth sensor values recorded by the receivers were reported as unitless values, a depth calculation for the sensor values was required. During range and detection efficiency testing the transmitter was anchored at six depth intervals (0.5, 2, 5, 10, 15, and 17 m) for time periods between ~21 to ~73 h. A standard calibration curve was developed by plotting the six depth intervals against the reported unitless depth sensor values, and the resulting equation (E1), which yielded a good fit to the data ($R^2 = 0.99, F_{1,13} = 1056, P < 0.001$), was used to calculate telemetry depth data.

\[(E1) \quad depth = 0.3892(sensor \ value) - 2.9175\]

### 4.3.4 Total dissolved gas modeling

In the present study, three TDG scenarios for the Columbia-Kootenay sector (henceforth Lower Columbia) were modeled using a TDG dissipation methodology following Kamal et al. (2019). See Appendix C for a more detailed description of the TDG modeling methodology. Operational data for the facilities were provided by BC Hydro and Columbia Power Corporation. Scenarios were chosen based on HLK and BRD operating conditions during periods of interest in 2016 and 2018 (Table 4.1). Acoustic tags were active for these periods except for Scenario 1. Data exploration of the HLK and BRD facilities revealed there was higher variation in BRD spillage in the 2016-2018 range relative to HLK during the same period, so scenarios were selected based on BRD operating conditions. Time periods for a given scenario were selected where the spillage rate was relatively consistent (coefficient of variation $< 15\%$, all scenarios) to
enhance TDG dissipation modeling outputs. Low, moderate, and high spillage scenarios that occurred in May and June were selected. These three scenarios were chosen because they represented realistic, biologically relevant scenarios that the fish present in the system would experience. The dissipation modelling output resulted in TDG point data for transects in the Lower Columbia system, which were extrapolated across the entire ~56 km sector using the Ordinary Kriging function in QGIS (version 2.142).

4.3.5 Data analysis

Telemetry data, statistical analyses, and maps were processed in R Studio (version 1.2.5042) using R (version 3.6.3). False negative detections, detected transmitter IDs that were not implanted into fish, were removed prior to data analysis. False positive detections, existing transmitter IDs deemed erroneous, were removed from the dataset by applying a minimum lag method whereby an a priori determined, biologically relevant minimum number of detections within a specified time interval window was used to identify and remove false positive detections (Pincock 2012). Since the duty cycle differed for the two tag types (LP-9 = 30-90 s, LP-7.3 = 90-120 s), the minimum lag was calculated separately for each of the tag types. In the present study a minimum of two detections within a one-hour period were considered “true” detections (Papastamatiou et al. 2010). Fish detection data were verified by visually inspecting individual abacus plots. Maximum detection range was determined by examining range testing data. Detection efficiency percentage was calculated at each distance and depth interval as the quotient of the number of observed detections divided by the number of possible detections while the receivers were active. The mean duty cycle of the two transmitter types (i.e., 105 s) was used to determine the number of expected detections for a given time period. Range and detection
efficiency testing results were not further applied to telemetry data analysis, but are presented to provide the level of certainty for interpretation of the detection data.

The individual receiver sites (stations) were grouped based on geographical proximity and location in similar fish habitat (Table 4.2). The mean coordinates (latitude and longitude) of each receiver group (location) were calculated for mapping purposes. If a location’s mean coordinates fell outside of the river boundary on terrestrial habitat (five instances), the latitude was retained, and the longitude was manually adjusted to a point in the middle of the river. In total there were 11 locations used for analyses (Figure 4.1, Table 4.2).

4.3.5.1 Reach residency index

A residence index (RI) was used to quantify site residency as a measure of reach use for individual fish in the present study. A residence index was selected to infer site residency over use of raw detection data because a RI reduces the potential for bias whereby site residency could be primarily driven by few individuals generating high numbers of detections at a given site (Kessel et al. 2014). To calculate RI, daily fish detections were enumerated within a 24 h time-bin at each location and divided by the total number of time-bins in which the fish was detected anywhere in the system. A fish was considered as resident at a site if there were > 9 detections within a 24 h time-bin at a location. Time-bins that did not meet this threshold were excluded from analyses. A recent lab study by Pleizier et al. (2020b) reported that 50% of Rainbow Trout in shallow depth (< 1m) exhibited loss of equilibrium within 48-96 h at 115% TDG, 20-48 h at 120%, and 5-24 h at 125-135%. A 115-135% TDG range can occur in the Lower Columbia system (Fidler 2003). Sufficient habitat is available for full or partial depth compensation throughout the study system which could mitigate or increase the time to effects of TDG exposure. The > 9 detection within 24 h threshold was chosen to represent a balanced time
frame among the realized exposure effects at the different TDG levels in Pleizier et al. (2020b) while also acknowledging the depth compensation availability to fish in the system. The resulting RI values vary between 0 and 1, with a value of 1 indicating that at least one fish was resident at that location for that 24 h period. The daily RI was then summed for each fish at each location within a season and divided by the total number of days corresponding to each season. In the present study September-November was considered as fall, December-February as winter, March-May as spring, and June-August as summer. The dataset encompassed seasons over multiple years (e.g., spring 2017, spring 2018). A Kruskal-Wallis rank sum test found no statistical difference for inter-annual RI in the MW data (Kruskal-Wallis chi-squared = 13.128, df = 9, $P = 0.157$). An overall inter-annual statistical difference was found for RT data (Kruskal-Wallis chi-squared = 19.1068, df = 9, $P = 0.02$), but a Dunn’s test with a Bonferroni correct factor for pairwise comparisons revealed that no relevant pairwise comparisons (e.g., winter 2017 and 2018) were statistically different ($P > 0.05$ all cases). Consequently, seasonal data were pooled across years where this occurred. To account for the difference in the number of receivers that could contribute to fish detections at a given location, the seasonal RI was weighted at each location by dividing the seasonal RI by the number of stations at the location. The resulting weighted RIs varied depending on the number of stations within a location (Table 4.2).

### 4.3.5.2 Depth residency index

A depth RI was also determined at each location following the same procedure as described for the reach use RI. Telemetry depth values were categorized into 1 m incremental bins (e.g., 0-0.9, 1-1.9 m, etc.). Depth RI was calculated by enumerating the number of detections grouped by depth-bin within a location divided by the total number of detections independent of location and depth bins. An overall inter-annual statistical difference in depth use
was found for MW data (Kruskal-Wallis chi-squared = 19.1068, df = 9, \( P = 0 \)), but a Dunn’s test with a Bonferroni correct factor revealed that no relevant pairwise comparisons were statistically different \((P > 0.05\) all cases). An overall inter-annual statistical difference was found for RT data (Kruskal-Wallis chi-squared = 28.569, df = 9, \( P = 0 \)). A Dunn’s test with a Bonferroni correct factor revealed only one relevant pairwise comparison (spring 2018 and 2019) was statistically different \((P > 0.011)\). Consequently, seasonal depth RI data were pooled across years to retain sample sizes.

4.3.5.3 Risk assessment

The modeled TDG levels in the present study are a discrete representation at a given location, and thus the TDG exposure risk resulting in harmful outcomes can be assessed as a function of reach and depth residency (i.e., reach use and hydrostatic compensation) at a given river location. The TDG exposure risk for MW and RT were analyzed separately and only included spring (March, April, May) reach RI and depth RI data. Spring data were chosen because they represent the high flow season when increased water spillage events are most likely, which are presumably associated with relatively greater TDG exposure risk (Fidler 2003).

A Monte Carlo method (MCM) was used to generate probability distributions of reach, depth, and TDG level occurrence using input distributions derived from the reach residency, depth residency, and TDG level data. For the reach occurrence input distribution, an empirical density function (EDF) was applied to MW and RT reach residency data to determine the cumulative probability of occurrence at a given location for each species. For the MCM reach residency output distribution, a uniform distribution of 100,000 randomly generated numbers between 0 and 1 was generated. The input reach residency cumulative probability distribution was then applied to the uniform distribution such that the location assigned to the randomly generated
value corresponded to the cumulative proportion range for that location. For example, if EDF determined the spill basin location accounted for 0.25 of the total proportion and the tailrace for 0.25, random number values between 0 and 0.25 (inclusive) in the uniform distribution were assigned as occurring in the spill basin and those > 0.25 but ≤ 0.50 were assigned as tailrace. For depth occurrence input distribution, an EDF was applied to MW and RT depth residency data at each location to determine the cumulative probability of occurrence at a given location for each species. For the MCM depth residency output distribution, a uniform distribution of 100,000 randomly generated numbers between 0 and 1 was generated for each location. The input depth residency cumulative probability distribution was then applied to the uniform distribution in the same manner as for reach occurrence above. For TDG occurrence, TDG levels were categorized into 5% incremental bins (e.g., 100-104%, 105-109%, etc.,) at each location and an EDF was applied to the TDG data determine the cumulative probability of TDG occurrence at each location. The MCM TDG output followed the same uniform distribution and cumulative proportion process as for depth occurrence. The location-conditional cumulative probability process used for depth and TDG occurrence ensured that values represented real possibilities at the corresponding locations. All EDF were determined using the “ecdfPlot” function in the EnvStats package (Millard and Kowarik 2020) and all uniform distributions were generated using the “runif” function in the R base stats package.

