

ECOLOGICAL IMPLICATIONS OF FLOW-MEDIATED SCOUR EVENTS FOR
SOCKEYE SALMON ALEVINS (*ONCORHYNCHUS NERKA*)

by

STEPHANIE ROBIN INGRAM

B.Sc., Vancouver Island University, 2008

A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF
THE REQUIREMENTS FOR THE DEGREE OF

MASTER OF SCIENCE

in

The Faculty of Graduate Studies
(Zoology)

THE UNIVERSITY OF BRITISH COLUMBIA
(Vancouver)
December 2011

© Stephanie Robin Ingram 2011

Abstract

Pacific salmon (*Oncorhynchus* spp.) life cycles involve completion of several developmental stages including the alevin stage. As alevins, sockeye salmon are found within freshwater gravel redds where they utilise yolk sacs for nutrition, growth and development. Flow mediated scour events pose a common threat of destruction to both redds and fragile alevins during a several month period of winter incubation. However, to date, there is very little research on the impacts of early forced emergence of alevins. Using sockeye salmon (*Oncorhynchus nerka*) as a model, simulated elevated discharge event (SEDE) experiments were conducted to examine the relationship between sockeye alevin development, SEDE exposure and alevin survival. Following five weeks of SEDE experiments, survival rates were found to be significantly correlated to both alevin developmental stage and length of elevated discharge exposure. SEDE experiments were followed by experiments designed to investigate the ecological competence level of alevins following forced early dislodgement. Repeated tests during a five week interval immediately following egg hatch indicated that alevins subjected to SEDE exposure took longer than unexposed alevins to rebury in gravel. Alevins exposed to SEDEs took longer to rebury as they developed, but increased their overall ability to rebury. Neither SEDE exposed or unexposed alevins exhibited abilities to initiate exogenous feeding given forced, early emergence. Survival rates of sockeye salmon alevins both during and after SEDE testing increased significantly with advances of developmental stage. Older, larger alevins also exhibited improved performance in responding to ecological challenges presented in laboratory experiments. Knowledge gained from this research has practical implications for water managers and suggests that: (a) the

probability of scour induced mortality of both unhatched eggs and alevins is likely similar up to at least 3 weeks after egg hatch, (b) survival rates and ecological competence of alevins has improved significantly by four weeks following egg hatch, and (c) survival of alevins forced into an epibenthic or water column environment as late as one week before volitional emergence is unlikely to differ greatly from that of unforced emergent fry.

Preface

Stephanie Ingram held primary responsibility for the experimental design, fieldwork, data analysis, and writing of the manuscript inherent to the present thesis. The following co-authors, will be named in the manuscript version of this thesis: Dr. Kim Hyatt and Dr. John Richardson, who provided important technical expertise and manuscript reviews

Table of contents

Abstract.....	ii
Preface	iv
Table of contents	v
List of figures.....	vi
Acknowledgements	vii
Dedication.....	viii
1 Introduction	1
1.1 Flow and stream geomorphology	2
1.2 Biological responses to floods	4
1.3 Salmonids	6
1.4 Environmental impacts on developing sockeye salmon.....	10
1.5 Sockeye salmon in the Okanagan River, BC	12
2 Methods and materials	16
2.1 Simulated elevated discharge experiment	18
2.1.1 General methods.....	18
2.1.2 Trials.....	8
2.2 Bury experiment	20
2.3 Statistical analysis.....	21
2.4 Supplementary experiments.....	23
3 Results	24
3.1 Simulated elevated discharge experiment	24
3.2 Bury experiment	27
4 Discussion	31
4.1 Simulated elevated discharge experiment	31
4.2 Ability to rebury after dislodgement.....	33
4.3 Remaining questions.....	35
4.4 Implications and management	36
References	36
Appendix A.....	45
A.1 Predator avoidance experiment.....	45
A.2 Exogenous feeding experiment.....	46

