INORGANIC FINE SEDIMENT DEPOSITION IN RIVERS WITH RUN-OF-RIVER HYDROPOWER PROJECTS AND COASTAL TAILED FROG (ASCAPHUS TRUEI) TADPOLES IN COASTAL BRITISH COLUMBIA

by

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Abstract

Freshwater species are the most threatened group among terrestrial, marine and freshwater ecosystems globally. Riverine species are particularly at risk and their conservation is likely to require an enhanced understanding of the effects of alterations to natural flow regimes. Run-of-river (RoR) hydropower has the potential to affect natural flow regimes and is an increasing component of energy portfolios. In particular, increased sedimentation due to decreases in discharge below RoR weirs may have deleterious biological effects on primary production and associated aquatic species. I hypothesized that primary production would decrease with higher fine sediment deposition, and in turn impair growth and survival of Coastal Tailed Frog (*Ascaphus truei*) tadpoles. I conducted tadpole surveys and quantified biofilm above three RoR weirs and in the diversion reach of each installation in British Columbia, Canada, during peak summer productivity. I also conducted an *in situ* mesocosm experiment with three levels of fine sediment deposition to determine the effects of fine sediment on tadpole growth and survival. I found that fine sediment deposition on the top surfaces of stones was higher in the diversion reach of two rivers with RoR hydropower projects, but varied in magnitude depending on the river. Fine sediment was positively associated with higher chlorophyll *a* biomass and ash-free dry mass on all three rivers. Tadpole density was consistently lower by nearly 50% in the diversion reach for all three rivers with RoR hydropower projects. The results from my mesocosm experiment suggested that survival and average tadpole growth tends to be lower as fine sediment amount increases. Although our experimental results were not conclusive, if fine sediment does decrease growth and survival of Coastal Tailed Frog tadpoles, this may indicate that higher fine sediment deposition in the diversion reach of rivers where discharge is reduced have the potential to impact Coastal Tailed Frog populations in these watersheds.

Preface

This research program was encouraged by Joshua Malt, who has a professional interest in the potential impacts of run-of-river hydropower projects on Coastal Tailed Frogs, although the focus of the study was left to the author. The observational study was done in collaboration with Rylee Murray, a Master of Science student from Simon Fraser University. The design of tadpole sampling procedures was jointly determined between the author and R. Murray, with the author responsible for determining the best way to collect biofilm samples for the thesis. Additionally, the experimental design, data analysis and writing of this thesis was the responsibility of the author. This project was approved under the Animal Care numbers 1130B-2014 (SFU) and A14-0170 (UBC).

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1 Freshwater conservation

Relative to terrestrial and marine species, freshwater species are the most threatened group globally (Dudgeon et al. 2006, Collen et al. 2014, World Wildlife Fund 2014). Between 1970 and 2010, populations of monitored species have declined in size by 76% (World Wildlife Fund 2014), most often due to anthropogenic land-use changes (Dudgeon et al. 2006, Collen et al. 2014). Habitat loss and degradation, water pollution, and invasive species are thought to be the main contributors of freshwater population declines globally, particularly for riverine species (Dudgeon et al. 2006, Collen et al. 2014, World Wildlife Fund 2014). Of these three drivers of decline, habitat loss and degradation is the most prevalent among threatened species (Collen et al. 2014).

It is estimated that 80% of threatened freshwater species are affected by habitat loss and degradation due primarily to urbanization, agriculture, and water impoundment schemes (Collen et al. 2014). All three can affect the availability of aquatic habitat, limiting the accessibility of important spawning and rearing habitat (Sparks 1995, Dudgeon 2000, Poff and Zimmerman 2010, Lesack and Proctor 2011). Other effects of habitat degradation, such as changes to thermal or sediment transport regimes, have been linked to population declines and extirpation (Dudgeon 2000, Kareiva et al. 2000), decreased recruitment success (King et al. 1999, Preece and Jones 2002, Humphries et al. 2007), and increased competition between native and non-native species (Vila-Gispert et al. 2005, Kirkwood et al. 2007, Johnson et al. 2008). While urbanization, agriculture, and water impoundment schemes all contribute to habitat loss and degradation, future increases in the demand for freshwater resources (Gleick 2010) is likely to require the use of more water impoundment or diversion schemes. This will necessitate a more comprehensive understanding of their impacts on aquatic species.

Large dams intercept approximately 66% of global freshwater discharge (Nilsson and Berggren 2000), and 77% in the Northern hemisphere alone (Dynesius and Nilsson 1994). The construction of large dams was quite popular during the 1950s, as they were believed to be not only a clean source of energy and water for human settlements downstream, but an excellent way to control for floods in rivers with highly variable discharges (Altinbilek et al. 2012). From the 1970s to the 1990s, growing evidence against the use of large dams became more widely known to the public. They had been shown to have not only terrestrial effects, such as flooding large areas of land during the construction of the large reservoirs and altering species composition in downstream riparian zones (Kondolf 1997, Nilsson and Berggren 2000, Altinbilek et al. 2012), but also aquatic impacts, such as by changing upstream lotic habitats into lentic habitats in the reservoirs and altering downstream habitats and coastal estuaries (Kondolf 1997). Ecologically and socially, large dams continue to be a less desirable method of obtaining freshwater resources. As such, the growth of small hydropower has increased dramatically since 2000 (Abbasi and Abbasi 2011).

Typically, projects with up to 25 MW of power output, and in some countries up to 50 MW outputs, are considered to be “small hydropower”, and are often comprised of run-of-river (RoR) hydropower projects (Abbasi and Abbasi 2011). Due to their smaller size and lack of water storage, they are perceived to have a smaller impact on aquatic ecosystems than large dams, but there have been few scientific studies to support or refute this claim (Gower et al. 2012). As the installation of RoR hydropower projects increases, it is critical to understand the ecological impacts they may have on riverine species through the alteration of the natural flow regime.

1.1 The natural flow regime

Biological communities dependent on freshwater ecosystems are greatly influenced by the natural flow regime (Busch and Smith 1995). The components of the natural flow regime are described as the magnitude of discharge in the river at a given time, the frequency with which changes in discharge occur, the duration of the change, the rate of change, and the timing or predictability of the change (Poff et al. 1997). Together, these characteristics play an important role in determining the identity and abundance of species occurring in these ecosystems.

Seasonal patterns of low flows and short-term floods give rise to communities of species that are specially adapted to resist desiccation and avoid getting washed out by high flows. Species that occur in intermittent rivers often evolve methods to avoid desiccation (Datry et al. 2014). For instance, some macroinvertebrates lay drought-resistant eggs while others emerge as winged adults before a drought to allow for faster recolonization once higher flows have returned (Lytle and Poff 2004, Strachan et al. 2015). Other macroinvertebrates develop a drought-resistant case, or take refuge in moist areas, such as hyporheic zones (Strachan et al. 2015). For flood-influenced systems, species can evolve behavioural and life history strategies to avoid getting swept downstream during high flows. As with desiccation avoidance, some macroinvertebrates time their metamorphosis into a winged adult form to coincide with periods with a low risk of flooding (Lytle 2002, Strachan et al. 2015). Other species often evolve behaviours which cause them to seek refuge in other habitats when a heavy rain event occurs to avoid getting washed downstream during floods, such as the Sonoran topminnow (*Poeciliopsis occidentalis*) which had to evolve such a mechanism to avoid getting swept downstream during flash floods (Meffe 1984).

Despite that species in riverine ecosystems often represent those species that are best adapted to persist under the specific flow regime of that ecosystem, even short-term droughts or floods can have large effects on communities by altering the relative abundance of species. One well-described example is from the South Fork Eel River in California, USA. Bed-scouring flows in winter wash out armoured caddisfly grazers which are invulnerable to fish predators, leaving only vulnerable grazers. This results in an increase of algal biomass in the following growing season as fish decrease the grazing pressure of vulnerable grazers on the algae (Power et al. 2008). In the same system, drought years which do not wash the armoured caddisflies grazers downstream are followed by low algal biomass accrual as fish predators are unable to prey on the armoured caddisflies, allowing them to reduce algal standing crops dramatically (Power et al. 2008).

Unlike naturally-occurring droughts and floods, changes to land-use by humans has resulted in long-term alterations of the hydrologic regime throughout the globe. For instance, high flows are often used to trigger spawning, egg hatching, and migration, cues which are lost when high flows are suppressed by dams (Poff et al. 1997). Flow-stabilized rivers are at risk of invasion by more competitive non-native species (Vila-Gispert et al. 2005, Kirkwood et al. 2007), and prolonged low flows can lead to the loss of access to floodplains and backwaters, important habitats for young fish and a source of nutrients (Poff et al. 1997). In the case of large water impoundment schemes, the change from lotic environments to lentic habitat make reservoirs susceptible to invasion of non-native species as well (Johnson et al. 2008). Additionally, release of water from large dams can either increase the temperature of downstream reaches by releasing epilimnetic water, or decrease the temperature by releasing limnetic water (Lessard and Hayes 2003, Olden and Naiman 2010). Alterations to the thermal regime can cause recruitment failure in native species (King et al. 1999, Preece and Jones 2002), decrease individual survival (Lessard and Hayes 2003, Todd et al. 2005), and shift communities from coldwater to warmwater species and vice versa (Olden and Naiman 2010). Additionally, the construction of large dams can cause the loss of sediment transport downstream, important for habitat maintenance and nutrient transport (Poff et al. 1997).

The development of environmental flows has been one management effort to reduce the impacts of altered flow regimes on ecological processes. Environmental flows are developed to balance water flow required for freshwater ecosystem functions and water flow required to support the human communities that rely on the freshwater source (Poff et al. 2010). This requires an understanding of how different ecological processes change with flow, with the knowledge that no single environmental flow requirement will be able to be applied to all riverine ecosystems (Arthington et al. 2006, Richter et al. 2006, Poff et al. 2010).

1.2 Sediment transport

The deposition and transport of sediment in rivers depends on the sediment supply and patterns of flow (Wood and Armitage 1997). Sediment can be supplied by external or internal sources in rivers. Hillslopes on the sides of rivers deliver inorganic sediment created by the natural weathering of rocks and soil erosion, while riparian vegetation is a source of organic material. As this sediment enters the stream, it can immediately be transported in the water column or be temporarily stored in back water areas, areas with low flow, or in interstitial spaces in the stream bed, which can later be re-entrained. Instream sources of sediment capable of being mobilized include that which is transported by tributaries, sediment due to the erosion of the stream bed or stream banks, and organic material (e.g. detritus, algae). Organic sediment can be processed in the ecosystem and taken up into the food web through macroinvertebrate and microbial ingestion (Boulton and Lake 1992, Wood and Armitage 1997, Tank et al. 2010), while inorganic sediment tends to remain in the ecosystem to be stored or transported.

Whether inorganic sediments settle on the stream bed or continue to be transported downstream depends not only on flow, but also on the size of the particle. The movement of coarse particles typically only occurs in high-flow events such as spring run-off or rainstorms. In this case, bedload movement can occur wherein coarser material can be transported via rolling, sliding, or saltation. Fine sediments often remain suspended except where flows are low enough to allow deposition. This often occurs in pools and stream edges during low flow periods and is temporary. Very fine particulate matter such as silts or clays typically do not settle if there is any water flow, except when they adhere together to create larger particles, called flocs, which deposit more readily (Droppo and Ongley 1994, Hill et al. 2000, Owens et al. 2005).

Land-use changes both increase and decrease sediment supply. Anthropogenic sources of sediment include forestry, urbanization, and agriculture. Clearing of land can lead to the destabilization of soils, increasing the risk of landslides and increase soil erosion. This sediment can cause increased embeddedness, particularly in pools (Wohl and Cenderelli 2000). Additionally, agriculture, the construction of forestry roads, and urbanization creates impervious surfaces making water move into rivers at a much faster rate, and increasing the sediment delivery rate and causing stream bed scour (Wood and Armitage 1997, Walters et al. 2003, Coffin 2007, Walling et al. 2007). In contrast, the construction of dams and reservoirs tend to decrease sediment load in water below the dams as large reservoirs cause sediment to settle out of the water column (Kondolf 1997). Often, river channels below dams experience greater rates of channel incision, armouring, and channel degradation as sediment-free water exits the dam and erodes the channel (Kondolf 1997).