The within-species realized risk for MW and RT were assessed by calculating the cumulative proportion of compensation occurring at a given location compared against the mean TDG and depth RI values for that location. The degree of compensation achieved by fish was determined using the 10% TDG supersaturation compensation per metre of depth rule (Pleizier et al. 2020a; 2020b). For example, a depth RI bin value of 2-2.9 m would compensate for all TDG
levels < 130%. A TDG level of 110% was chosen as the benchmark to evaluate risk because 110% TDG is the threshold above which GBT effects begin to be observed (Pleizier et al. 2020a) and British Columbia has a water quality objective requiring that TDG not exceed 110% (Fidler and Miller 1994).

4.3.6 Statistical analysis

For all statistical analyses, $\alpha$ was set to 0.05 for purposes of determining significant differences. A Pearson’s Chi-square test with Yate’s continuity correction was used to determine if there was a difference in the relative proportions of transmitter types that were detected in the array. The weighted seasonal reach RI data (reach RI hereafter) were used to test for statistical differences in seasonal MW and RT reach use. Samples sizes at each location were not sufficient to include location in the model, so statistical testing focused on overall drivers of residency. Because the response data were bounded by 0 and 1, a generalized linear mixed model (GLMM) with a beta distribution and logit link function was used to test for differences in seasonal reach RI among species (categorical), season (categorical), and body length (TL, continuous). A random intercept for individual fish (fish ID) was included in the GLMM because there were multiple observations from each individual fish. The GLMM was modelled using the “glmmTMB” function in the glmmTMB package (Magnusson et al. 2020). Model fit was verified by plotting the residuals against the fitted values for all the factors. A Type III Wald Chi-square analysis of deviance test was used to determine the significance of main factor effects on response variables. Multiple comparisons were conducted with a Tukey’s HSD method using the “lsmeans” function in the eemeans package (Length et al. 2020).

The weighted depth residency RI data (depth RI hereafter) were used to test for statistical differences in seasonal MW and RT depth use. A GLMM with a beta distribution and logit link
function was used to test for differences in seasonal depth RI among species (categorical), season (categorical), location (categorical), depth bin (categorical), and body length (TL, continuous). A depth bin interaction term with species, season, or location was of primary interest for the purposes of this study, but sample sizes were either not sufficient for testing or interaction terms were not found significant and consequently removed for statistical testing. A random intercept for individual fish (fish ID) was included in the GLMM because there were multiple observations from each individual fish. The GLMM model, analysis of deviance for main effects, and any multiple comparisons were completed using the same functions and packages for reach RI data. Model fits were verified as outlined above for reach RI data.

A Pearson’s Chi-square test with Yate’s continuity correction was used to test if there was a difference in overall depth compensation between species (i.e., independent of location). To test if there was a difference in TDG exposure risk at a given location, within-species cumulative proportions were compared using a Marascuilo method for pairwise multiple comparisons (Wagh and Razvi 2016). Briefly, the absolute value of the difference between two cumulative proportions was compared to a critical range value. The difference was considered statistically significant if the absolute value was greater than the critical range value. Locations with an occurrence of < 110% TDG were automatically categorized as low regardless of fish depth compensation because the 110% guideline threshold was not exceeded. If the TDG exceeded 110%, risk was categorized according to depth compensation percentages whereby 0-25% compensation was considered high risk, 26-50% as of concern, 51-75% as moderate, and 76-100% as low risk.
4.4 Results

4.4.1 TDG models and detection data

The range of TDG levels varied among and within the three scenarios (Figure 4.2, Table 4.3). Scenario 2 and Scenario 3 produced the highest TDG levels, ranging from 107 to 129% and 108 to 131%, respectively. Scenario 1 produced relatively lower TDG levels that ranged from 108 to 124%. The highest TDG levels were generated at the Kootenay Confluence or downstream thereof.

A total of 92 (RT = 51, MW = 41) fish were tagged and released. After removing false negative and positive detections, a total of 66 of the 92 tagged fish were detected in the receiver array, resulting in 1,265,723 detections. The relative proportion of the LP-9 and LP-7.3 transmitters detected were similar (LP-9 = 76%, LP-7.3 = 24%) to the relative proportion originally deployed for the study (LP-9 = 79%, LP-7.3 = 21%) and were statistically equivalent ($\chi^2 = 1.145$, df = 1, $P = 0.285$).

Maximum detection range was > 150 m, as indicated by detections on the 150-m receiver at all depth intervals and time periods (Table 4.4). Detection efficiency was lowest when near the surface, and increased until 10 m depth, where it remained relatively high across depths and distances (Table 4.4).

4.4.2 Reach residency index

Reach and depth RI calculation criteria (i.e., fish with > 9 detections) further excluded five fish, resulting in 61 fish (RT = 42, MW = 19) included for RI analyses. The body length of the 61 fish ranged from 307 to 540 mm TL.
The GLMM model indicated that there were no statistical differences in seasonal reach RI among any of the factors included in the model (Table 4.5). Examining location-based fish reach residency (Figure 4.3), MW were most commonly observed in the upper half of the ~56 km Lower Columbia sector in all seasons, with the majority of fish resident at locations upstream of the Genelle location (rkm 22). Residency downstream of Genelle in the lower reaches of the system was only observed in the fall. The highest MW residency was in the spring at Raspberry (rkm 9) and Norns Creek (rkm 7.5). Residency was lowest in summer, which also produced the fewest detections of MW throughout the system overall. Genelle, Robson Ferry (rkm 5), and Kinnaird Bridge (rkm 15) had moderate MW residency in the spring and winter seasons. Rainbow Trout residency was documented at locations upstream of Genelle in all seasons (Figure 4.3). The highest RT residency during the study period was at Norns Creek in spring and Raspberry in the summer. Fall RT residency was evenly distributed among all locations, and primarily at/or upstream of Kootenay Confluence in winter.

4.4.3 Depth residency index

The GLMM revealed that season and location had an effect on depth residency, but was independent of species, body length, and depth bin (Table 4.5). Examining species-pooled depth residency among locations and seasons (Figure 4.4), fish exhibited relatively consistent within-season residency at each location, with consistently higher residency values in winter and spring across depth bins. Multiple comparisons for season revealed that fish exhibited higher depth residency in the winter compared to fall and summer ($P < 0.001$, all cases), and in spring compared to fall ($P = 0.011$) and summer ($P = 0.003$). Fish at Norns Creek, the Tailrace, and Raspberry consistently produced the highest within-location depth residency values. Multiple comparisons for location revealed that fish exhibited higher depth residency at Norns Creek area.
compared to Kootenay Confluence \((P = 0.007)\), Robson Ferry \((P < 0.001)\), Robson West \((P = 0.016)\), and the Spill Basin \((P = 0.012)\), and at Raspberry compared to Robson Ferry \((P < 0.001)\).

Of primary interest in this study was depth use (i.e., hydrostatic compensation). The GLMM revealed no significant interaction terms between depth bin and any of the other factors, meaning that that fish in this study did not exhibit a depth preference according to season, species, location, or body size. Graphical representations of the main effects differences in depth residency among seasons and locations independent of other factors are presented in Appendix C.

4.4.4 Risk assessment

The MCM TDG frequency distributions resulted in TDG levels that fell entirely within the 105-109% range at locations downstream of HLK but upstream of the Kootenay Confluence (Figure 4.5A). The highest TDG values were produced at the Kootenay Confluence and Kinnaird Bridge locations. Kinnaird Bridge had an even frequency distribution of TDG levels and the highest mean TDG level, and thus posed the highest risk purely from a TDG exposure standpoint (i.e., when not incorporating consideration of reach or depth use). The TDG values at locations upstream from the Kootenay Confluence fell within the 110% water quality guidelines whereas locations at or downstream of the Kootenay Confluence did not.

The reach use distributions revealed that MW occurrence would extend from Robson Ferry downstream to Genelle (Figure 4.5B). The highest frequency of MW occurrence would be at the Genelle \((> 25\%)\), but the spatial mean of MW occurrence was at Raspberry and cumulatively occurred more frequently \((> 50\%)\) in the locations directly upstream of the Kootenay Confluence (Figure 4.5B). The Kootenay Confluence location produced the lowest MW occurrence. The MCM revealed that RT occurrence would extend from the spill basin
downstream to Genelle. The highest (> 35%) and spatial mean frequency of RT occurrence was at Norns Creek, with the occurrence distribution being fairly equal upstream and downstream of Norns Creek.