List of figures

- Figure 2.1 Features of the study area and relative location within British Columbia (inset). Laboratory location abbreviated: Pacific Biological Station (PBS). (Adapted from: http://en.wikipedia.org/wiki/Okanogan_River) Scale is approximat 16
- Figure 2.2 Schematic of the experimental apparatus used to create SEDEs..... 20
- Figure 3.1 SEDE Experiment. Cumulative mortality rates of sockeye salmon alevins over 60-minute simulated SEDE trials conducted every week (n = 3 per week) until volitional emergence at 11 weeks. Each trial contained 10 alevin sockeye salmon. Symbols indicate means with 95% CI..... 25
- Figure 3.2 Regression for the cumulative mortality rates of sockeye salmon alevins during 60-minute SEDE trials conducted every week (n = 3 per week) until volatile emergence at 11 weeks after hatch. Each trial contained 10 alevin sockeye salmon. Symbols indicate means with 95% CI..... 26
- Figure 3.3 The fork length (A), mass (B) and yolk sac mass (C) of all tested alevins were measured to the nearest 0.1 mm and 0.01 g. Mass was recorded as total wet mass of alevin. Symbols indicate means with 95% CI, n = 42, 28, 29, 26, 19 for each week in sequential order 27
- Figure 3.4 The time in which individual alevin sockeye salmon completely buried within a simulated gravel bed. Each trial contained 10 alevin (n = 3 per week). Alevins were subjected to a 30 minute SEDE prior to placement in an aquarium containing a 5 cm deep gravel bed. Controls were carried out where alevins were not previously subjected to an SEDE event. Symbols indicate means with 95% CI 28
- Figure 3.5 Comparison of cumulative mortality rates of sockeye salmon alevins exposed to a 30-minute SEDE versus unexposed control groups of alevins. For the purpose of this experiment mortality is classified as either failure to completely conceal in the gravel after 60 minutes or dead from exposure to the SEDE. Individual alevins were given 60 minutes to completely bury within a 5 cm deep simulated gravel bed before being classified as deceased. Each trial contained 10 alevins (n = 3 per week). Symbols indicate means with 95% CI..... 29
- Figure A.1 Comparison of exogenous feeding responses exhibited by sockeye alevins exposed to an SEDE versus those of an unexposed control group. The experiment commenced 7 weeks after hatch and ceased upon volitional emergence at 11 weeks (n = 3 per week). Controls were carried out where alevins were not previously subjected to an SEDE. Bars represent 95% CI.. 46

Acknowledgements

I would sincerely like to thank both of my co-supervisors Dr. John Richardson of UBC and Dr. Kim Hyatt of DFO for both of their continuous direction and support. I would also like to thank Dr. Scott Hinch for his expertise. I would also like to thank Paul Rankin and Rick Ferguson for lab assistance. A big thank you to everyone at the Okanagan Nation Alliance Fisheries Department for all of their help collecting the broodstock, specifically Howie Wright and Keri Long (Animal transfer permit number: 11582 for Fisheries and Ocean Canada, Fisheries and Oceans Canada's Animal Care Protocol number: 09-002). Thank you to Carol Cooper and Adrienne Horbas for assistance with stomach analysis. A great big thanks to Tony Kozak for all of assistance with the statistical analysis for this project. I am indebted to Bill Damon and his many volunteered hours in incubating my alevins. Thanks to Ben Chalmers for moral support as well as his help with general editing. This project was funded by the Douglas County Public Utility District through the direction of Fisheries and Ocean Canada.

Dedication

To my husband, for everything, always.

“...to undreamed shores...”

1 Introduction

The growing demands on freshwater resources create an urgent need to improve the scientific foundation for water management to meet the human and about and natural system needs. Freshwater quality and quantity impacts both the natural environment and human needs, for example drinking water, irrigation, aquaculture, recreation, flood control and habitat for aquatic life. Currently at least 90% of the total water discharge from US rivers is strongly affected by channel fragmentation from dams, reservoirs, and irrigation (Jackson et al. 2001). Human impacts coupled with climate change are affecting the quality of the world's freshwater, and globally 20% of modern freshwater fish species are threatened or extinct (Moyle and Leidy 1992; Dudgeon et al. 2006; Vörösmarty et al. 2010). The management and conservation of species in flowing water environments is both necessary and problematic. Thus, natural resource managers face a major challenge of maintaining water quantity and quality to meet the competitive requirements of both human and biological systems.

In the British Columbia interior, the Okanagan Nation Alliance Fisheries Department (ONAFD) and Fisheries and Oceans Canada (DFO) are currently working to restore the highly engineered Okanagan River to a more normative, natural system state. This involves several projects, one of which is focused on restoring Okanagan sockeye salmon to their historic distribution and abundance levels (Hyatt and Rankin 1999). One potential problem with this recovery program is the threat of lost or depleted year classes due to potential flood and scour events that may occur during the alevin incubation stage. These flood and scour events generally occur in late spring to early summer in rivers of the British Columbian interior where the natural hydrograph is primarily snowmelt

driven (Farley 1979). Although the Okanagan River generally follows this same seasonal pattern, the frequency, magnitude and precise timing of flood-and-scour events are also influenced by water management decisions associated with the operation of flood control and irrigation works on the Okanagan River and Lake System (Alexander et al. 2008).