Both large and small changes in sediment loads can have large effects on riverine species. Decreases in sediment loads can lead to channel erosion and bed coarsening, which can cause loss of fish spawning habitat as gravels are swept downstream and the remaining substrate becomes too large for females to move (Kondolf 1997). Similarly, a large increase in sediment to rivers can fill in pools, resulting in habitat loss due to infilling of interstitial spaces, which are important refuges from high flows and predators (Kondolf 1997, Wood and Armitage 1997, Wohl and Cenderelli 2000, Kemp et al. 2011). There are several ways that fine sediment deposition could negatively affect biofilm, an important food resource for grazers that is a mixture of algae, bacteria and protozoans. Increased inorganic fine sediment can prevent attachment by primary producers and cause smothering or abrasion of established biofilm (Wood and Armitage 1997, Izagirre et al. 2009). Additionally, increased suspended sediment loads can decrease photosynthetic capabilities and productivity by decreasing light penetration and abrading biofilm (Wood and Armitage 1997, Henley et al. 2000, Francoeur and Biggs 2006, Izagirre et al. 2009). Biofilm quality can also be decreased when there is high suspended sediment loads as particles infiltrate biofilm and decrease the organic content that consumers are able to ingest, thus reducing the growth of grazers (Graham 1990, Wood and Armitage 1997, Henley et al. 2000, Kiffney et al. 2003). While fine sediment can negatively affect higher trophic levels by decreasing primary producer quality and quantity, it can also play a more direct role: suspended particles can adhere to gills or other external respiratory organs, as well as filter-feeding apparatuses, decreasing breathing and feeding efficiencies (Wood and Armitage 1997). Changes in macroinvertebrate communities have been found with increasing embeddedness, due to shifts from drifting individuals to burrowing species, which are less accessible to predators (Suttle et al. 2004). Suspended sediments can also impede visual hunters if turbidity is high enough (Wood and Armitage 1997). Even episodic events causing short-term increases in fine sediment deposition can decrease macroinvertebrate populations (Doeg and Milledge 1991, Waters 1995, Shaw and Richardson 2001), which could cause decreases in prey abundance and result in decreased growth and survival of higher trophic levels. In light of these effects and the scale at which rivers have been affected globally, sedimentation within rivers is a leading cause of concern for the conservation of freshwater species (Waters 1995).

1.3 Water diversion schemes

During the 1950s, large dams were viewed as an efficient and clean method of creating energy as water could be released from the reservoir as required, regardless of the discharge in the supplying rivers. They were also a boon as reservoirs could be used as flood control for communities downstream, or supply water during droughts (Abbasi and Abbasi 2011, Altinbilek et al. 2012). But over time, the environmental impacts of large dams have become well known.

The installation of large dams impacts not only the terrestrial environment the reservoir takes up, but also downstream ecosystems. The decomposition of inundated terrestrial plants in reservoirs is estimated to release methane equal to 20% of emissions released by other anthropogenic sources such as rice paddies and fossil fuel emissions, and carbon dioxide equivalent to 2% of emissions (St. Louis et al. 2000). In addition, the dam itself interrupts the continuity of the stream, inhibiting the movement of nutrients, debris, and organisms between upstream and downstream reaches (Kondolf 1997). Lack of sediment transport past reservoirs causes erosion of the stream bed in downstream reaches, reducing habitat quality including on coastal beaches which depend on fine sediment transport to replace naturally eroded sand (Kondolf 1997). And while it is known that dams create barriers to migration, the installation of fish passages to mitigate this problem tend to be ineffective or negatively impact spawning success (Bunt et al. 2000, Aarestrup et al. 2003, Naughton et al. 2006, Roscoe et al. 2011). In addition, thermal regimes below dams can cause community shifts and alter recruitment success, growth, and survival of fish (King et al. 1999, Preece and Jones 2002, Lessard and Hayes 2003, Todd et al. 2005, Olden and Naiman 2010). Finally, warmer temperatures and decreased discharge below dams have been linked with increased parasite infections in amphibians (Kupferberg et al. 2009). As these impacts have become more widely known, there has been a societal push for more environmentally friendly alternatives.

Believed to have fewer environmental impacts, the use of small hydropower has become increasingly popular and has nearly doubled between 2001 and 2010 (Abbasi and Abbasi 2011). Run-of-river (RoR) hydropower projects are primarily favoured as there are more rivers that are suitably large enough for their construction. They also require little water storage, relying on the natural flow regime of the river to generate energy, and impacts are believed to be limited to the area between the weir and where the water is reintroduced downstream (i.e. the diversion reach).

Similar to large dams, there are concerns that rivers with RoR hydropower projects may cause changes to sediment transport. It is possible that coarse materials may get trapped in the headpond while finer particles pass over the weir. As the small particles naturally adhere together, they may be more likely to deposit in the diversion reach where flows are depressed. Studies investigating fine sediment changes in rivers with RoR hydropower projects are few (but see Baker et al. 2011, Csiki and Rhoads 2014) and often lack consideration of aquatic species.

1.4 Coastal Tailed Frog ecology

Endemic to North America, the Coastal Tailed Frog is one of two species in the genus *Ascaphus*. Coastal Tailed Frogs are distributed along the Pacific Northwest from northern California to the southern half of British Columbia (Fig. 1-1) and inhabit cool, fast-flowing waters. Breeding is believed to occur in late summer to early fall (Bull and Carter 1996a) and eggs are laid under rocks in the headwater streams during mid-summer (Bury et al. 2001). Tadpoles emerge after approximately 6 weeks (Brown 1975) and take 2-4 years to complete metamorphosis (Bury and Adams 1999). Coastal Tailed Frog tadpoles prefer areas with lower embeddedness (Hawkins et al. 1988, Bull and Carter 1996b) as interstitial spaces are important refuges from predators and high-flow events.

Coastal Tailed Frog larvae may be the dominant biofilm-grazer in the ecosystems in which they occur (Lamberti et al. 1992, Kiffney et al. 2004). As the growth season for tadpoles is limited to a few months in the summer when river temperatures are warm enough to support adequate biofilm resources, impacts to the quality or quantity of their food source decrease their survival or slow their growth (Wood and Richardson 2009) and may increase the time to metamorphosis as found in other frog species (Gillespie 2002). By increasing the length of time to metamorphosis, they experience higher cumulative risk of predation and if metamorphosis is delayed until the following summer, Coastal Tailed Frog tadpoles may experience another opportunity to get washed downstream or killed during winter high flows or spring freshet. As Coastal Tailed Frog habitat overlaps in distribution with current and potential RoR hydropower projects in Pacific northwest rivers, there is concern about the possibility of impacts by RoR operations in these riverine ecosystems.

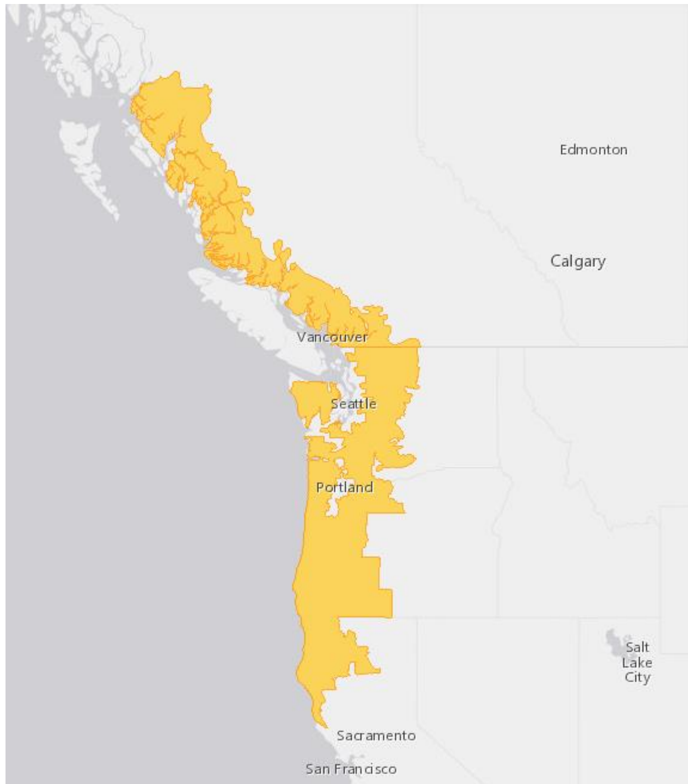

Figure 1-1. Distribution of Coastal Tailed Frog (*Ascaphus truei*) along the Pacific northwest coast (from IUCN SCC Amphibian Specialist Group 2015).

1.5 Study objectives

RoR hydropower projects have become more popular as a source of energy, and hence it is important to understand what ecological impact they may have on aquatic species. Although some studies investigating the effects of RoR installations on sediment deposition and transport have been conducted (Baker et al. 2011, Csiki and Rhoads 2014), none have considered potential impacts on amphibians.

The objectives of this study are firstly, to investigate the spatial distribution of fine sediment, biofilm, and Coastal Tailed Frog tadpoles in relation to RoR weirs. My second objective was to determine if fine sediment deposition affected tadpole growth and survival. The first objective was completed by conducting an observational study on three rivers with RoR hydropower projects. To complete the second objective, I conducted a mesocosm experiment where tadpoles were exposed to several fine sediment deposition levels to measure the effect on tadpole growth and survival.

2 Observational and experimental data

2.1 Introduction

Disturbance can drive evolutionary change (Macnair 1987, Tabashnik 1994) and shape natural communities by affecting the habitats species occupy (Busch and Smith 1995, Poff et al. 1997, Olden and Naiman 2010). Disturbance regimes can therefore play a key role in the conservation of threatened species. In riverine ecosystems, natural flow regimes can act as a somewhat predictable disturbance regime. For example, annual patterns of high flows or drought-like conditions play a large role in structuring communities (Rood and Mahoney 1995, Poff et al. 1997, Vinson 2001, Poff and Zimmerman 2010). Many stream species are adapted to specific disturbance types that shape their physical habitat, such as seasonal change in the duration, magnitude, frequency and timing of flooding (Meffe 1984, Poff et al. 1997, Lytle 2002). As such, alterations to natural flow conditions can have detrimental impacts on individuals which can have long-term effects on populations (Poff et al. 1997, Dudgeon 2000, Kareiva et al. 2000).

Downstream sediment transport patterns in rivers depend on sediment supply and water flow patterns (Walling et al. 2007). Sediment supply can be influenced by sediment that is already in the river system, such as in tributaries, or from the erosion of soils and rocks located on streambanks and in other regions of the watershed (Wood and Armitage 1997). The size and amount of sediment transported by rivers is heavily dependent on streamflow, which can vary seasonally. Coarse sediments tend to only be transported during peak flows, while fine sediments tend to remain suspended except at very low flows. During natural periods of low flow, areas with slow-moving water, such as pools and stream edges, tend to become fine sediment deposition sites (Walling et al. 2007). But both sediment supply and sediment transport can be affected by changes in land-use. For instance, forestry practices can cause the destabilization of soils, and the construction of affiliated roads can lead to an increase of suspended and deposited sediments in riverine ecosystems (Wood and Armitage 1997, Coffin 2007). Alternatively, large dams typically limit sediment movement downstream as particles tends to settle out in the large reservoirs, causing channel incision and bed coarsening below the dam (Kondolf 1997). Whether fine sediment loads increase or decrease in rivers, alterations to sediment transport in rivers can have large impacts on aquatic habitat.

Large changes in fine sediment supplies and deposition in rivers can have drastic impacts on the geomorphology of ecosystems, such as channel erosion or filling of pools, resulting in habitat loss for aquatic species (Kondolf 1997, Wohl and Cenderelli 2000). More subtle increases in sediment supply can lead to increased streambed embeddedness or higher suspended sediment loads (Wood and Armitage 1997, Wohl and Cenderelli 2000). Such changes to aquatic habitat can have various impacts on grazers. The loss of interstitial spaces is often associated with the loss of refuge from predators and high-flow events (Wood and Armitage 1997, Kemp et al. 2011), while suspended sediment can reduce standing stocks of primary producers by decreasing light availability or scouring (Wood and Armitage 1997, Francoeur and Biggs 2006), as well as infiltrate biofilm and decrease the food quality for herbivores (Graham 1990, Wood and Armitage 1997, Henley et al. 2000, Kiffney et al. 2003). These alterations to biofilm quantity and quality can cause decreased growth and survival for grazers (Gillespie 2002, Kiffney et al. 2004, Wood and Richardson 2010). These impacts are of increasing concern in the light of growing demands for freshwater resources (Gleick 2010, Abbasi and Abbasi 2011).