The depth use distributions revealed Mountain Whitefish depth occurrence that varied by location (Figure 4.5C). Depth use at locations upstream of the Kootenay Confluence was most frequently in the 0-0.9 m range. Mean depth use for MW was in the 0-0.9 m depth range at all locations except for the Kootenay Confluence and Kinnaird Bridge areas, where MW were deeper, being predominantly confined to ≥ 3 m depth at these locations. The MCM also indicated RT depth use that varied according to location. In the areas directly downstream of HLK, RT mean depth use in the Spill Basin and Tailrace areas was ≥ 3 m, and < 2 m in the other locations. Rainbow Trout depth occurrence was deepest in the Spill Basin area, largely confined to the 4+ m depth bin. Depth occurrence was fairly evenly distributed among depth bins at the Tailrace, Robson West and Norns Creek areas, and was largely confined to shallower 0-0.9 depth bins at Robson Ferry, Raspberry, Kootenay Confluence, Kinnaird Bridge, and Genelle locations.

Mountain Whitefish were more frequently depth compensated than RT (MW = 43%, RT = 39%), and this difference was statistically significant ($\chi^2 = 2263.800$, df = 1, $P < 0.001$). Mountain Whitefish cumulative depth compensation and risk level varied by location (Table 4.6). The highest risk locations were at Norns Creek and Raspberry in terms of compensation, but the TDG level was < 110% at these locations received so they were assigned a low risk categorization. Genelle was the only location for MW occurrence where TDG levels consistently exceeded compensation and thus risk was high. Within-species multiple comparisons revealed that MW depth compensation percentages were statistically different among the locations in all cases except for the Norns Creek-Robson Ferry comparison (i.e., both 0%). Rainbow Trout were
most frequently compensated at the Spill Basin and Tailrace locations, which also had < 110% TDG, and thus were at a low exposure risk in these locations. At the Robson West, Robson Ferry, Norns Creek, and Raspberry locations, RT were infrequently or minimally depth compensated but the TDG level was < 110% so they were assigned low risk. The high risk locations for RT were the Kootenay Confluence and downstream thereof where TDG levels consistently exceeded sufficient depth compensation. Within-species multiple comparisons revealed that RT depth compensation percentages were statistically different among the locations in all cases.

4.5 Discussion

I used acoustic telemetry to quantify and examine the reach and depth residency of resident Mountain Whitefish and Rainbow Trout in a system impounded by two hydropower facilities. I then used this telemetry data to conduct a risk assessment and determine the location-based risk exposure in relation to TDG levels within the system for these species. The reach residency analysis revealed no differences in residency between MW and RT, or according to season or body length, which led us to reject the hypothesis that reach residency would vary by species, season, and/or body length. The depth residency analysis revealed that there was a difference among seasons and locations, but no differences between species, according to body length, or among depth bins which partially supported the hypothesis that depth use would vary by species, season, body length, and depth bin. As hypothesized, the risk assessment revealed that MW were fully depth compensated more frequently than RT. The risk assessment also revealed that MW and RT were at highest TDG exposure risk at locations close to or downstream of BRD. The result thus only partially supported the hypothesis that species-specific elevated TDG exposure risk would be highest for fish at locations closer to dams.
4.5.1 Reach and depth residency

Fish movement and migration decision are ultimately made at the individual level (Chapman 2012). Although interesting from a biological perspective, a TDG management approach catered to individual fish movement patterns is not feasible from a hydropower operational perspective. For this reason, I focused on examining location-based residency patterns independent of individual fish movements. Mountain whitefish can substantially vary in their seasonal movement patterns among systems and within the same population (Ford et al. 1995, Baxter 2002). In the present study, within-species trends in MW reach residency appeared to be reflective of habitat selection for seasonal spawning, foraging, and refuge movements characteristic of fluvial or fluvial-adfluvial potadromous species (Northcote 1997). Mountain Whitefish reach and depth residency at locations within the Lower Columbia were comparable in winter-spring relative to the other seasons. The timing of MW spawning tends to be population specific, driven largely by temperature (Benjamin et al. 2014) and varies according to altitude and longitude of the system (Pettit and Wallace 1975; Thompson and Davies 1976; Wydoski 2001; Boyer et al. 2017). The main spawning season for MW in the Lower Columbia study system, or those close by, occurs between late October and February with a peak in January (Ford et al. 1995; Irvine et al. 2017). I found that MW were most often resident at Norns Creek, Kinnaird Rapids, and the Kootenay Confluence areas in the winter, which have been identified as primary and secondary spawning locations in the system (Golder Associates Ltd. 2014). In a Montana system, Boyer et al. (2017) found no evidence that MW select for specific depths, water velocity or substrate composition at spawning sites. This was evident in the fish in my study which showed increased depth residency in winter and spring, but no depth bin preference. In the spring, MW in the present study were largely resident in the same locations as winter, which
contrasts with the post-spawning movements of adult MW reported in other systems (Thompson and Davies 1976; Wydoski 2001; Pierce et al. 2012; Benjamin et al. 2014). However, these studies were conducted on MW populations in high elevation streams or tributaries where spawning timing is earlier (October/November) than in the Lower Columbia (January/February) (Ford et al. 1995) and overwintering in the spawning habitats in some of these systems may not be possible. Furthermore, these systems have more pronounced differences in upstream-downstream habitat relative to the Lower Columbia system. With the later spawning timing in the Lower Columbia system and the relatively system-wide habitat homogeneity, the sustained winter-spring residency suggests that larger, potentially spawning MW in this study do not undertake post-spawn migrations from the spawning areas. Alternatively, the MW included in this study may have been facultative spawners which did not spawn. Pierce et al. (2012) noted that over 30% of the adult MW showed no migratory spawning movements during the spawning season. Boyer et al. (2017) also noted that a proportion of adult MW remained in close proximity to spawning grounds throughout the spawning period. As I did not directly monitor specimens to confirm spawning activity, it is also possible that MW selected these locations for foraging or overwintering purposes (Northcote 1997). As movement can be energetically costly relative to residency (Forseth et al. 1999; Morinville and Rasmussen 2003), environments supporting both spawning and overwintering requirements are likely to be occupied for both purposes as data from the fish in this study suggest.

There was a system-wide lack of MW reach and depth residency results for the summer, thus it is somewhat unclear where MW spent their time in Lower Columbia during the summer season. In other systems, fluvial/fluvial-adfluvial MW migrate to deeper, slower moving areas for foraging (Pettit and Wallace 1975; Benjamin et al. 2014). Pettit and Wallace (1975) found
MW exhibited a high degree of residency in deep pools throughout the summer months. In the fall I found an increased residency at sites across the study system, including in the lower reaches where they were absent in the other seasons. Hence, I suggest that the MW in this study moved to foraging areas in the summer and fall in the downstream reaches of the system, thereby evading detection in the summer. As MW seasonal movement patterns appeared to largely follow that of their key life history activities, a TDG abatement strategy for the Lower Columbia MW should consider seasonal movement patterns to lower exposure risk.

Rainbow Trout exhibited consistent residency in the same locations across seasons, as previously demonstrated by BC Hydro long-term monitoring studies where RT exhibited high (50-75%) site fidelity (Golder Associates Ltd. et al. 2016; 2018). Consistent locational residency made it difficult to discern patterns in RT seasonal movements. However, RT reach residency appeared to follow habitat association patterns reflective of RT ecology. For example, previous research on the Kootenai River, a comparable river to the Lower Columbia, found that RT were positively associated with faster water velocities, shallower depths, and cobble-boulder riverbanks and substrates (Smith et al. 2016). The reach from Kinnaird Bridge upstream to HLK, that accounted for the bulk of the RT residency in this study consists largely faster water habitats with deep riffle, pool and back eddy areas with varying substrate types. Many of these habitat characteristics align with those reported in Smith et al. (2016), suggesting that areas downstream of HLK to the Kootenay Confluence provide habitats sufficient for year-round RT refuge, foraging, and spawning activities.

4.5.2 Risk Assessment

I examined residency patterns of MW and RT to determine if TDG exposure risk differed according to species and the location of hazardous areas for each species. As predicted, RT
exhibited less cumulative depth compensation and were found to be at a greater TDG exposure risk relative to MW. Some species and life stages are more likely than others to experience harmful outcomes from exposure to elevated TDG levels owing to differences in physiology, morphology, or habitat use (Weitkamp and Katz 1980; Jensen et al. 1986; Fidler and Miller 1997; Beeman et al. 2003; Weitkamp et al. 2003). Rainbow Trout, in particular, appear to be one of the more susceptible salmonids. In a field study at Bonneville Dam, Backman and Evans (2002) found that adult Steelhead Rainbow Trout and Sockeye Salmon (*O. nerka*) had a higher incidence of GBT relative to Chinook Salmon (*O. tshawytscha*) despite the latter's exposure to higher TDG levels. In lab experiments, Mesa et al. (2000) reported that juvenile Steelhead mortality occurred in shorter timespans than juvenile Chinook Salmon exposed to the same TDG levels. Dawley and Ebel (1975) also noted that larger Steelhead were less tolerant than small Chinook to elevated TDG levels.