1.1 Flow and stream geomorphology

The structure of a fluvial system depends on the various natural influences present within a geographical area. The climate variability of a region affects the hydrology of the surrounding streams while the chemistry and sediment sources are affected by parent geology, topography and other processes. This, coupled with the anthropogenic changes occurring within a given watershed, help determine the nature of a stream's morphology (Valett et al. 1993; Poole 2010). These distinctions in morphology are partially due to the differences in discharge, channel slope and dominant bed materials (Rosgen 1994; Poole 2010). Streams with fluctuating flow regimes often transport a high percent of the total sediment load during infrequent but elevated water levels (Wolman and Miller 1960; Ma et al. 2010). Gravel-bed streams are organized such that transport of the median bed sediment size occurs at near-threshold conditions during bankfull discharge (Jerolmack and Brzinski 2010).

Scour is a natural phenomenon caused by the erosive action of a flowing stream on alluvial beds. As the tractive force of water acts on the bed, the build up of power eventually overwhelms the frictional forces of bed materials and transportation is initiated (Wang 1999). There are various types of flood and scour events that occur within a stream system. Tregnaghi et al. (2010) found that the scouring process of stream

beds occur either during the rising limb of a short flood or throughout floods with longer recession times. These types of scour events are referred to as local scour.

Large-scale scour events are often a result of a stream discharge having both an unsaturated sediment load and a strong hydraulic force. They can occur within long reaches of a channel that are unimpeded by structures. A section of stream bed may be subject to continuous scour when the sediment transport capacity (defined by Wang and Pullar 2005 as corresponding to the rate of energy dissipation against the bed and banks of a stream per unit downstream length and the width-integrated bed shear stress across section along a stream profile) is much higher than the sediment load it carries (Wang 1999). A long section of the stream bed can be scoured hundreds of meters down a reach during a flood event, although, the reduction in the sediment-carrying capacity of the stream near the end of a flood results in the discharge depositing sediment back into the bed further downstream (Wang 1999). The outcome of the flood, therefore, produces a partial or complete recovery of the geological structure of the bed (Wang 1999).

Currently hydrologists use a standardized approach to predict sediment transport in stream channels. They expect that there is an unrestricted supply of material within the channel, and that the movement of the material is fundamentally correlated to the pressure imposed by the tractive force of water. This force versus volume must first pass a certain threshold to begin entrainment of any material (Hassan et al. 2005). Beyond bankfull, additional waters do not increase the velocity or tractive force within the channel, as excess water spreads out over the floodplain and slows (Matthews 1986).

Watercourses and their floodplains have been used and modified for hundreds of years around the world. Humans have altered fluvial systems to support a multitude of

needs, such as water supply, irrigation, flood protection, transportation, wastewater discharge and hydropower generation. The effects of these uses have inadvertently caused pollution, eutrophication, and loss of both aquatic and riparian biodiversity as well as flooding problems (Jähnig et al. 2008). The hydromorphological degradation of streams, caused by channelization, dams and the separation of streams from their floodplains represents one of the greatest impacts on fluvial systems (Jähnig et al. 2008). In a study conducted by Jähnig et al. (2008) it was found that multiple-channel systems had higher diversity of hydromorphological features, current velocity, depth, substrate and aquatic habitats versus anthropogenically produced single channel reaches.

Flood extremes, particularly spates, are common disturbances in stream ecosystems. During such events, shear forces and abrasion by transported bed sediments severely damage or eliminate organisms living at the channel surface and in the top layers of sediments (Uehlinger and Naegeli 1998). When the flows reach $> 30 \text{ m}^3/\text{s}$, in streams such as the Okanagan River, the scour potential is threatening to biological systems within the gravel bed (Alexander et al. 2008). The geology of a stream is capable of returning to a state of balance by the end of a scour event (Wang 1999), however, the ecology of a stream may take longer to recover. The modifications in the configuration of a streambed impact all organisms that rely on the fluvial ecosystem.

1.2 Biological responses to floods

Ecological disturbances occur when a temporary change in the average environmental conditions causes a pronounced change in the local ecosystem. The highly variable nature of stream currents can greatly affect the biological make-up of a streambed, specifically the benthic communities (Bain et al. 1988; Death 2010).

Disturbances can arise from a broad array of both physical and biological effects varying in size, frequency and intensity (Michener and Haeuber 1998; Jurajda et al. 2006). Changes in discharge volume and velocity may impact the stability of aquatic habitats of local fauna. For example, macroinvertebrates are known to be periodically decimated by various natural catastrophes, such as scour-inducing floods (Gray and Fisher 1981; Sponseller et al. 2010). Flood events large enough to produce scour disturb the local substrates and can eliminate 80-100% of the benthic fauna (Gray and Fisher 1981).