Although not a new technology, run-of-river (RoR) hydropower projects are becoming an increasingly popular method of producing energy globally. They are purported to have fewer impacts on flow patterns than traditional dams as they are smaller and retain less water in the headpond, thus minimizing impoundment effects (Abbasi and Abbasi 2011, Gower et al. 2012). RoR hydropower projects are typically installed on relatively small rivers with large gradient changes, and can divert all or a portion of the water in a river into a pipe or “penstock”, reintroducing the water many kilometers downstream of the intake (Paish 2002, Egré and Milewski 2002; Fig. 2-1). By only removing water from a small section of the river, impacts are presumed to be limited to the diversion reach located between the weir and the point where water is reintroduced at the tailrace downstream. A review of RoR installations in British Columbia (Conners et al. 2014) proposed that RoR hydropower weirs may act as a barrier for coarse sediments as large particles could settle in the slower-moving water in the headpond. However, finer silts and clays, which take longer to settle out in still water (Henley et al. 2000), may continue to pass over the weir and migrate downstream. As the fine sediment particles collide and adhere together, forming flocs, they become more likely to settle out in the diversion reach where there is less water discharge compared to the undiverted reach above the weir (Droppo and Ongley 1994, Hill et al. 2000, Owens et al. 2005).

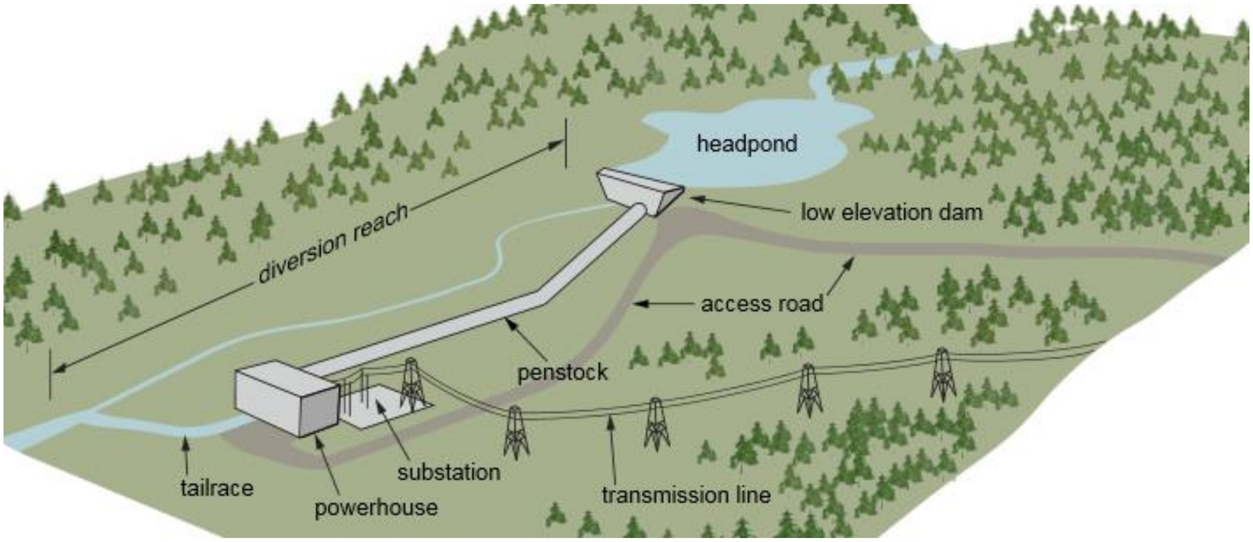

Figure 2-1. A generalized schematic of a run-of-river (RoR) hydropower project (from Gower et al. 2012). A small weir is installed in the river creating a small headpond which raises water levels to allow water to enter the penstock.

Some RoR hydropower projects periodically allow sediment to pass by the weir during high-flow events via sluice gates which minimizes annual changes to average bed-sediment size downstream of the weir. However, low flows during the summer may increase the deposition of fine sediment in the diversion reach, which may have negative impacts on primary production and aquatic grazers. This is particularly important in oligotrophic rivers in the Pacific Northwest where species do most of their growth during the warmer summer months. Although fine sediment has been the focus of many studies looking at the effects on macroinvertebrates (Waters 1995, Henley et al. 2000, Zweig and Rabeni 2001), few have focused on the effects on amphibians (but see Flecker et al. 1999a, Gillespie 2002, Wood and Richardson 2009), particularly for those species whose larval stages take several years to reach metamorphosis. Slow larval growth or delayed metamorphosis can increase predation risk and lower survival rates of larval stages (Semlitsch 1990, Altwegg and Reyer 2003), thus making these species of particular concern. Any impacts due to changes in sediment deposition during summer could affect multiple larval stages, and may therefore have a large effect on adult population sizes in the affected watershed.

Tadpoles of some frog species are biofilm specialists (Flecker et al. 1999) and thus may be highly affected by changes in inorganic fine sediment deposition in biofilm. Fine sediment can directly affect biofilm quantity via smothering or abrasion (Wood and Armitage 1997, Henley et al. 2000, Francoeur and Biggs 2006, Izagirre et al. 2009), reducing the availability of resources for tadpoles. Other studies have shown that fine sediment can be incorporated into biofilm which increases the proportion of inorganic matter (Cline et al. 1982, Graham 1990, Kiffney et al. 2003). An increase in the proportion of inorganic matter could cause reduced growth rates and survival, as tadpoles may be required to consume more low quality biofilm to meet their nutritional requirements and therefore expend more energy foraging (Wood and Richardson 2009). Additionally, higher fine inorganic matter may cause damage to mouthparts via abrasion, depending on the coarseness of the sediment. Changes to biofilm quality may also change behaviour, such that tadpoles may seek out areas with low sediment deposition (e.g. nearer to the thalweg of a river, where water velocity tends to be faster), as has been found in invertebrates (Doeg and Milledge 1991). Thus, alterations to sediment deposition rates may be an important consideration for RoR operations.

This study was conducted to identify whether Coastal Tailed Frog populations may be threatened by higher fine sediment deposition in the diversion reach of rivers with RoR hydropower projects. The mechanism through which this threat may manifest is that higher fine sediment deposition has the potential to negatively impact tadpole food resources and thus decrease the growth and survival of Coastal Tailed Frog tadpoles in the diversion reach. In this study, I investigated the spatial distribution of inorganic fine sediment in biofilm and of a biofilm-grazing amphibian, the tadpoles of the Coastal Tailed Frog (*Ascaphus truei*) in relation to RoR weirs. I hypothesized that tadpole densities would be lower in areas with higher fine sediment deposition. To determine if inorganic fine sediment deposition affected the spatial distribution of Coastal Tailed Frog tadpoles, I conducted an observational study on three rivers with RoR hydropower projects and compared tadpole densities above the weir and in the diversion reach. I was also interested in whether increased fine sediment deposition negatively affected the growth and survival of tadpoles. I hypothesized that tadpole growth and survival would decrease as fine sediment deposition increased. To test this hypothesis, I used a mesocosm experiment in which I manipulated fine sediment levels to determine if fine sediment negatively affected tadpole growth and survival.

2.2 Methods

2.2.1 Sample sites

During July – September 2015, I sampled sites located in three rivers with RoR hydropower projects in the Harrison Lake watershed in southwestern British Columbia, Canada (Fig. 2-2). Hydrology in the Pacific Northwest is such that these three rivers are influenced by a combination of rainfall, snowmelt, and glacier melt. Discharge is high during the fall when the region experiences high rainfall, and decreases as air temperatures become cold enough for snow to accumulate. In the spring, discharge increases as the snow melts and decreases again during the summer when there is little precipitation. To maintain a semblance of this flow variability, RoR hydropower projects are required to maintain minimum environmental flows which change seasonally, but are nevertheless very low during summer periods.

At the time of sampling, all RoR hydropower projects in this study had been in operation for six years, and the rivers naturally had enough discharge that the projects were in operation throughout the summer. Basin size of the rivers ranged from 63.2 – 105.2 km^2, with gradients ranging between 3.6% – 9.1% from the highest point sampled to the lowest (Table 2-1).

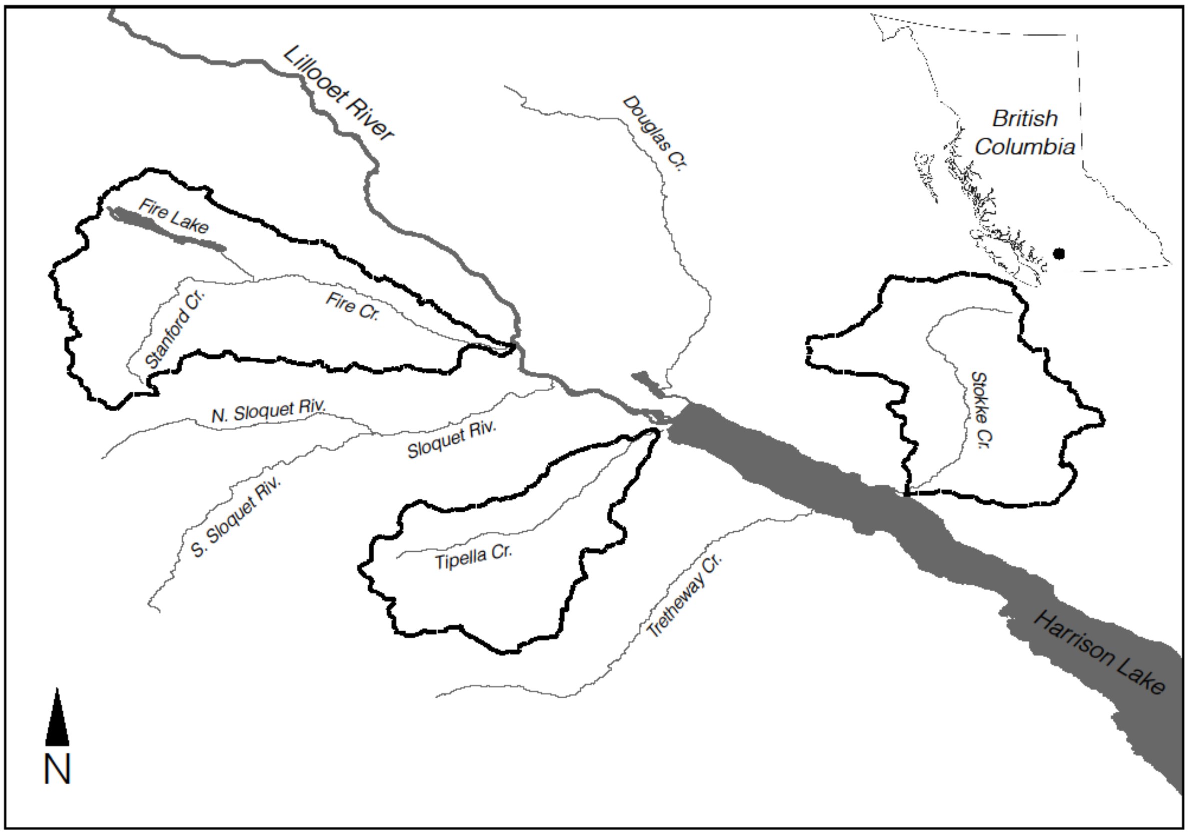

Figure 2-2. Map of the three study rivers located in the Harrison Lake watershed with basins outlined in heavy black lines. Map of British Columbia, Canada inset in top right corner.

Table 2-1. Characteristics of the study rivers. Basin size, slope above the weir, slope in diversion reach, total slope, and average bankfull width measured within 800 m above and 800 m below the weir.