I found TDG risk in the spring season varied by location for each species within the Lower Columbia. Upstream of the Kootenay Confluence to HLK, the TDG levels fell within the 110% guidelines, and despite RT and MW lacking full depth compensation at these locations the risk of GBT occurrence was low. Previous research has found that TDG levels < 110% are generally not lethal for salmonids even when they are lacking full depth compensation (Ryan et al. 2000; Antcliffe et al. 2002; Weitkamp et al. 2003). Downstream of the Kootenay Confluence to the United States border had TDG levels that posed greater risk to fish in the Lower Columbia. The highest TDG levels exceeding the 110% guideline (120-124% in the present study) are associated with mortality and other harmful effects when fish are not fully depth compensated (Pleizier et al. 2020a; 2020b). In lab experiments, Mesa et al. (2000) reported that 20% of Steelhead died (LT20) within 25-30 h exposure to 120% TDG and within 5-7 h at 130% when
lacking depth compensation. However, previous field studies in other hydropower impounded systems have found most fish to be depth compensated during TDG exposure. Weitkamp et al. (2003) reported minimal GBT symptoms in salmonids and non-salmonids exposed to 120-130% because fish were sufficiently depth compensated. Studies on the Columbia River in the United States that tracked depth use of migrating Rainbow Trout and Chinook Salmon in relation to modeled TDG levels found that these migratory salmonids used water depths sufficient for full depth compensation (Johnson et al. 2005; 2007; 2010). The high risk areas in the Lower Columbia have sufficient habitat available for full depth compensation, but the risk assessment results indicated that MW and RT occurrence in those deeper waters is relatively low.

The TDG risk appeared to be divided into two zones – upstream and downstream of the Kootenay Confluence. The fish residency results generally followed this same pattern with increased winter-spring residency at locations upstream of the Kootenay Confluence and lower residency downstream. The fish residency patterns suggest that the Kootenay Confluence may be a transition zone in the Lower Columbia. The residency patterns follow known zonation (i.e., ranges within the longitudinal section of the river) and habitat association patterns for RT and MW in the region (Smith et al. 2016). Current hydropower management regimes operate at a more localized scale whereby the system is broken up into the reaches between dams/facilities and management plans are typically developed at this reach level. However, where the TDG and fish residency appear to follow the same patterns such as in the Lower Columbia, dividing a reach into zones according to habitat association and the functional guilds of the fish assemblage (fish zonation) may be an effective tool for TDG management outcomes like exposure risk in a river system. Using fish zonation as a standardized method specifically for TDG management is not common, but frameworks exist for broadscale hydropower management outcomes. In
Europe, regulators and environmental managers are exploring using a fish zonation approach to assess the ecological status of rivers and to support decision making for restoring river connectivity for diadromous and potadromous fish (Lasne et al. 2007; Breve et al. 2014). In these fish zonation regimes, migratory fish assemblages are categorized into ecological fish guilds to identify their sensitivities and habitat requirements, then fish zonation (via spatial analyses) is used to identify the most disruptive connectivity barriers for the fish guilds. Other similar standardized frameworks are suggested for more broadscale ecological assessment of rivers. Fish-based assessment methods that take a standardized approach using environmental data, ecological guilds, reference sites, impact sites, and spatial based modeling are used to assess human disturbance of rivers (Schmutz et al. 2007; Virbickas and Kesminas 2007). Because these fish zonation and fish-based methods are standardized approaches, they have broad applicability and could likely be scaled for facility level operations such as TDG management strategies.

4.5.3 Study Limitations

Detection range and efficiency can be affected by environmental conditions such as high flows and noise generated from hydropower facilities (Kessel et al. 2014). In the present study, logistic and economic constraints meant that range and detection efficiency testing was conducted post-hoc and limited to a relatively short duration. Additionally, I conducted testing to a maximum distance of 150 m, which could add some uncertainty for the detection data in the lower reaches where distance between receivers was greater (i.e., downstream of Genelle). A study by Newton et al. (2016) that used the same Thelma Biotel LP-7.3 transmitters for range testing identified a detection range of 450 m, suggesting that the 150 m range may be conservative. Moreover, the testing location was close to the HLK facility and a navigation lock representing a noisy environment in the system, and thus performance was expected to yield a
decreased range and detection efficiency relative to other areas in the system. Consequently, I expected range and detection efficiency results to be similar in other time periods and noisy areas, and to improve in the lower reaches given that it is presumably a less noisy environment.

4.6 Management Implications

The telemetry and risk assessment results indicated that TDG exposure risk depends on the interplay between species-specific ecology and the patterns of TDG generated by the hydropower facilities. While the risk assessment results indicated that RT were at a higher TDG exposure risk relative to MW, the high habitat suitability reaches near the hydropower facilities are likely to pose an increased risk for both species. Given that spring is the high flow season, the risk assessment results likely represent a worst-case scenario under the HLK/BRD operational regime in this study, but the risk levels would likely change under other operational regimes. The ecological and TDG patterns suggest that system-specific studies will be necessary if detailed TDG exposure predictions are required for decision-making.
Table 4.1: Date range, spillage rate at Brilliant Dam and reason for scenario selection.

<table>
<thead>
<tr>
<th>Scenario</th>
<th>Date Range</th>
<th>BRD Spillage (m³s⁻¹)</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>May 01-31, 2016</td>
<td>895.5</td>
<td>Low</td>
</tr>
<tr>
<td>2</td>
<td>June 01-10, 2017</td>
<td>1837.8</td>
<td>Moderate</td>
</tr>
<tr>
<td>3</td>
<td>May 26-27, 2018</td>
<td>2375.5</td>
<td>High</td>
</tr>
</tbody>
</table>

Table 4.2: Name, downstream distance from Hugh L Keenleyside (HLK) dam, number of receivers, coordinates, and potential minimum and maximum weighted seasonal reach residency index (RI) values for locations. Locations with a * indicate manually adjusted longitudes.

<table>
<thead>
<tr>
<th>Location name (~rkm)</th>
<th>Mean coordinates (lat, lon)</th>
<th># Receivers</th>
</tr>
</thead>
<tbody>
<tr>
<td>Spill Basin (0)</td>
<td>49.3421, -117.7695</td>
<td>2</td>
</tr>
<tr>
<td>Tailrace Area (0.5)</td>
<td>49.3408, -117.7657</td>
<td>4</td>
</tr>
<tr>
<td>Robson West (2.5)</td>
<td>49.3402, -117.7388</td>
<td>3</td>
</tr>
<tr>
<td>Robson Ferry (5)</td>
<td>49.3315, -117.6904</td>
<td>3</td>
</tr>
<tr>
<td>Norns Creek (7.5)</td>
<td>49.3319, -117.6732</td>
<td>1</td>
</tr>
<tr>
<td>Raspberry (9)</td>
<td>49.3286, -117.6522</td>
<td>1</td>
</tr>
<tr>
<td>Kootenay Confluence (11)*</td>
<td>49.3122, -117.6563</td>
<td>2</td>
</tr>
<tr>
<td>Kinnaird Bridge (15)*</td>
<td>49.2771, -117.6421</td>
<td>2</td>
</tr>
<tr>
<td>Genelle (22)*</td>
<td>49.2162, -117.6796</td>
<td>2</td>
</tr>
<tr>
<td>Rivervale-Trail (38)*</td>
<td>49.1094, -117.7141</td>
<td>3</td>
</tr>
<tr>
<td>Upstream Waneta (50)*</td>
<td>49.0300, -117.6076</td>
<td>3</td>
</tr>
</tbody>
</table>

Table 4.3: Location and TDG level at each location from dissipation modeling.

<table>
<thead>
<tr>
<th>Location (rkm)</th>
<th>Scenario 1 (%)</th>
<th>Scenario 2 (%)</th>
<th>Scenario 3 (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Spill Basin (0)</td>
<td>108</td>
<td>107</td>
<td>108</td>
</tr>
<tr>
<td>Tailrace Area (0.5)</td>
<td>108</td>
<td>107</td>
<td>108</td>
</tr>
<tr>
<td>Robson West (2.5)</td>
<td>108</td>
<td>108</td>
<td>109</td>
</tr>
<tr>
<td>Robson Ferry (5)</td>
<td>108</td>
<td>107</td>
<td>109</td>
</tr>
<tr>
<td>Norns Creek (7.5)</td>
<td>108</td>
<td>107</td>
<td>109</td>
</tr>
<tr>
<td>Raspberry (9)</td>
<td>108</td>
<td>107</td>
<td>109</td>
</tr>
<tr>
<td>Kootenay Confluence (11)</td>
<td>122</td>
<td>127</td>
<td>130</td>
</tr>
<tr>
<td>Kinnaird Bridge (15)</td>
<td>117</td>
<td>118</td>
<td>121</td>
</tr>
<tr>
<td>Genelle (22)</td>
<td>117</td>
<td>119</td>
<td>122</td>
</tr>
<tr>
<td>Rivervale-Trail (38)</td>
<td>116</td>
<td>119</td>
<td>121</td>
</tr>
<tr>
<td>Upstream Waneta (50)</td>
<td>115</td>
<td>118</td>
<td>120</td>
</tr>
</tbody>
</table>
Table 4.4: Range and detection efficiency testing results.