River	Basin size (km^2)	Slope above the weir (%)	Slope in diversion reach (%)	Total slope (%)	Average bankfull width (m)	Annual average discharge (m^3/s)
Fire Creek	105.2	4.5	3.1	3.6	21.4	5.4
Stokke Creek	73.9	5.4	14.1	9.1	18.7	5.2
Tipella Creek	63.2	8.6	8.4	9.1	25.6	4.6

2.2.2 Comparison of environmental variables and tadpole density above RoR weirs and in diversion reaches, and at river edges versus near the thalweg

I selected 6 transects randomly within an 800 m distance above the RoR weirs and 6 transects within 800 m of the RoR weir in the diversion reach (total N = 12) in each of the three rivers. To test the hypothesis that fine inorganic sediment deposition would be higher in shallower water where fine sediment is hypothesized to be less likely to settle, I sampled two 1 m^2 quadrats in each transect: one near the river edge and one closer to the thalweg.

Prior to conducting tadpole surveys, three rocks were removed for chlorophyll *a* and three were removed for ash-free dry mass (AFDM) samples. Field assistants held nets downstream while removing the rocks to catch any tadpoles that might be dislodged during the process. The top surface of all six rocks per quadrat were thoroughly scrubbed with a toothbrush, then the scrubbed material was rinsed into clean plastic containers with distilled water. Each rock was photographed on lined paper, which acted as a reference scale, to estimate the scrubbed surface area using the computer software Image-J (Abràmoff et al. 2004) at a later time. Samples were either immediately filtered using Whatman™, Mississauga, ON, glass microfiber filters (GF/F, 47 mm diameter) or put into Falcon™ centrifuge tubes for filtering at a later time. Filters used for AFDM were ashed and weighed prior to sample collection. Both AFDM and chlorophyll *a* samples were frozen until they could be processed. AFDM samples were dried for 24 hrs at 105°C until a constant weight was achieved (to the nearest 0.1 mg), then ashed for 4 hrs at 500°C and re-weighed. I extracted chlorophyll *a* from samples by putting filters in 90% acetone over a 24 hr period, after which a TD-700 fluorometer was used to determine chlorophyll *a* concentration, which was then corrected for dilution to determine chlorophyll *a* biomass.

After collecting temperature, canopy cover and water velocity data in each quadrat, surveyors conducted area-constrained surveys, taking care to remove all rocks from the 1 m^2 quadrat until only gravel was left, then sifting through the gravel by hand looking for tadpoles (modified methods from RIC 2000). They used aquarium nets downstream to catch tadpoles that were displaced by the movement of cobbles and rocks, and a large net placed downstream of the sampling area to catch tadpoles that may have drifted past the smaller aquarium nets. All tadpoles were put into a bucket until the completion of the survey, after which they were photographed so their body length could be measured using Image-J as described previously (Abràmoff et al. 2004).

2.2.3 Experimental methods

From July to August 2015, I grouped 30 enclosures into five spatially distributed blocks within a 100 m reach of Fire Creek. Each block had 6 enclosures which were all within a 6-m radius, and were similar in canopy cover, initial flow, and depth to reduce variability within each block. I used Rubbermaid® (Atlanta, GA) Roughneck totes (189 L) as enclosures. After cutting openings at the upstream and downstream side of the enclosures, I covered the openings with 1.6 mm screening to prevent tadpoles from escaping while allowing water to flow through. Each tote was filled with a 10 cm layer of substrate ranging from 22.6 mm to 90 mm in size (percentage by area for each size class: 90 mm = 20%, 64 mm = 22%, 45 mm = 20%, 32 mm = 7%, 22.6 mm = 31%). The substrate was collected from the stream bank to ensure no initial biofilm growth, except all 90 mm cobbles were taken from the stream and randomly assigned to enclosures to facilitate biofilm regrowth. Each enclosure had a temperature data logger (Maxim's iButtons®, San Jose, CA, waterproofed using Plasti Dip®, Blaine, MN) to allow me to calculate degree days. I applied three fine sediment (< 0.7 mm) addition treatments in a randomized block design, with two replicates within each block. Every two weeks, I applied the following fine sediment treatment to the enclosures: 0 g/m^2 (control; C), 250 g/m^2 (low sediment addition treatment; L), or 1000 g/m^2 (high sediment addition treatment; H).

Prior to the addition of tadpoles, enclosures were left in the stream for a week to allow for biofilm growth and invertebrate colonization. I collected tadpoles from Fire Creek and its tributaries by lifting cobbles from the stream bed and catching tadpoles in aquarium nets. Then I randomly assigned each tadpole to an enclosure until there were four per enclosure. Each group of four tadpoles were weighed together using a field scale (Ohaus®, Parsippany, NJ, Scout II model SC2020) and took photos to determine the average length. The average length and averaged biomass per tadpole by enclosure at the start of the experiment was 1.158 cm (SE = ±0.011; N = 120) and 0.414 g (SE = ±0.009), respectively.

One replicate of each treatment per block was removed after 4.5 weeks, while the second replicate was removed after 7 weeks. At the completion of the experiment, surviving tadpoles were removed, weighed in groups of surviving tadpoles by enclosure, and photographed to measure length using Image-J (Abràmoff et al. 2004). I collected four rocks per enclosure for AFDM and chlorophyll *a* analysis and processed them as described above.

2.2.4 Data analysis

I used a model selection and multi-model averaging approach, using an AICc weight cut-off of 0.95 (Burnham and Anderson 2002) to determine the relative influence of fixed effects on the distribution of inorganic fine sediment, chlorophyll *a,* organic matter (AFDM), and tadpole densities above RoR weirs compared to in the diversion reaches. Analysis was completed using the statistical program R (R Core Team 2015). I used the function *lme* from the package *nlme* to create linear mixed models and explore how inorganic fine sediment was related to location in relation to the weir (above weir or in diversion reach) and stream position (edge or closer to the thalweg), using water velocity and slope of the transect (as measured using GIS) as a covariate. Linear mixed models were also used to investigate how chlorophyll *a* and AFDM varied with inorganic fine sediment deposition, location in relation to the weir, and stream position, with canopy cover and water velocity as covariates. Models for AFDM included a term for chlorophyll *a* biomass. I used the function *glmer*, with a poisson distribution, from the package *lme4* to create generalized linear mixed models and explore the relationship between tadpole density and the following fixed effects: location in relation to the weir, inorganic fine sediment deposition in biofilm, and stream position, with temperature, slope, water velocity, and canopy cover as co-variates. The abundance of Rocky Mountain Tailed Frog tadpoles is known to decrease as basin size increases (Dupuis and Friele 2006), and Coastal Tailed Frog tadpole densities are expected to change in a similar manner. To ensure that tadpole density showed no relationship with basin size and would not unduly influence my results, I plotted the residuals from my tadpole density model versus basin size and found no obvious pattern (Fig. S1). All models included river as a random intercept term to account for differences between rivers independent of the main effects. Prediction variables were standardized to a mean = 0 and a SD = ±0.5 to account for categorical data with binary results and allow me to directly compare effect sizes of the predictor terms on the response variables (Schielzeth 2010). To identify outliers in my data, I used the function *CookD* from the package p*redictmeans* which calculates a significance level based on the Mahalanobis distances of data compared to the predicted model (Pinheiro et al. 2015), then creates Cook's distance plots. I used a cut-off of 0.1 to determine if any outliers were influential in my models (Luo et al. 2014). I used the function *dredge* from the package *MuMin* to generate and rank all candidate models, using all combinations of fixed random effects from the global model for each given response variable. As there was no single model for any given response with an AICc weight ≥ 0.9, I averaged all ranked models that fell within the 0.95 AICc weight (Burnham and Anderson 2002) using the function *mod.avg* from the package *MuMin*.

To determine if fine sediment deposition in the mesocosms experiment had any effect on Coastal Tailed Frog tadpole growth or survival, I used model selection on unstandardized variables (all candidate models are located in the Appendix). As I did not expect mortality, all tadpoles per enclosure were weighed together. The response of average growth was thus calculated as

$$change\ in\ mass = \frac{m_t}{N_t} - \frac{m_{t+1}}{N_{t+1}}$$

Where *m* is the mass of all tadpoles weighed and *N* was the number of tadpoles weighed. I used the package *lme4* to model tadpole survival, using a poisson distribution and the function *glmer*, and *nlme* to model tadpole growth, using the function *lmes*. My fixed effects for both analyses included treatment and the length of the experiment (4.5 or 7 weeks), as well as an interaction between the two factors. I included the mass of all the tadpoles at the start of the experiment as a covariate and weighed the model by the number of tadpoles per enclosure that survived to the end of the experiment. I used the package *MuMin* as described above to determine which models fell within 0.95 AICc weight.

2.3 Results

2.3.1 Comparison of environmental variables and tadpole density above RoR weirs and in diversion reaches, and at river edges versus near the thalweg

Inorganic fine sediment – There were four models that encompassed 0.95 AICc weight (Table S1) which all contained a term for location in relation to the weir (above or in the diversion reach) and stream position (edge or nearer to the thalweg). Location in relation to the weir and stream position had high relative importance (w = 0.91) and were present in all top ranked models, while water velocity had a lower relative importance (w = 0.51; Table 2-2). Mean inorganic fine sediment as collected from the tops of rocks, was higher in the diversion reach compared to above RoR weirs ($\beta = 0.77$, CI = 0.24 to 1.29), although the magnitude of difference varied by river and stream position (Fig. 2-3), and higher at the edge of the stream compared to the thalweg ($\beta = -0.95$, CI = -1.48 to -0.42; Fig. 2-3). Finally, mean inorganic fine sediment tended to be lower in areas with higher water velocity ($\beta = -0.52$, CI = -1.07 to 0.02; Fig. 2-4A).

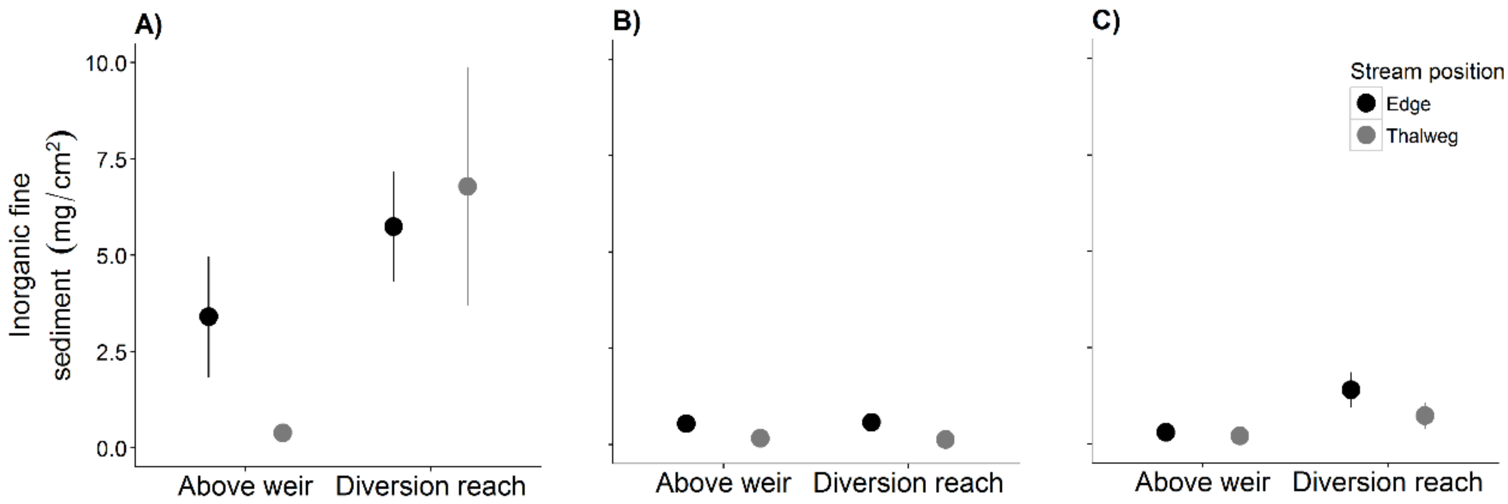

Figure 2-3. Mean inorganic fine sediment (mg/cm^2) above RoR weir and in the diversion reach of three rivers with RoR hydropower projects: A) Fire Creek, B) Stokke Creek, and C) Tipella Creek. Black points represent samples taken at the edge of the river and gray points indicate samples were taken closer to the thalweg. Error bars extend one standard error. In some cases, the symbols cover the error bars.

Table 2-2. Relative importance of each term in the top ranked models (within 0.95 AICc weight), measured as the summed Akaike weight of all models containing the term. NA indicates the term was not included in the global model.

Response	Total models averaged	Above weir or in diversion reach	Slope	Canopy cover (%)	Water velocity (m/s)	ln (Inorganic fine sediment (mg/cm^2))	Temperature (°C)	Stream position (near edge or near thalweg)	ln (Chlorophyll *a* (μg/cm^2))
ln (Inorganic fine sediment (mg/cm^2))	4	0.91	0.18	na	0.51	na	na	0.91	na
ln (Chlorophyll *a* (μg/cm^2))	8	0.09	na	0.67	0.11	0.93	na	0.13	na
ln (AFDM (mg/cm^2)) (all data)	20	0.18	na	0.13	0.18	0.95	na	0.41	0.23
ln (AFDM (mg cm-2)) (outliers removed)	7	0.09	na	0.11	0.08	0.94	na	0.07	0.94
Tadpole density (individuals/m^2)	64	0.91	0.52	0.34	0.3	0.26	0.22	0.21	na

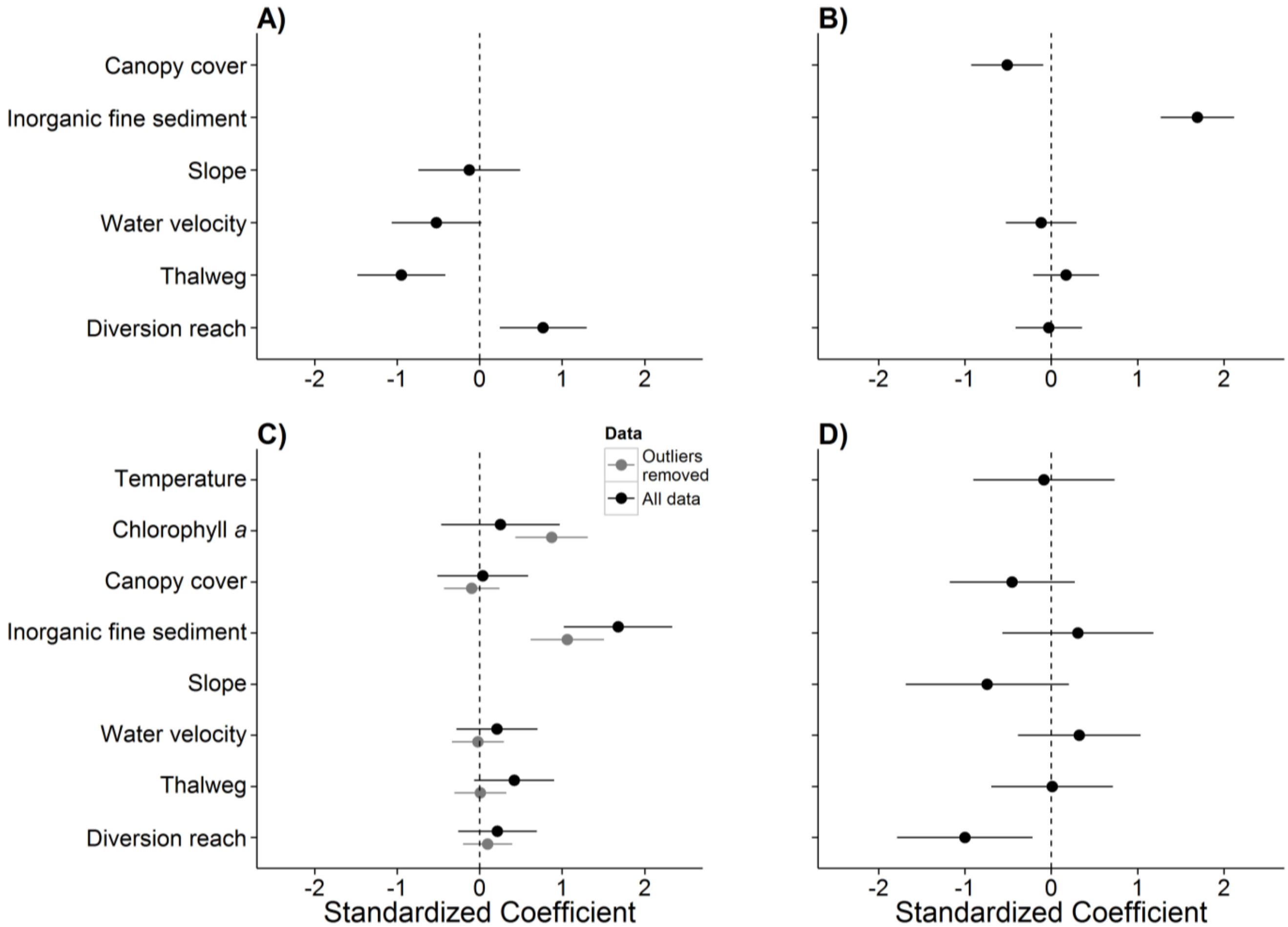

Figure 2-4. Standardized model average coefficients (±0.95 CI) for the relative effect of habitat variables on A) inorganic fine sediment (mg/cm^2) found in biofilm on top of rocks, B) chlorophyll a (µg/cm^2), C) ash-free-dry mass (AFDM; mg/cm^2) (black points indicate all data was used, while gray indicates data with three outliers removed) and D) tadpole density (individuals/m^2). Habitat variables without a corresponding standardized coefficient indicate that the term was not included in the global model. Values to the left of the dashed line indicate a negative relationship with the response variable, while values on the right denote a positive relationship. The dashed line indicates no relationship between the variable of interest and the response variable.

Chlorophyll a – All top ranked models that encompassed 0.95 AICc weight for chlorophyll *a* included a term for the amount of inorganic fine sediment (w = 0.93), which had a positive relationship with chlorophyll *a* levels (β = 1.69, CI = 1.27 to 2.12; Fig. 2-4B; Fig. 2-5A). Although canopy cover had a lower relative importance in the top ranked models (w = 0.67; Table 2-2), it was negatively related to chlorophyll *a* measurements (β = -0.51, CI

= -0.93 to -0.09). Stream velocity, stream position, and location in relation to the weir had no effect on chlorophyll *a* levels.

Ash-free dry mass (AFDM) – I have included two analyses for AFDM, as there were three influential outliers. One analysis has all data points included, while the other has the outliers removed. When all data were used in the analysis, all top ranked models encompassing 0.95 AICc weight included a term for inorganic fine sediment (w = 0.95; Table 2-2; Table S1), which had a strong positive effect on AFDM measurements (β = 1.68, CI = 1.02 to 2.33; Fig. 2-4C; Fig. 2-5B). Stream position was of lower relative importance than inorganic fine sediment (w = 0.41), but tended to be positively related with AFDM (β = 0.42, CI = -0.07 to 0.90). Location in relation to the weir, chlorophyll *a*, and water velocity tended to be positively associated with AFDM, although they had lower overall relative importance in the top ranked models. Canopy cover showed no relation with AFDM measurements.

When the three outlier data points were removed from the analysis, there were only seven models that encompassed 0.95 AICc weight, all which contained terms for inorganic fine sediment and chlorophyll *a* (Table S1). Of the seven models, the top ranked model had 0.60 AICc weight and contained only terms for inorganic fine sediment and chlorophyll *a*. Each had high relative importance (w = 0.94; Table 2-2), and were positively associated with AFDM measurements ($\beta_{inorganic}$ = 1.06, $CI_{inorganic}$ = 0.62 to 1.51; $\beta_{chlorophyll}$ = 0.87, $CI_{chlorophyll}$ = 0.43 to 1.31; Fig. 2-4C). Water velocity, stream position, and weir position no longer showed any relation with AFDM measurements.

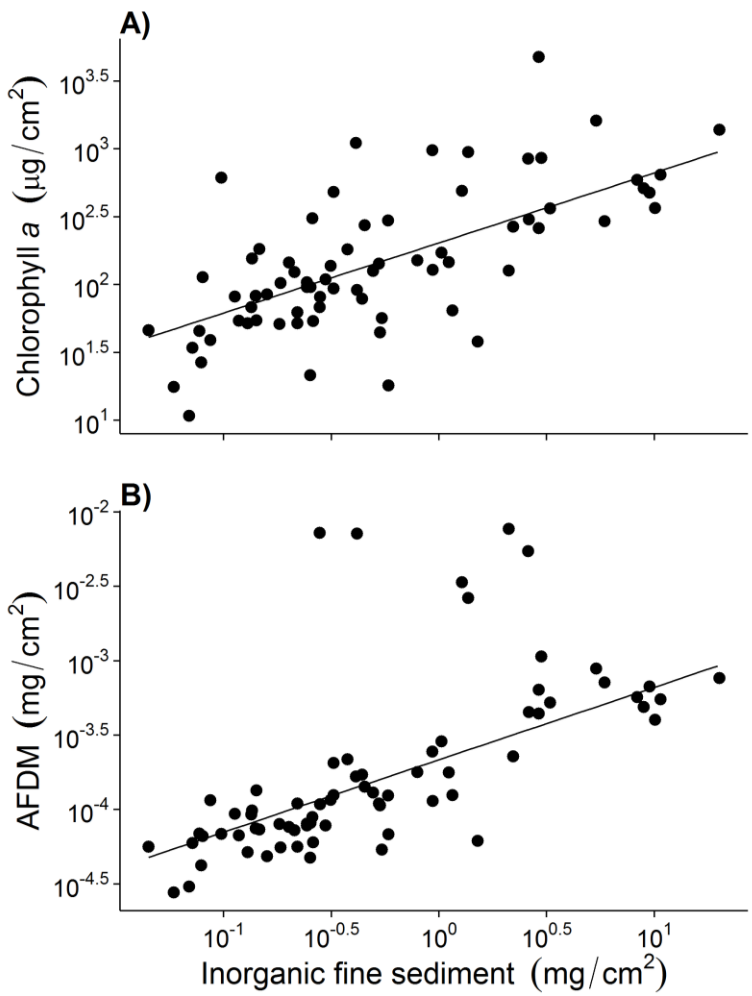

Figure 2-5. The effect of inorganic fine sediment from the top of rocks on A) chlorophyll a and B) ash-free dry mass in biofilm. Regression line represents the coefficients from the averaged model using a 0.95 AICc weight cut-off.

Tadpole density – Tadpole density was consistently lower in the diversion reach than above the RoR weir (β = -1.00, CI = -1.78 to -0.22; Fig. 2-6). Location in relation to the weir was in most top ranked models (Table S1) and had high relative importance (w = 0.91; Table 2-2). While of lower relative importance, inorganic fine sediment and water velocity tended to be positively associated with tadpole density ($\beta_{inorganic}$ = 0.31, $CI_{inorganic}$ = -0.56 to 1.18; β_{water} = 0.32, CI_{water} = -0.20 to 0.85), while canopy cover and slope tended to be negatively associated (β_{canopy} = -0.45, CI_{canopy} = -1.18 to 0.27; β_{slope} = -0.74, CI_{slope} = -1.69 to 0.20). Stream position and temperature did not show any relation with tadpole density.