<table>
<thead>
<tr>
<th>Depth (m)</th>
<th>Distance (m)</th>
<th>Efficiency (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.5</td>
<td>50</td>
<td>11.6</td>
</tr>
<tr>
<td></td>
<td>100</td>
<td>8.2</td>
</tr>
<tr>
<td></td>
<td>150</td>
<td>1.6</td>
</tr>
<tr>
<td>2.0</td>
<td>50</td>
<td>44.7</td>
</tr>
<tr>
<td></td>
<td>100</td>
<td>38.2</td>
</tr>
<tr>
<td></td>
<td>150</td>
<td>14.7</td>
</tr>
<tr>
<td>5.0</td>
<td>50</td>
<td>64.9</td>
</tr>
<tr>
<td></td>
<td>100</td>
<td>60.0</td>
</tr>
<tr>
<td></td>
<td>150</td>
<td>36.6</td>
</tr>
<tr>
<td>10.0</td>
<td>50</td>
<td>88.3</td>
</tr>
<tr>
<td></td>
<td>100</td>
<td>85.0</td>
</tr>
<tr>
<td></td>
<td>150</td>
<td>63.2</td>
</tr>
<tr>
<td>15.0</td>
<td>50</td>
<td>88.9</td>
</tr>
<tr>
<td></td>
<td>100</td>
<td>87.4</td>
</tr>
<tr>
<td></td>
<td>150</td>
<td>56.5</td>
</tr>
<tr>
<td>17.0</td>
<td>50</td>
<td>90.4</td>
</tr>
<tr>
<td></td>
<td>100</td>
<td>87.7</td>
</tr>
<tr>
<td></td>
<td>150</td>
<td>81.6</td>
</tr>
</tbody>
</table>

Table 4.5: Outputs of statistical tests for seasonal reach RI (residence index) depth RI. Depth bins are 1 m incremental depth bins. Locations are found in Table 4.3. Significant terms are denoted in boldface. Multiple comparisons for significant interaction terms are found in text.

<table>
<thead>
<tr>
<th>Response</th>
<th>Factor</th>
<th>$\chi^2$</th>
<th>df</th>
<th>$P$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Reach RI</td>
<td>Intercept</td>
<td>44.475</td>
<td>1</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>Species</td>
<td>0.001</td>
<td>1</td>
<td>0.974</td>
</tr>
<tr>
<td></td>
<td>Season</td>
<td>6.158</td>
<td>3</td>
<td>0.104</td>
</tr>
<tr>
<td></td>
<td>Body Length</td>
<td>1.812</td>
<td>1</td>
<td>0.178</td>
</tr>
<tr>
<td>Depth RI</td>
<td>Intercept</td>
<td>27.479</td>
<td>1</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>Species</td>
<td>0.026</td>
<td>1</td>
<td>0.871</td>
</tr>
<tr>
<td></td>
<td><strong>Season</strong></td>
<td>26.542</td>
<td>3</td>
<td><strong>&lt;0.001</strong></td>
</tr>
<tr>
<td></td>
<td>Body Length</td>
<td>2.839</td>
<td>1</td>
<td>0.092</td>
</tr>
<tr>
<td></td>
<td>Depth Bin</td>
<td>5.989</td>
<td>4</td>
<td>0.200</td>
</tr>
<tr>
<td></td>
<td><strong>Location</strong></td>
<td>59.711</td>
<td>10</td>
<td><strong>&lt;0.001</strong></td>
</tr>
</tbody>
</table>
Table 4.6: Cumulative percentage and exposure risk level of Mountain Whitefish (MW) and Rainbow Trout (RT) depth compensation resulting from a Monte Carlo simulation process. The compensation depth-bin value indicates the minimum depth occurrence required for compensation at that location. Locations denoted with * indicate the 110% threshold is not exceeded and receive a low risk level regardless of compensation %. No telemetry observations were noted at Rivervale-Trail or Upstream Waneta locations for MW and RT. Within-species Marascuilo pairwise multiple comparisons found compensation at all locations statistically different except MW Norns Creek-Robson Ferry.

<table>
<thead>
<tr>
<th>Location (rkm)</th>
<th>Mean TDG (%)</th>
<th>Comp depth-bin (m)</th>
<th>MW Comp (%), risk level</th>
<th>RT Comp (%), risk level</th>
</tr>
</thead>
<tbody>
<tr>
<td>Spill Basin (0)*</td>
<td>105-109</td>
<td>1.0-1.9</td>
<td>-</td>
<td>80, low</td>
</tr>
<tr>
<td>Tailrace Area (0.5)*</td>
<td>105-109</td>
<td>1.0-1.9</td>
<td>-</td>
<td>86, low</td>
</tr>
<tr>
<td>Robson West (2.5)*</td>
<td>105-109</td>
<td>1.0-1.9</td>
<td>0, low</td>
<td>64, low</td>
</tr>
<tr>
<td>Robson Ferry (5)*</td>
<td>105-109</td>
<td>1.0-1.9</td>
<td>0, low</td>
<td>34, low</td>
</tr>
<tr>
<td>Norns Creek (7.5)*</td>
<td>105-109</td>
<td>1.0-1.9</td>
<td>0, low</td>
<td>57, low</td>
</tr>
<tr>
<td>Raspberry (9)*</td>
<td>105-109</td>
<td>1.0-1.9</td>
<td>40, low</td>
<td>6, low</td>
</tr>
<tr>
<td>Kootenay Confluence (11)</td>
<td>115-119</td>
<td>2.0-2.9</td>
<td>100, low</td>
<td>14, high</td>
</tr>
<tr>
<td>Kinnard Bridge (15)</td>
<td>120-124</td>
<td>2.0-2.9</td>
<td>99, low</td>
<td>12, high</td>
</tr>
<tr>
<td>Genelle (22)</td>
<td>115-119</td>
<td>2.0-2.9</td>
<td>20, high</td>
<td>0, high</td>
</tr>
<tr>
<td>Rivervale-Trail (38)</td>
<td>115-119</td>
<td>2.0-2.9</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Upstream Waneta (50)</td>
<td>115-119</td>
<td>2.0-2.9</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>
Figure 4.1: The Columbia-Kootenay system (A) and the Lower Columbia study system (B). The 
~56 km Lower Columbia system extends from the Hugh L. Keenleyside Dam (HLK) on the 
Columbia River, Brilliant Dam (BRD) on the Kootenay River, and Waneta Dam (WAN) at the at 
the Pend d’Oreille River confluence. Filled circles denote receiver sites; filled triangles denote 
locations used in analyses. See Table 4.2 for details about locations used in analyses.
Figure 4.2: System-wide modeled TDG profile and frequency of TDG levels for Scenario 1 (A), Scenario 2 (B), and Scenario 3 (C).
Figure 4.3: Mountain Whitefish and Rainbow Trout seasonal reach residency index at each location in the Lower Columbia system. See Table 4.2 for location details and minimum/maximum possible residency index values at each location.
Figure 4.4: Seasonal depth residency index at each 1-m depth bin and location in the Lower Columbia system. Depth residency is pooled between species.
Figure 4.5: Monte Carlo model risk assessment outputs for TDG level occurrence (A), reach occurrence (B), and depth occurrence (C) of Mountain Whitefish (MW) and Rainbow Trout (RT). Dashed line denotes mean value. The solid line in (A) denotes the 110% TDG threshold guideline, values to the right exceed the guideline. The solid line in (C) denotes the depth bin required for compensation at that location, values to the right indicate lack of depth compensation.
Chapter 5: General Discussion, Concluding Remarks and Future Directions

5.1 General Discussion

The overall goal of my thesis was to apply conservation behaviour and risk analysis approaches to guide decision-making for avoiding or mitigating hydropower-related hazards to freshwater fish. To this end, each data chapter quantified and assessed risk levels associated with entrainment and TDG exposure at hydropower facilities for freshwater fish. In Chapter 2, I systematically reviewed the hydropower literature and quantified the magnitude of injury/mortality risk associated with entrainment/impingement during downstream passage across hydropower facilities and infrastructure types. In Chapter 3, using biotelemetry I empirically evaluated the vulnerability of re-entrainment risk of salvaged Kokanee salmon at a large hydropower facility with no fish passage. In Chapter 4, using biotelemetry I assessed the exposure risk of Mountain Whitefish and Rainbow Trout to elevated levels of TDGs in a system impounded by two hydropower facilities. The data chapters collectively demonstrated that empirical behaviour research generates data that serves as effective inputs for risk assessment, and the resulting risk assessment outputs can be used for decision-making purposes in avoiding/mitigating entrainment and TDG exposure at hydropower facilities. In the following sections, I summarize the key findings and make some general conclusions for each data chapter.