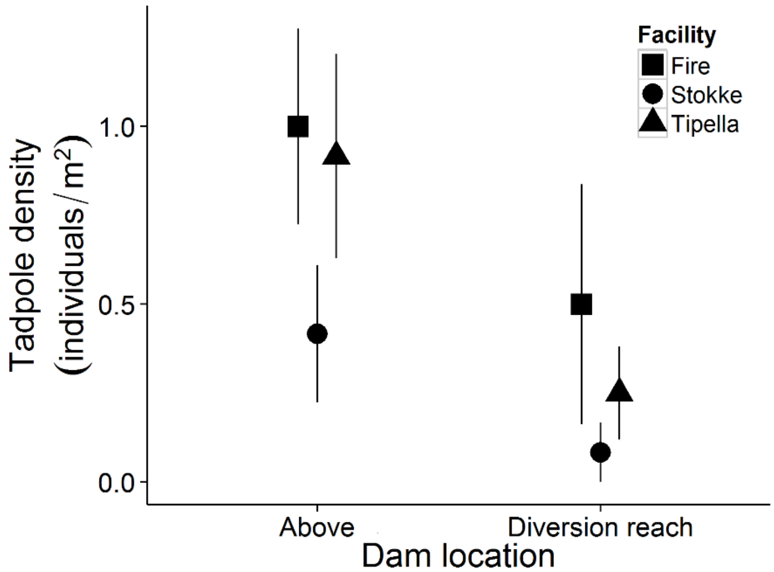

Figure 2-6. Tadpole densities (individuals/m^2) found above RoR weirs and in the diversion reach. The shapes indicate the three different facilities.

2.3.2 Experimental results

The initial hypothesis for this experiment predicted a decrease in individual growth rates as fine sediment inputs increased. However, I observed a high rate of mortality of tadpoles in many enclosures, which could be due to higher sediment deposition rates compared to observational measurements taken in the rivers (Table 2-3). This mortality confounds consideration of growth rates alone. Thus, there are two outcomes for an individual: 1) mortality or 2) if it survives, a change in weight. This outcome reduced my power to use growth as my response measure. Here I will first consider survival rates, and then growth rates of survivors.

Table 2-3. Range and average measurements of inorganic fine sediment (mg/cm^2) for observational samples taken from natural conditions, and those found in the mesocosm experiment by treatment level.

	Inorganic fine sediment (mg/cm^2)		
Treatment	Average	Minimum	Maximum
Observational	1.70	0.04	20.11
Control	16.67	2.77	64.88
Low	34.77	13.97	77.65
High	88.12	20.03	282.80

Survival – The mean number of the four tadpoles per enclosure that survived to the end of the experiment for both time periods was 1.83 (SE = ±0.25). There were 5 models that encompassed 0.95 AICc weight (Table S2), and treatment was only found in one model and had low relative importance (w = 0.07). The two top ranked models encompassed 0.66 AICc weight, with the top ranked model including only the intercept, and the second including the initial mass of all tadpoles per enclosure. Tadpole survival tended to be random among treatments (Fig. 2-7), but it is worth noting that at the end of 7 weeks, the high sediment treatment had no enclosures with more than two tadpoles (Fig. 2-7B).

Growth – There was one top ranked model that encompassed 0.64 of the AICc weight, while the second top ranked model encompassed 0.33 of the AICc weight (Table S2). Mean change in averaged tadpole growth at 4.5 weeks was 0.02 g (SE = ±0.02) and at 7 weeks was -0.03 g (SE = ±0.02). Although averaged growth tended to decrease with higher sediment loads as predicted for enclosures left in the stream for 4.5 weeks (Fig. 2-7A), neither top ranked models included a term for treatment. The top ranked model included a term for length of the experiment, while both models indicated that initial mass was the best predictor for the difference in average tadpole mass.

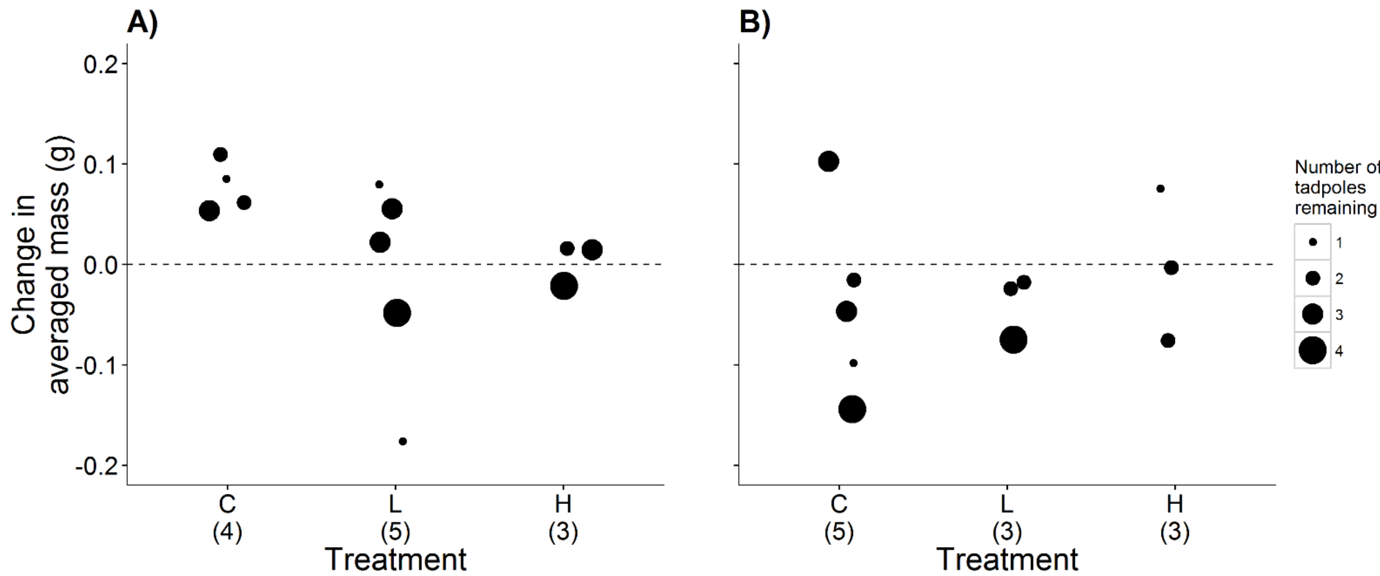

Figure 2-7. Change in averaged mass (g) of surviving tadpoles compared to the averaged mass of tadpoles at the beginning of the experiment for enclosures left in for A) 4.5 weeks and B) 7 weeks by treatment level. The symbols represent the number of tadpoles that survived to removal of the enclosures. Fine sediment addition treatments included control (C; 0 mg/2 weeks), low (L; 250 mg/2 weeks) and high (H; 1000 mg/2 weeks). The dashed line indicates no change in mass. Numbers in parentheses indicate the number of enclosures that had one or more tadpoles at the time of collection.

2.4 Discussion

The purpose of the study was to determine if low flows during summer in rivers with RoR hydropower projects may have different spatial distributions of deposited inorganic fine inorganic sediment found in biofilm on top of rocks above weirs compared to in the diversion reach. I also investigated whether tadpole densities were lower in areas with higher fine sediment deposition. I used both an observational study and conducted an *in situ* mesocosm experiment to determine if fine sediment deposition had any effect on Coastal Tailed Frog tadpole survival or growth to strengthen the implication of my results. Generally, tadpole densities were lower in the diversion reach where inorganic fine sediment was higher. My experiment shows inconclusive results for the effects of fine sediment deposition on survival and growth of Coastal Tailed Frog tadpoles, although the results tended to show a decrease in change in averaged biomass at higher fine sediment addition treatments.

2.4.1 Comparison of environmental variables and tadpole density above RoR weirs and in diversion reaches, and at river edges versus near the thalweg

A review of the potential impacts of RoR hydropower projects suggests that reduced flows in the diversion reach during naturally low-flow summer conditions may lead to higher fine sediment deposition (Conners et al. 2014). My results support this hypothesis as fine sediment deposits were times higher in the diversion reach than upstream of the weir of RoR hydropower projects during summer in at least two of my study rivers, suggesting that the water turnover rate in the headponds of these RoR projects is short enough that fine particles do not have the time to settle at the bottom of the headpond. Combined with reduced flows, my results suggest the fine particles that pass over the weir tend to settle in the diversion reach. Baker et al. (2011) and Csiki and Rhoads (2014) found similar results, however, this pattern was more pronounced in rivers with low gradients. Although the slope of the sample location did not have a strong effect in my models for inorganic fine sediment, my lowest gradient river, Fire Creek, had the highest percentage of fine sediment deposition in the diversion reach (edge: 1.7%; thalweg: 17.4%). While Tipella Creek showed slightly higher fine sediment deposition in the diversion reach (edge: 4.6%; thalweg: 3.5%), Stokke Creek showed very little difference between above the weir and in the diversion reach (edge: 1.1%; thalweg: 08%). This may be because the diversion reach in this system has a slope approximately 2.5 times that of above the weir, and therefore fine sediments are less likely to settle. In all cases, there was no obvious visual difference in suspended sediment as waters were clear during the sampling period, although water samples were not taken to quantify the amount of suspended fine sediment.

Coastal Tailed Frog tadpole densities are strongly linked to substrate size (Hawkins et al. 1988, Corn and Bury 1989, Richardson and Neill 1995). Other studies have attributed higher densities of tadpoles to streams which regularly are able to flush fine sediments (Corn and Bury 1989, Welsh and Ollivier 1998, Adams and Bury 2002). Consistent with these studies, my results showed that tadpole densities were 20 – 50% lower in the diversion reach of RoR hydropower projects, while inorganic fine sediment deposition was higher. I hypothesized that lower biofilm quantity could result in lower tadpole densities in the diversion reach, but chlorophyll *a* and AFDM both had a positive relationship with inorganic fine sediment, and location in relation to the weir had little effect in my models, suggesting that this may not be the case. While it could be possible that an increase in fine sediment allows for more surface area upon which biofilm can grow, it may also be possible that the sticky surface of the biofilm captures fine sediment, such that an increase in biofilm results in an increase in fine sediment "deposition" in biofilm (Cline et al. 1982, Graham 1990, Kiffney et al. 2003). If this is the case, my result of lower tadpole densities in the diversion reach of RoR hydropower projects is consistent with the hypothesis that biofilm in the diversion reach is of lower quality due to more fine sediment deposition (Wood and Richardson 2009).

Although it is possible that tadpoles could change behaviour and move closer to the thalweg where there is less fine sediment deposition, my results did not support this hypothesis. If biofilm quality is the cause of lower tadpole densities, my results and those results from other studies (i.e. Baker et al. 2011, Csiki and Rhoads 2014) could indicate that low-gradient sections of rivers with RoR hydropower projects are at higher risk of sediment deposition, and therefore, tadpoles in these areas may experience higher inorganic fine sediment deposition. I was unable to find a significant effect of fine sediment on tadpole density, which could be that the amount of inorganic fine sediment that deposited in the biofilm was not enough to affect tadpole density across all three rivers and that there is another mechanism driving this pattern. Other explanations unrelated to biofilm quality that may explain lower tadpole densities in the diversion reach of RoR hydropower projects include: 1) higher temperatures in the diversion reach which could cause higher metabolic requirements that are difficult to meet in these cool and relatively unproductive rivers; 2) the installation of a weir may act as a barrier to the downstream movement of tadpoles from tributaries where they hatch (Bury et al. 2001); and 3) alterations to the flow regime could cause changes to the structure of biofilm (Furey et al. 2014), making it more difficult for tadpoles to digest.

2.4.2 Experiment

Although my observational results were congruent with the hypothesis that tadpole densities are lower where inorganic fine sediment deposition is higher (i.e. in the diversion reach), my experimental results showed no clear effect of the different sediment addition treatments on tadpole growth or survival. Due to high variability in survival, I was unable to find any significant trends in survival or growth, although I noted that at 7 weeks, the maximum survival of tadpoles per enclosure was 50% at the highest sediment treatment, while maximum survival was 100% in some enclosures in the control and lowest sediment treatment. Additionally, the change in averaged tadpole mass after 4.5 weeks tended to decrease as fine sediment increased and was overall lower at 7 weeks. These two results are consistent with my hypothesis of negative effects of increased inorganic fine sediment deposition, although treatment was not in my top ranked models. Coastal Tailed Frog tadpoles tend to respond quickly to changes in biofilm, whether due to changes in light availability (Kiffney et al. 2004), nutrient availability (e.g. Kiffney and Richardson 2001, Mallory and Richardson 2005) or increased sediment deposition (Kiffney et al. 2004), which may explain my higher than anticipated tadpole mortality at 4.5 weeks.

It is also worth noting that the range of fine sediment experienced by tadpoles in the experiment exceeded ambient levels of fine sediment deposited in biofilm, even in the enclosures where no fine sediment was added, due to the design of the enclosures (Fig. S2). Water flow through the enclosures was limited, causing more sediment than expected to settle out in the enclosures in comparison to levels typically found in the river. It may be possible that the tadpoles in my experiment were experiencing low resource availability even in the control treatment due do the high amounts of deposited fine sediment, and therefore the effects of additional fine sediment were limited.

2.4.3 Implications

While there has been little evidence of the accumulation of sediment above RoR weirs (Ashley et al. 2006, Orr et al. 2006, Csiki and Rhoads 2014), my results add to the peer reviewed literature that fine sediment are higher the diversion reach where flows are diverted during naturally occurring periods of low flow (Baker et al. 2011, Csiki and Rhoads 2014), and suggest that tadpole densities are lower in the diversion reach. However, my results are limited to the regions directly above RoR weirs and directly below prior to any major tributary influences, and I lack data from before the weirs were installed and thus cannot directly attribute my results to the construction of the RoR weirs. Despite this, my results suggest that fine sediment deposition may be of concern in some RoR hydropower projects as two of my study rivers showed higher deposition below the weir, and that tadpole densities tend to be lower in the diversion reach in all three rivers which could not be attributed to other predictors of tadpole abundance, such as basin size. While it is unlikely that there will be higher embeddedness measures in the diversion reach below most RoR weirs which could affect the availability of refuges from predators or high-flow events, as suggested by Conners et al. (2014), my results suggest there may be subtler impacts to biofilm quality in rivers with higher deposition of inorganic fine sediment, which could affect Tailed Frog tadpole growth and survival, and in turn potentially have long-term impacts on Coastal Tailed Frog populations.

In the Pacific northwest, summer is the important period for growth of many riverine species as this is when these oligotrophic rivers are most productive. Decreased biofilm quality has been associated with increased fine sediment deposition (Graham 1990, Kiffney and Bull 2000, Gillespie 2002, Kiffney et al. 2003, Wood and Richardson 2009). For amphibians such as the Coastal Tailed Frog, which take up to 4 years to metamorphose, the effect of decreased quality of biofilm can cause delays in metamorphosis (Gillespie 2002), slower growth, and decreased survival (Wood and Richardson 2009) which can increase their vulnerability to predators. In light of growing implementation of RoR hydropower projects (Abbasi and Abbasi 2011), lower tadpole growth and survival may be of particular concern in watersheds with multiple RoR hydropower projects. This is because Coastal Tailed Frog tadpoles show more genetic variation between neighbouring streams than within a stream (Wahbe et al. 2005), therefore a reduction in the adult population size in one river has the potential to affect neighbouring streams and rivers more than might initially be predicted.

There is an increasing global demand for freshwater resources (Gleick 2010, Abbasi and Abbasi 2011) which are expected to become more limited in the near future (Gleick 2010). Small hydropower projects are rapidly becoming a more favoured form of hydroelectric power generation to meet these demands, as they are hypothesized to have a smaller ecological impact than large dams, however there have not been many studies to evaluate the ecological impacts of these types of hydropower projects. As RoR hydropower projects are meant to more closely mimic the natural flow regime and affect a smaller region than large dams, functions such as annual sediment deposition and annual discharge may not be as altered in these small rivers as in large dammed systems. Yet research focusing on annual changes in flow or sediment deposition may overlook subtler effects, as even short-term impacts can have large impacts on communities if individuals do not survive (Shaw and Richardson 2001). Thus, although RoR hydropower projects may have fewer perceived environmental impacts than large dams, it is imperative to explore the ecological effects of these projects to ensure proper protection of threatened species.

3 Conclusion

3.1 Summary

The objectives of this study were to determine if inorganic fine sediment deposition, biofilm biomass, and tadpole density was different above RoR weirs or in the diversion reaches during naturally occurring low flow periods. I also investigated whether tadpoles were negatively affected by increased fine sediment deposition. The spatial distribution of fine sediment, biofilm and tadpoles was conducted through observational surveys on three rivers with RoR hydropower projects, while a mesocosm experiment was used to test the effects of fine sediment deposition on tadpole growth and survival.

Through the observational surveys conducted, I found that inorganic fine sediment deposition and tadpole density appeared to differ in the diversion reach of the three RoR hydropower projects during the summer low flow period, while chlorophyll *a* and AFDM appeared to be more closely related to inorganic fine sediment deposition. Fine sediment tended to be higher in diversion reaches, as found elsewhere (Baker et al. 2011, Csiki and Rhoads 2014), while tadpole density was lower. This could not be explained by lower chlorophyll *a* biomass or AFDM as these had a positive relationship with fine sediment, nor by basin size alone.

Although my observational study suggested that there may be an effect of fine sediment on tadpole densities, I was unable to show this explicitly in my mesocosm experiment. My results suggest that mortality was random throughout all treatments and that initial mass was the most important predictor for tadpole growth. However, trends in my data generally follow the expected outcome of my hypothesis of lower growth and survival with increased fine sediment deposition, as average tadpole mass tended to be lower as fine sediment increased for the 4.5 week treatments, and continued to be depressed for enclosures left during the entire 7 week period.

3.2 Limitations

Our observational study was limited to three rivers with RoR hydropower projects that were all managed by the same company and were also approximately the same age. Although I was able to compare the impacts of the weirs without taking into account the length of time they have been installed, I was unable to determine whether these impacts persist over longer periods of time. Also, since I used the section of river directly above the RoR weirs as my control, I cannot directly attribute changes in fine sediment deposition directly to the installation of the weirs and not a change in stream slope or an increase in fine sediment inputs. To minimize these possibilities, I chose streams which had no or little tributary inputs within the study area and kept our study area within 1km upstream or downstream of the weir when possible. This limits my results to account for only sections directly above and directly below weirs, and may not accurately represent areas farther downstream in the diversion reach where river slope is likely to increase. Additionally, the total number of tadpoles caught during surveys was low (n = 38). This makes it difficult to statistically determine if density differs along a gradient of inorganic fine sediment deposition.

It is also worth noting that the range of fine sediment experienced by tadpoles in the experiment exceeded ambient levels of fine sediment deposited in biofilm, due to the design of the enclosures (Fig. S2). Water flow through the enclosures was limited, causing more sediment than expected to settle out in the enclosures in comparison to levels typically found in the stream. It may be possible that the tadpoles in my experiment were experiencing low resource availability even in the control treatment due to the high amounts of deposited fine sediment, and therefore the effects of additional fine sediment deposition were limited.

3.3 Implications and future research

Although studies have shown that RoR hydropower projects have minimal impacts on annual sediment fluxes in rivers (Ashley et al. 2006, Orr et al. 2006, Baker et al. 2011, Csiki and Rhoads 2014), my research suggests that there may be subtler impacts of inorganic fine sediment deposition in diversion reaches that have not been considered, such as changes in biofilm quality or composition which add to the cumulative impacts that such developments cause. The deposition of fine sediment can alter the composition of biofilm (Izagirre et al. 2009) in addition to decreasing quality as the proportion of inorganic material increases (Graham 1990). Changes to quality of primary production can lead to decreased growth and survival of grazers (Gillespie 2002, Wood and Richardson 2010), but may also cause tadpoles to change their behaviour such that they move closer to the thalweg of the river where less fine sediment deposition occurs, although this behaviour change is not supported by my data. To determine whether decreased biofilm quality could have population-level effects on Coastal Tailed Frogs, it is necessary to estimate the amount of habitat that could be affected by fine sediment deposition in the diversion reach and then model the predicted impact of depressed tadpole densities and growth or survival on the number of adults in the area. It would be possible to use the results from my experiment as a starting point for estimates in such a model.

While I only considered whether fine sediment deposition differed above or in the diversion reach of RoR hydropower projects, lower tadpole densities could be explained by other factors, such as limited downstream movement, changes to water temperature, and changes to biofilm composition. Coastal Tailed Frogs lay their eggs in headwater streams during mid-summer, which then hatch 6 weeks later (Bury et al. 2001). Newly hatched tadpoles stay in the nesting area until spring, then move downstream during spring run-off (Bury et al. 2001). Due to the creation of a headpond, albeit relatively small, this lentic area may hinder the movement of tadpoles from regions higher in the watershed if they move downstream primarily by periodic flushing during high flow events. If this is the case, although my results indicate 20 – 50% lower tadpole densities in the diversion reach, this difference may be smaller below tributary inputs as tadpoles hatched in those streams migrate into the diversion reach. While studies have shown that Coastal Tailed Frog tadpoles experience mortality at 22°C (Hossack et al. 2013), a companion study found that the study systems I used never reached levels high enough to cause mortality during summer (maximum temperature = 18°C; Murray, unpublished). Despite no direct mortality due to increased temperature, it could be possible that slightly higher temperatures could cause an increase in metabolic requirements which may be more difficult to meet in oligotrophic systems, particularly tadpoles much expend more energy to meet their nutrient requirements with low quality biofilm. Also, higher temperatures could also have interactive effects with other stressors, such has been found with parasites (Berven and Boltz 2001, Kupferberg et al. 2009) and insecticides (Broomhall 2004)for other frog species. There is currently ongoing research at Simon Fraser University to investigate whether temperature may play a role in causing lower tadpole densities. Finally, it may be possible that the altered flow regimes in the diversion reach may be altering biofilm structure such as was found in two streams in California (Furey et al. 2014). Flow regulation was linked to an increase in stalked diatoms abundance in biofilm, which are more difficult to feed upon and may be of lower nutritional quality (Furey et al. 2014). But to more clearly determine whether RoR hydropower projects affect Coastal Tailed Frog tadpole abundance, there is a Before-After-Control-Impact study currently underway in British Columbia (Malt, pers. comm.) which will be able to exclude other river attributes, such as slope or basin size, as drivers of any potential differences in tadpole abundance in the diversion reach and above RoR weirs.

Current environmental flows implemented by RoR hydropower projects may need to be revised to ensure the ecological integrity of the rivers, as we learn more about the impacts of RoR hydropower projects on riverine ecological processes. Although I did not test river gradient explicitly, I did find that inorganic fine sediment deposition was much higher in the low gradient river, as has been found in other sediment studies on RoR hydropower projects (Baker et al. 2011). While my experimental results did not unequivocally show that increased fine sediment deposition leads to decreased growth and survival, they also do not completely refute that fine sediment may be a concern for Coastal Tailed Frog tadpoles, particularly in low gradient sections of rivers where deposition was highest. Further studies to determine whether the levels of fine sediment I found in my study systems affects the nutritional quality of biofilm would be able to determine whether levels of fine sediment deposition in low gradient rivers may be detrimental to grazers. If so, it may be necessary to re-evaluate the environmental flow requirements for low-gradient rivers to better manage for inorganic fine sediment deposition in these ecosystems.

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Appendix

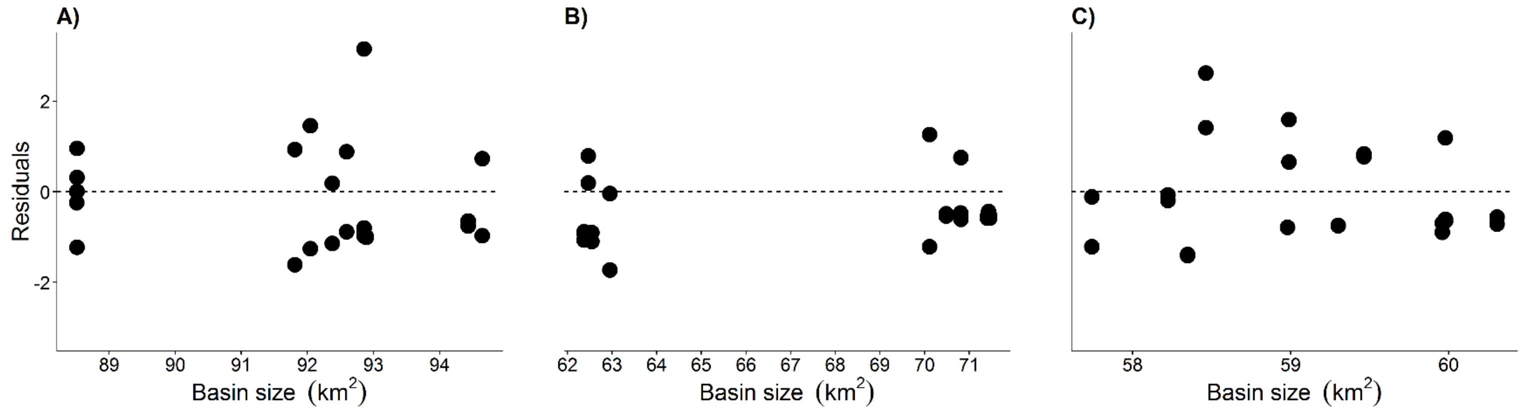

Figure S1. Plot of residuals for generalized, linear mixed model with tadpole density (individuals/m2) by basin size for the three rivers A) Fire Creek, B) Stokke Creek, and C) Tipella Creek. The horizontal line indicates a residual value of zero.