5.1.1 Chapter 2 Discussion

The systematic review and meta-analysis of the literature evidence base revealed that downstream passage over/through hydropower infrastructure increased the overall risk of freshwater fish injury and immediate mortality in temperate regions, and the results were consistent regardless of the effect size metric used (i.e., relative and absolute risk). Injury and immediate mortality risk varied among intervention type with turbines and spillway passage
associated with higher risk. The most “fish-friendly” downstream passage route was via bypasses, which resulted in decreased fish injury and a marginal non-significant increase in immediate mortality risk. These results supported the findings highlighted in earlier traditional literature reviews (OTA 1995; FERC 1995; Coutant and Whitney 2000; Pracheil et al. 2016).

Injury and mortality can vary according to species at hydropower facilities (Bevelhimer et al. 2017; Knott et al. 2019). A taxonomic analysis revealed that downstream passage increased injury and immediate mortality risk for genera *Alosa* (river herring), *Oncorhynchus* (Pacific salmonids), and delayed mortality risk for *Anguilla* (freshwater eels). As reported in other traditional reviews on the subject (Roscoe and Hinch 2010; Pracheil et al. 2016), the evidence base for this systematic review lacked studies on resident and other fish not deemed economically important. Importantly, the absence of underrepresented species or lack of statistical significance in the taxonomic analyses does not imply that injury and mortality risk is lower for these species or that they are not affected by hydropower infrastructure. Rather, this is more suggestive that there is a lack of data in the evidence base to quantify injury and mortality risk or that an effect was not detected which could be attributable to low statistical power.

Targeting specific species is not necessarily problematic from a management perspective, but can be if mitigation efforts are extrapolated onto other non-target species for which they might be an ineffective solution. For example, river herring, prominent target species for fish passage on the east coast of North America (Gephard and McMenemy 2004; Haro and Castro-Santos 2012), were found to have a high risk of injury and immediate mortality in this meta-analysis. River herring are known to be sensitive to the conditions that occur during passage through hydropower infrastructure (Castro-Santos 2012) that are typically targeted at salmonids (Gephard and McMenemy 2004).
Interestingly, there was a difference in risk according to study setting such that lab-based turbine studies resulted in higher risk outcomes than field-based studies. This finding highlighted that lab studies cannot wholly replicate the complexity of conditions present in the field, and that ground-truthing lab-based results in a field setting is imperative. Demonstrating consistency between field and lab testing results for injury/mortality from entrainment/impingement would presumably lead to increased uptake by regulators and hydropower operators to implement changes to hydropower facilities. Lab studies are often used to justify conducting field studies because comprehensive field studies are time consuming and resource intensive for hydropower operators. Moreover, owing to the unique equipment and setup at each facility, results can be site-specific and make results extrapolation difficult. Rather than looking for consistency among field and lab studies, hydropower researchers could develop standardized methods of injury and mortality assessment that are able to identify the mechanism(s) responsible (i.e., turbine blade strike) for different injuries that would be applicable across sites (e.g., Mueller et al. 2017; Alves et al. 2019).

5.1.2 Chapter 3 Discussion

Using acoustic telemetry to track the movements of Kokanee salvaged from turbine infrastructure, I demonstrated that salvaged fish are at low risk to re-entrainment events. The most recent system-wide population indexing surveys on the fish community in the reservoir indicated that the Kokanee abundance increased in the reservoir from previous surveys, suggesting that dam operations do not appear to be a major driver of Kokanee decline in the system. By extension, stranding/entrapment in turbine infrastructure did not appear to have a measurable effect on Kokanee recruitment at present.
For all intents and purposes, fish that are entrapped in the surge towers should be considered as lost to the system, thus salvaging them would give them a chance for survival. Monitoring, assessment, and mitigation of fish stranding and entrapment due to discharge reductions and flow ramping salvage efforts are commonplace (Nagrodski et al. 2012; Munn et al. 2016; Golder Associates Ltd. 2020). The results of this study would be encouraging from a management perspective because the fish do not demonstrate a propensity for entrapment after release and fish salvage presents an option to reduce entrapment related mortality. Thus, if allowed by regulatory frameworks, salvage-related efforts for turbine infrastructure such as surge towers could be included as part of fish stranding and mitigation strategies for hydropower operators. A large portion of the fish in the turbine intakes were in visibly poor condition, presumably because their condition degrades over time due to the poor environmental conditions found in the surge towers. These anecdotal observations suggested that to minimize the time spent in the surge towers (or other structures that fish can become entrapped) and maximize survival after release, hydropower operators should increase the frequency of salvage efforts.

Tracking fish movements using telemetry is considered an effective tool for estimating reservoir use, forebay use, and entrapment vulnerability for potadromous fish like Kokanee (Harrison et al. 2019). The results of this Kokanee salvage study can be used by decision-makers as inputs into BC Hydro’s two-tiered fish entrapment risk strategy (i.e., risk assessment and risk evaluation; BC Hydro 2006). The results of this study can contribute to the risk assessment stage (the first stage), more specifically towards consequence assessment and likelihood of risk. The low forebay use and entrapment vulnerability for Kokanee in this study suggest low consequence and likelihood of risk in the BC Hydro fish entrapment risk strategy framework. However, salvaged Kokanee that were already entrained were used in this study and non-
salvaged fish may have a different risk factor. Consequently, studies should be conducted on non-salvaged Kokanee to validate and confirm that the findings and risk assessment inputs in this study are in fact more widely applicable to the overall Kokanee population in the system.

5.1.3 Chapter 4 Discussion

Using acoustic telemetry to track resident fish movements in relation to modeled TDG levels, I demonstrated how distinguishing fish behaviour can inform conservation decision-making. Specifically, I demonstrated that by tracking resident Mountain Whitefish and Rainbow Trout reach and depth residency, and then using that data in risk assessment techniques, conservation behaviour research can inform managers and operators in decision-making with the goal of reducing TDG exposure risk for these species.

As predicted, Mountain Whitefish reach residency and depth use trends followed that of their seasonal spawning patterns in the system (Northcote 1997). Rainbow Trout exhibited relatively consistent residency at a few locations in the system throughout the study duration, making it difficult to distinguish a clear pattern akin to following key life history. However, Rainbow Trout appeared to demonstrate habitat association patterns that are typical of fish assemblages in the region (Smith et al. 2016). Despite being a ubiquitous species throughout systems in northwestern North America and regarded as a prominent secondary sportfish, few studies in the literature have tracked movement patterns of Mountain Whitefish using biotelemetry, thus this chapter contributed to the knowledge base of this species. Being an economically and socially valued fish, Rainbow Trout are a highly studied species, but relatively few studies have focused on potadromous variants.

As predicted, the risk assessment revealed that Rainbow Trout had an overall higher TDG exposure risk relative to Mountain Whitefish during the high-flow spring season, and within-
species exposure risk was high at relatively few locations in the system. There was a clear
delineation in risk levels in the system whereby the system was divided into two zones – one
with low risk that met provincial TDG water quality guidelines, and another zone with relatively
higher TDG levels known to cause GBT and other harmful effects. Given that Rainbow Trout
and Mountain Whitefish residency in the spring was also largely divided into two zones that
aligned with the TDG zones, a fish zonation (i.e., longitudinal patterns of habitat association and
fish assemblages) approach could potentially be used as a TDG management strategy for this
impounded system. However, this approach may not be suitable under different operational
regimes if the TDG profile of the system changes. The results of this study suggest that system-
specific data are required for TDG operational decision-making on TDG risk abatement
strategies.

Hydropower managers can build upon the approach and results of Chapter 4 in this thesis
for decision-making regarding TDG abatement strategies. Modeling TDG generation, tracking
fish movements and depth use over targeted periods of interest, determining residency and depth
use, and altering the facility’s operational regime to avoid high TDG generation during periods
when fish are at high risk (i.e., occupy areas with high TDG or shallow depths) would likely
suffice to minimize or ideally avoid system specific TDG exposure (Politano et al. 2012). To
develop an optimal TDG abatement strategy, comparisons to alternative operational regimes
would be necessary. Implementing and optimizing a TDG exposure abatement strategy in
systems with multiple facilities, like the Lower Columbia, is more complex because of
cumulative effects from cascading hydropower facilities. To address cumulative effects,
hydropower managers could build on the approach used in this thesis and incorporate
simulations with alternative operational scenarios of the facilities operating singly and/or in
concert (see Politano et al. 2017; Witt et al. 2017; Ma et al. 2018). Coupling the simulation results with fish telemetry data to generate the risk degree posed by each scenario would allow decision-makers to identify the optimal TDG abatement strategy (or strategies) and sensitivity analyses could be conducted to increase the understanding of the drivers of TDG generation and fish exposure risk. Witt et al. (2017) used this strategy for multi-reservoir systems with cascading low and medium head facilities, whereas Ma et al. (2018) used this strategy for high head facilities.