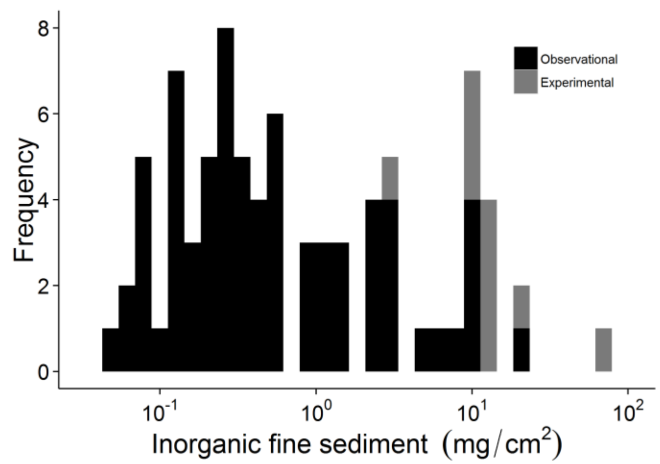

Figure S2. Frequency of inorganic fine sediment measurements from observational samples in three rivers with RoR hydropower projects (black) and in the experiment (control enclosures only; grey).

Table S1. Top-ranked models that encompass 0.95 AICc (Akaike's Information Criterion for small sample sizes) weight. Responses are inorganic fine sediment (mg/cm^2), chlorophyll *a* (µg/cm^2), ash-free dry mass (AFDM; mg/cm^2), and tadpole density (individuals/m^2). CC = canopy cover (%), Ch = chlorophyll *a* (µg/cm^2), F = inorganic fine sediment (mg/cm^2), L = above weir or in diversion reach, P = stream position (edge or closer to thalweg), S = slope of surveyed quadrat, T = temperature (˚C), v = water velocity (m/s). Fixed variables and co-variates were standardized to a mean of 0 and a standard deviation of 0.5. df = degrees of freedom, LogLik = log likelihood.

Response	Rank	Model	df	LogLik	AICc	Δ	Weight
ln (Inorganic fine sediment)	1	L + P + v	6	-110.61	234.52	0.00	0.41
	2	L + P	5	-112.08	235.07	0.55	0.31
	3	L + P + v + S	7	-110.83	237.42	2.90	0.10
	4	L + P + S	6	-112.21	237.70	3.18	0.08
ln (Chlorophyll *a*)	1	ln (F) + CC	5	-83.17	177.25	0.00	0.44
	2	ln (F)	4	-85.30	179.19	1.94	0.17
	3	ln (F) + CC + P	6	-83.46	180.21	2.96	0.10
	4	ln (F) + CC + ln (v)	6	-83.81	180.91	3.66	0.07
	5	ln (F) + L	6	-83.88	181.06	3.81	0.06
	6	ln (F) + ln (v)	5	-85.51	181.93	4.68	0.04
	7	ln (F) + P	5	-85.74	182.39	5.15	0.03
	8	ln (F) + L	5	-86.03	182.97	5.72	0.02
ln (AFDM) (all data)	1	ln (F)	4	-101.00	210.59	0.00	0.20
	2	ln (F) + P	5	-99.93	210.77	0.18	0.18
	3	ln (F) + ln (Ch)	5	-100.86	212.62	2.03	0.07
	4	ln (F) + L	5	-101.03	212.98	2.38	0.06
	5	ln (F) + ln (v)	5	-101.08	213.06	2.47	0.06
	6	ln (F) + P + ln (Ch)	6	-99.89	213.07	2.48	0.06
	7	ln (F) + P + L	6	-100.18	213.65	3.05	0.04
	8	ln (F) + P + ln (v)	6	-100.18	213.65	3.06	0.04
	9	ln (F) + CC	5	-101.39	213.68	3.09	0.04
	10	ln (F) + CC + P	6	-100.34	213.98	3.39	0.04
	11	ln (F) + ln (Ch) + ln (v)	6	-100.84	214.97	4.38	0.02
	12	ln (F) + L + ln (Ch)	6	-100.92	215.13	4.54	0.02
	13	ln (F) + L + ln (v)	6	-101.07	215.43	4.84	0.02
	14	ln (F) + CC + ln (Ch)	6	-101.16	215.62	5.03	0.02
	15	ln (F) + P + ln (Ch) + ln (v)	7	-100.07	215.89	5.29	0.01
	16	ln (F) + CC + L	6	-101.33	215.95	5.36	0.01
	17	ln (F) + P + L + ln (Ch)	7	-100.14	216.03	5.44	0.01
	18	ln (F) + CC + ln (v)	6	-101.42	216.14	5.55	0.01
	19	ln (F) + CC + P + ln (Ch)	7	-100.24	216.24	5.64	0.01
	20	ln (F) + P + L + ln (v)	7	-100.39	216.53	5.93	0.01
ln (AFDM) (outliers removed)	1	ln (F) + ln (Ch)	5	-64.13	139.21	0.00	0.61
	2	ln (F)+ ln (Ch) + CC	6	-64.85	143.06	3.85	0.09
	3	ln (F)+ ln (Ch) + L	6	-64.91	143.18	3.96	0.08
	4	ln (F) + ln (Ch) + ln (v)	6	-65.06	143.47	4.26	0.07
	5	ln (F) + ln (Ch) + P	6	-65.06	143.48	4.26	0.07
	6	ln (F) + ln (Ch) + CC + L	7	-65.68	147.20	7.99	0.01

ln (AFDM) (outliers removed)	7	ln (F) + ln (Ch) + CC + ln (v)	7	-65.75	147.34	8.12	0.01
Tadpole density	1	L + S	4	-66.24	141.08	0.00	0.09
	2	L	3	-67.60	141.56	0.47	0.07
	3	L + CC + S	5	-65.74	142.39	1.30	0.05
	4	L + CC	4	-67.02	142.63	1.55	0.04
	5	L + v + S	5	-65.94	142.80	1.71	0.04
	6	L + ln (F) + S	5	-66.16	143.23	2.14	0.03
	7	L + v	4	-67.37	143.33	2.25	0.03
	8	L + S + T	5	-66.24	143.40	2.31	0.03
	9	L + P + S	5	-66.24	143.40	2.31	0.03
	10	L + ln (F)	4	-67.46	143.51	2.43	0.03
	11	L + T	4	-67.53	143.65	2.57	0.03
	12	P	4	-67.60	143.80	2.72	0.02
	13	L + CC + v + S	6	-65.37	144.03	2.95	0.02
	14	L + CC + ln (F)	5	-66.65	144.20	3.12	0.02
	15	L + CC + v	5	-66.65	144.21	3.13	0.02
	16	L + CC + ln (F) + S	6	-65.55	144.39	3.30	0.02
	17	L + v + ln (F) + S	6	-65.60	144.50	3.41	0.02
	18	L + CC + P + S	6	-65.73	144.75	3.66	0.02
	19	L + CC + S + T	6	-65.74	144.77	3.68	0.01
	20	L + v + ln (F)	5	-66.96	144.83	3.75	0.01
	21	L + CC + v + ln (F)	6	-65.77	144.84	3.76	0.01
	22	L + CC + T	5	-66.99	144.88	3.80	0.01
	23	L + CC + P	5	-67.01	144.92	3.84	0.01
	24	L + P + v + S	6	-65.88	145.05	3.96	0.01
	25	L + v + S + T	6	-65.94	145.18	4.09	0.01
	26	L + CC + v + ln (F) + S	7	-64.76	145.27	4.19	0.01
	27	S	3	-69.51	145.38	4.29	0.01
	28	L + v + T	5	-67.27	145.44	4.36	0.01
	29	L + P + v	5	-67.31	145.53	4.45	0.01
	30	L + P + ln (F) + S	6	-66.14	145.57	4.48	0.01
	31	L + ln (F) + S + T	6	-66.16	145.61	4.52	0.01
	32	L + ln (F) + T	5	-67.36	145.63	4.54	0.01
	33	L + P + ln (F)	5	-67.41	145.73	4.65	0.01
	34	L + P + S + T	6	-66.24	145.78	4.70	0.01
	35	L + P + T	5	-67.53	145.96	4.88	0.01
	36	L + CC + P + ln (F)	6	-66.50	146.29	5.21	0.01
	37	L + CC + P + v + S	7	-65.35	146.46	5.37	0.01
	38	L + CC + v + S + T	7	-65.37	146.48	5.40	0.01
	39	L + CC + v + T	6	-66.60	146.49	5.41	0.01
	40	L + CC + ln (F) + T	6	-66.61	146.50	5.42	0.01
	41	v + S	4	-68.96	146.51	5.43	0.01
	42	L + CC + P + v	6	-66.63	146.55	5.46	0.01
	43	L + CC + P + ln (F) + S	7	-65.46	146.66	5.58	0.01
	44	L + CC + ln (F) + S + T	7	-65.55	146.85	5.76	0.01
	45	CC + S	4	-69.14	146.88	5.80	0.01
	46	L + v + ln (F) + T	6	-66.80	146.88	5.80	0.01
	47	L + v + ln (F) + S + T	7	-65.60	146.94	5.86	0.01
	48	L + P + v + ln (F) + S	7	-65.60	146.95	5.86	0.01

Tadpole density	49	S + T	4	-69.21	147.02	5.94	0.00
	50	L + CC + v + ln (F) + T	7	-65.66	147.08	6.00	0.00
	51	L + CC + P + S + T	7	-65.73	147.21	6.12	0.00
	52	L + P + v + ln (F)	6	-66.96	147.21	6.13	0.00
	53	L + CC + P + v + ln (F)	7	-65.75	147.25	6.16	0.00
	54	L + CC + P + T	6	-66.98	147.25	6.16	0.00
	55	Ln (F) + S	4	-69.36	147.32	6.23	0.00
	56	L + P + v + S + T	7	-65.88	147.50	6.42	0.00
	57	P + S	4	-69.51	147.62	6.54	0.00
	58	L + P + v + T	6	-67.20	147.70	6.62	0.00
	59	L + CC + v + ln (F) + S + T	8	-64.74	147.76	6.67	0.00
	60	L + CC + P + v + ln (F) + S	8	-64.75	147.79	6.70	0.00
	61	L + P + ln (F) + T	6	-67.31	147.91	6.82	0.00
	62	CC + v + S	5	-68.51	147.93	6.84	0.00
	63	L + P + ln (F) + S + T	7	-66.13	148.02	6.93	0.00
	64	v + S + T	5	-68.65	148.21	7.12	0.00

Table S2. Top-ranked models that encompass 0.95 AICc (Akaike's Information Criterion for small sample sizes) weight. Responses are change in averaged tadpole mass (g) and tadpole survival. M = initial mass (g), t = length of experiment (4.5 or 7 weeks), SA = treatment (control, low, high), df = degrees of freedom, LogLik = log likelihood.

Response	Rank	Model	df	LogLik	AICc	ΔAICc	Weight
Survival	1	Intercept	2	-50.67	105.8	0.00	0.38
	2	M	3	-49.725	106.4	0.59	0.29
	3	t	3	-50.589	108.1	2.31	0.12
	4	M + t	4	-49.713	109.0	3.24	0.08
	5	SA	4	-49.854	109.3	3.52	0.07
Change in mass	1	M + t	4	30.035	-46.5	0.00	0.64
	2	M	5	27.720	-45.2	1.32	0.33