5.2 Concluding Remarks

The chapters in this thesis each provide novel scientific contributions to research in avoiding and/or mitigating entrainment/impingement and elevated TDG exposure for freshwater fish. The key findings of the systematic review (Chapter 2) highlight what has been known for several decades – that hydropower facilities increase injury and mortality risk for freshwater fish, turbines are typically the infrastructure associated with the strongest effects, and bypasses are associated with a decreased risk outcomes. However, the evidence base and meta-analyses also quantified risk for effects modifiers including between source of fish (i.e., wild or hatchery), fish life stage (e.g., juveniles or eggs), study site type (e.g., field or lab), and assessment time (e.g., < 24 hr or >=24-48 hr) which have not been assessed in this manner before. These biological and methodological effects modifiers have been compared in the hydropower literature (Murchie et al. 2008) but are rarely quantified in terms of risk. The Kokanee entrainment vulnerability study (Chapter 3) offers novel contributions in that it is the first study to empirically evaluate the outcomes of fish salvage efforts on Kokanee, and on a general level, fish salvaged from turbine infrastructure. The TDG exposure risk study (Chapter 4) offers novel contributions in that it is one of few studies to track reach and depth residency in relation to modeled TDG levels, and to
use the resulting telemetry data as inputs for risk assessment to quantify the risks associated with TDG exposure for Mountain Whitefish and Rainbow Trout. Additionally, few studies exist tracking Mountain Whitefish or potadromous Rainbow Trout movements, so this thesis contributes to the knowledge base for these species in that regard.

Taken together, the data chapters in this thesis demonstrate the complexity of problems and decision-making that hydropower managers and regulators face in striking a balance between mitigating exposure to hazards and operational requirements for economics purposes. For example, the systematic review results demonstrated that risk of turbine injury and/or mortality is increased, but spilling water over spillways to facilitate non-turbine fish passage can lead to increased risk of TDG generation and GBT occurrence. If prioritizing resources for addressing either entrainment or TDG hazards, from a management perspective, I think that entrainment is more difficult to address. Legacy facilities are difficult and costly to retrofit with appropriate “fish friendly” infrastructure. Furthermore, retrofits at large hydropower facilities may not be feasible at all (e.g., screens) and cost-effective mitigation technologies remain unproven (e.g., behavioural guidance devices). In the case of TDG, changes to operational regimes (i.e., reduced spillage) directly leads to avoidance or minimized risk, which remains a simpler and more cost-effective solution to implement relative to those for entrainment avoidance/mitigation. It is clear that balancing power generation and other anthropogenic uses of dams (e.g., flood and/or invasive species control) with avoiding and/or mitigating harm to freshwater fish is a wicked problem (Rittel and Webber 1973) with no “silver bullet” solutions.

5.3 Future Directions

Hydropower facilities are currently optimized for energy production, not for “fish friendliness”. Hydropower-related research must transcend towards researching the proximate
and ultimate reasons of how and why fish are affected by hydropower (e.g., physiologically, behaviourally) to generate a more predictive knowledge base, rather than continue to rely on the reactive approach that has dominated the past few decades. Moreover, freshwater fish are in serious decline (Reid et al. 2019, Deinet et al. 2020), so hydropower research must generate actionable, practical results that produce real-world beneficial outcomes for freshwater fish. Thus, there are far reaching research avenues to explore for reducing or avoiding the harm that hydropower developments can place on freshwater fish. A general theme evident across all data chapters is the lack of data on resident freshwater fish in hydropower impounded systems. Here I highlight future research avenues in a focused perspective that directly relates to the studies conducted in this thesis.

The systematic review highlighted several knowledge gaps which can be applied to fish in general, as well as more specifically to resident freshwater fish. First, I was unable to directly address the fish productivity component in the primary question because the studies in the hydropower literature rarely scaled up their results to the population level. Resident fish studies were rare in the evidence base, thus tracking resident fish movement to determine entrainment risk would be a starting point for hydropower researchers. Acoustic telemetry could be used to track broad scale resident fish movements in relation to hydropower infrastructure. Entrainment risk could be determined by establishing an entrainment zone (Harrison et al. 2019) and comparing the time spent in the entrainment zone relative to outside the zone (e.g., Harrison et al. 2020). Species deemed at high risk could then be examined more closely to determine realized entrainment rates that could be incorporated into population level analyses. Second, I was unable to quantify delayed mortality risk in the systematic review. Addressing the effects of delayed injury/mortality from downstream passage at hydropower facilities is difficult and
remains a research priority among hydropower operators and conservation managers (Lennox et al. 2019; Ammar et al. 2020; Baker et al. 2020). Studying delayed mortality in a conservation behaviour approach would be beneficial because fish are subjected to multiple stressors during entrainment events, and relatively few studies have been conducted at the individual level to examine the effects of entrainment events on fish behaviour. For example, studies have found delayed mortality of migrant fish via increased predation directly downstream of hydropower infrastructure (e.g., Muir et al. 2006; Shreck et al. 2006). To see if there are behavioural differences between fish that experience entrainment events and controls, future work could implant fish with acoustic telemetry transmitters and conduct controlled release trials directly into various hydropower infrastructure. By tracking entrained fish movements and behaviour downstream, comparisons relative to control groups could elucidate overall behavioural differences in entrained fish, and factors such as infrastructure types and species could be examined. Lastly, the focus of this systematic review was on temperate fish. With the rapid expansion of hydropower developments in the equatorial regions of the world, a similar review on (sub)tropical systems would be useful from a hydropower management perspective because these (sub)tropical systems encompass a different array of species. Applying risk levels associated with facilities/fish in temperate regions may not be appropriate for species in (sub)tropical regions. Furthermore, this will fill a knowledge gap and may allow for a synthesis of generalized global injury and mortality risk associated with downstream passage at hydropower facilities.

In Chapter 3, salvaged Kokanee had low re-entrainment rates and spent little time in the forebay area once salvaged from the intake towers. Future work should seek to identify why resident fish are drawn to a hydropower forebay area. A conservation behaviour approach could
be used to address this whereby Kokanee movements are tracked in the system in relation to habitat variables, forage base, predator species movements, and spawning activity. This behavioural approach would allow for testable hypotheses of factors that drive Kokanee forebay presence or residency such as habitat association, foraging, predator avoidance, or spawning activity. Understanding why fish are entering the forebay would allow hydropower managers to adjust operations to potentially avoid entrainment. By extension, Kokanee are an underrepresented salmonid in the literature, thus conducting research on Kokanee spatial ecology would be valuable to better understand the species’ movement patterns. Given that the fish in the study were previously entrained, a logical question is: what is the entrainment rate of Kokanee in the system? Conducting a study using biotelemetry to track Kokanee movements in the system would be an ideal approach to answer this question. Coupling the telemetry data with computational fluid dynamics of the forebay could be used to identify hazardous entrainment areas and whether fish enter these zones. An alternative approach could be to conduct frequent capture-mark-recapture (CMR) studies in the turbine intakes to estimate the number of fish that become entrained in the intake towers and compare the data to known population data. One of the CMR assumptions, no immigration/emigration occurs, leads to another interesting question: do fish navigate out of the turbine intakes? Biotelemetry could be used to monitor for tagged fish exiting the intake towers back into the forebay. However, this question would be very difficult to answer from a hydropower operational and logistical standpoint because equipment would have to be placed within/near turbine intake infrastructure.

In Chapter 4, I demonstrated that Mountain Whitefish appeared to follow movement patterns that followed key life history patterns. However, studies in the literature suggest that Mountain Whitefish life history can vary considerably across its natural range (Ford et al. 1995; Baxter
2002), so the residency results in this study may differ from those in other systems. Despite
being an important species ecologically and recreationally, comprehensive studies on Mountain
Whitefish movements are lacking. Additional studies that track Mountain Whitefish movement
in other systems is needed to fill behavioural knowledge gaps, generate a greater understanding
of proximate reasons for movement, and ultimately support managers in decision-making for
management outcomes for this species. No difference was found in residency according to body
length. Juvenile fish typically exhibit different movement patterns than adults, and the effects of
TDG exposure can vary according to life stage (Weitkamp and Katz 1980). Future work tracking
juvenile fish movements is required to fill spatial ecology knowledge gaps and identify TDG
exposure risks for juvenile and small bodied fish. Potadromous resident fishes were monitored
for this study but other species’ behavioural movement patterns should be monitored to quantify
TDG exposure risk. From a management perspective movement data from a wider representation
of species would provide a clearer picture of TDG risk at the fish community level. By
extension, because the Lower Columbia system is comprised entirely of resident fishes,
characterizing the spatial ecology of resident fish assemblages in this system would be a valuable
contribution to the literature. From a fish behaviour standpoint, a key question to answer for
TDG exposure risk is whether fish can detect elevated TDG levels and respond to avoid harmful
outcomes of TDG exposure. To date, the consensus is that fish cannot detect TDG levels, but
past studies have produced conflicting results (Dawley et al. 1976; Stevens et al. 1980; Lund and
Heggberget 1985). Future work should include additional physiology- and behaviour-based
research to determine if fish are able to detect and respond to elevated TDG levels.
Appendix A

Additional files

The Additional files are available online through the following links:

Additional file 1  https://static-content.springer.com/esm/art%3A10.1186%2Fs13750-020-0184-0/MediaObjects/13750_2020_184_MOESM1_ESM.docx
Additional file 5  https://static-content.springer.com/esm/art%3A10.1186%2Fs13750-020-0184-0/MediaObjects/13750_2020_184_MOESM5_ESM.xlsx

Search terms

The following search string was used to query publication databases, Google Scholar, and specialist websites.

*Population terms* [Fish* AND (Reservoir$ OR Impoundment$ OR Dam$ OR "Hydro electric*" OR Hydroelectric* OR "Hydro dam*" OR Hydrodam* OR "Hydro power" OR Hydropower OR "Hydro")]

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AND

*Intervention terms* (Turbine$ OR Spill* OR Outlet* OR Overflow* OR Screen$ OR Tailrace$ OR “Tail race” OR Diversion OR Bypass* OR Tailwater$ OR Penstock$ OR Entrain* OR Imping* OR Blade$ OR In-take$ OR "Trash rack"$ OR "Draft tube")

AND

*Outcome terms* (Productivity OR Growth OR Performance OR Surviv* OR Success OR Migrat* OR Passag* OR Reproduc* OR Biomass OR Stress* OR Mortalit* OR Abundance$ OR Densit* OR Yield$ OR Injur* OR Viability OR Sustainability OR “Vital rate” OR Persistence OR “Trauma”)

**Publication databases**

The following bibliographic databases were searched in December 2016 using Carleton University’s institutional subscriptions:

1) ISI Web of Science core collection
2) Scopus
3) ProQuest Dissertations and Theses Global
4) WAVES (Fisheries and Oceans Canada)
5) Science.gov

Note, the Fisheries and Oceans Canada database (WAVES) became a member of the Federal Science Library (FSL) in 2017 after this search was conducted (see Additional file 1).

**Search engines**

Internet searches were conducted in December 2016 using the search engine Google Scholar (first 500 hits sorted by relevance). Potentially useful documents that had not already been found
in publication databases were recorded and screened for the appropriate fit for the review questions.

Specialist websites

Specialist organization websites listed below were searched in February 2017 using abbreviated search terms [i.e., search strings (1) fish AND hydro AND entrainment; (2) fish AND hydro AND impingement; (3) fish AND hydro AND mortality; and (4) fish AND hydro AND injury]. Page data from the first 20 search results for each search string were extracted (i.e., 80 hits per website), screened for relevance, and searched for links or references to relevant publications, data and grey literature. Potentially useful documents that had not already been found using publication databases or search engines were recorded.

1) Alberta Hydro (https://www.transalta.com/canada/alberta-hydro/)
2) British Columbia Hydro (https://www.bchydro.com/index.html)
3) Centre for Ecology and Hydrology (https://www.ceh.ac.uk/
4) Centre for Environment, Fisheries and Aquaculture Science (https://www.cefas.co.uk/)
6) Electric Power Research Institute (https://www.epri.com/)
9) Fisheries and Oceans Canada (https://www.dfo-mpo.gc.ca/index-eng.htm)
10) Fisheries Research Service (https://www.gov.scot)
12) Hydro Québec (http://www.hydroquebec.com/)
13) Land and Water Australia (http://lwa.gov.au/)
14) Manitoba Hydro (https://www.hydro.mb.ca/)
16) Ministry of the Environment New Zealand (https://www.mfe.govt.nz/)
17) National Institute of Water and Atmospheric Research New Zealand (https://niwa.co.nz/)
18) Natural Resources Canada (https://www.nrcan.gc.ca/home)
19) Natural Resources Wales (https://naturalresources.wales/?lang=en)
20) Newfoundland and Labrador Hydro (https://nlhydro.com/)
23) Pacific Fisheries Environmental Laboratory (https://oceanview.pfeg.noaa.gov/projects)
26) Trout Unlimited (https://www.tu.org/)
27) United Nations Environment Programme (https://www.unenvironment.org/)
28) US Fish and Wildlife Service (https://www.fws.gov/)

Other literature searches
Reference sections of accepted articles and 168 relevant reviews were hand searched to evaluate relevant titles that were not found using the search strategy (see Additional file 2 for a list of relevant reviews). Stakeholders were consulted for insight and advice for new sources of
information. I also issued a call for evidence to target sources of grey literature through relevant mailing lists (Canadian Conference for Fisheries Research, American Fisheries Society), and through social media (e.g., Twitter, Facebook) in February and November 2017. The call for evidence was also distributed by the Advisory Team to relevant networks and colleagues.

Appendix B

Figure B1: Free-swimming fish in the intake towers.

Figure B2: Intake towers at the W.A.C. Bennett facility.
**Figure B3:** Overhead shot looking down into the intake towers.

**Figure B4:** Net used to salvage Kokanee from the intake towers.
**Figure B5:** Cross sectional depiction of the intake towers at W.A.C. Bennett Dam. See text in *Study site* for dimensions.
Figure B6: Range testing array upstream and downstream of W.A.C. Bennett Dam. Hydropower infrastructure is indicated with dark gray fill colour. Open circles denote hydrophone receivers; black “x” denotes a JSATS tag; the black open square denotes the release point of salvaged fish. Note that in some cases receivers and tags were anchored on the same line, see text for description.
Appendix C

TDG Modeling Methods

Total dissolved gas supersaturation levels were modeled following Kamal et al. (2019), which provides a detailed account of the TDG modeling methodology. Kamal et al. (2019) modeled TDG dissipation in the Columbia-Kootenay sector, the same river sector for which the acoustic telemetry array and transmitters were active in the present study. In summary, to model TDG dissipation, field measurements of TDGs were collected for two test periods. In the first test period (July 26-30, 2016), four different low-level outlet gate operational combinations were implemented at HLK (Scenario A). Generation flow from the HLK powerhouse was consistent among the scenarios and BRD was limited to powerhouse releases (i.e., no spillway discharge) during the test period. In the second test period (June 7-8, 2017), at BRD three spillways were operated with generation flow from both powerhouses and three gates at HLK were operated (Scenario B). For both TDG field work sessions, discharge and water level data were sourced from Water Survey Canada station 08NE049. Spatial and temporal variation of TDG were continuously monitored using stationary floating platforms and spot measurements were taken across representative river transects by boat. The floating platforms were custom-built PVC platforms that housed measurement probes and a data logger encased in a waterproof container. Floating platforms were anchored ~3 to 5 m from the riverbank. Probes were calibrated to record data at 2 min intervals and were submerged ~1 to 1.5 m below the platform. Spot measurements were taken from an anchored boat with probes submerged ~1 to 1.5 m for 10 to 20 min. Measurements taken included total gas pressure, barometric pressure, and water temperature (Lumi4 DO-TGP and PT4 Smart TGP probes, Pentair Aquatic Eco-Systems, Apopka, Florida). For Scenario A, spot measurements were taken at seven transects and six continuous monitoring
stations were deployed on the Columbia River. For Scenario B, spot measurements were taken at six transects on the Kootenay River and Columbia River and no continuous monitoring stations were deployed.

To estimate discharge, water velocity and depth measurements were taken at the seven Scenario A transects using an acoustic Doppler current profiler (ADCP; 600 kHz RiverRay, Teledyne RD Instruments, Poway, California). Measurements at each transect were replicated three or four times. Due to time constraints, hydraulic measurements could not be taken at all transects in all operational scenarios, so velocity and depth were calculated using the Hydrologic Engineering Center River Analysis Software (US Army Corps of Engineers, https://www.hec.usace.army.mil/software/hec-ras/) where applicable. Flows from HLK and BRD were used as input boundary conditions and the model extended downstream to a Water Survey of Canada measurement station. The model was calibrated to the fourth iteration of Scenario A. However, field observations and previous research on the system indicated that the river section upstream of the Columbia-Kootenay river confluence is backwater affected, so Manning’s roughness coefficient was adjusted. The final Manning’s roughness coefficient was calibrated by first matching the calculated water surface elevation with the tailwater levels of both dams, and then matching the modeled velocities with the ADCP measured mean velocities. The cumulative discharge at individual transects was estimated using the mean velocity profile, which was obtained by fitting the ADCP measurements with Manning’s equation or a modified Manning’s equation. An analytical transverse mixing model was developed to obtain final TDG level estimates in the Columbia-Kootenay downstream of HLK and BRD through to the WAN dam at the Canada-US border. See Kamal et al. (2019) for explicit discussion of the equations used.
Depth Residency Results

Figure C1: Depth residency according to season (A) and at each location in the Lower Columbia (B). Depth residency is pooled across Mountain Whitefish and Rainbow Trout. Significant multiple comparisons are found in text.
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