The impacts of floods on native species can vary within a given habitat. Power et al. (2008) found flood scour to have either a positive or negative effect on algae blooms; the effect being dependent on the predator-specific vulnerabilities of the primary consumers of the area during a given year. That said, one of the most consistent characteristics of benthic communities is that although their density and diversity is reduced by disturbances they have a tendency to recover rapidly (Death 2010). Community dynamics in other habitats are dominated by population growth through reproduction, however, community dynamics in streams are dominated by immigration and emigration through drift, when dealing with short-term disturbances (Williams and Hynes 1976; Death 2010).

Macroinvertebrates are not the only organisms to be affected by erosive floods, fish populations (Collins et al. 1981; Tew et al. 2002) and/or community structures may be altered as well (Harrell 1978). Redistribution of some fish occurs during large flood events, however, others are able to find refuges within deep pools, stable substrates, side channels or other permanent physical features. These refuges can act as within-stream centers of dispersal (Matthews 1986) that allow fish to repopulate a disturbed reach of a

stream. Redistribution and recovery of the ecosystem can occur after large-scale scour events occur, but if the scour event was to occur during a sensitive period of an organisms' development it may be excessively damaging to the population.

Floods, even small in nature, that occur during the reproductive season (which varies between species) can have greater consequences for fish communities than floods of a larger scale that occur at other times of the year (John 1964). Alterations to fish populations occur, however, adult fish often survive floods and are able to remain within a given stream reach (John 1964; Young et al. 2010). Individual fish that survive floods, often the adult and larger juvenile fish, provide the population's capacity to recolonise the watershed following a disturbance (John 1964). Pacific salmon are a group of fish for which several key life history events (adult migration, spawning, egg incubation, hatching, alevin development, fry emergence and migration to rearing habitats) are generally completed within the highly variable environments provided by streams and rivers of the north Pacific Rim.

1.3 Salmonids

The five species of Pacific salmon found in North America (*Oncorhynchus* spp.) exhibit an incredibly diversity of life history strategies (Quinn et al. 2009), and range throughout the northern Pacific Ocean from Japan to Alaska and down to California (Groot and Margolis 1991). Most populations are anadromous, i.e., spawn in freshwater but rear in oceanic waters, and semelparous, i.e., each individual only spawns once in a lifetime (Groot and Margolis 1991).

The lifecycle of salmonids is divided into five stages (egg, alevin, fry, smolt and adult) and depending on the species they can reach reproductive maturity within three to five years (Groot and Margolis 1991). Mature salmonids generally spawn between midsummer and late autumn, but there are variations among species and stocks as local climatic conditions, such as temperature, differ (Groot and Margolis 1991). Eggs are laid and fertilized within gravel nests referred to as redds. Redds are depressions in the gravel bed created by an adult with the use of the body and fins (Gottesfeld et al. 2004). Female salmonids tend to choose redd locations based on their ability to successfully remove fine sediment from the area and allow sufficient intergravel flow for oxygenation of the eggs and alevins (Lisle 1989). This also allows emerging fry to escape from the redd (Lisle 1989). After hatching, salmonids enter the alevin stage. Once an alevin's yolk sac has been depleted it is then called a fry and is ready to emerge into the water column (Groot and Margolis 1991).

Salmonid spawning habitat preference varies between species. The variation in nesting sites is related to the geologic, topographic and climatic conditions of the region (Groot and Margolis 1991). Most salmonid redds require water flows that maintain a relatively consistent oxygen supply and cool temperatures, but beyond these elements suitable spawning sites are highly variable within and among populations of the five species (Groot and Margolis 1991). For example, pink salmon (*Oncorhynchus gorbuscha*) typically spawn in riffles with clean gravel, or along the borders between pools and riffles of streams, whereas, sockeye (*Oncorhynchus nerka*) commonly spawn near spring-fed ponds, side channels, riffles, or next to shoal beach areas along lake shores (Groot and Margolis 1991).

The egg incubation stage typically lasts four months, but is highly dependent on the mean temperature during this time (Velsen 1980). The rate of development of eggs is a direct function of the temperature regime within the gravel, and because environmental temperatures fluctuate in both time and space, the result is varying times to first hatch between and within stocks (Velsen 1980). Egg development requires a certain number of accumulated growing degree-days (GDDs) for hatching to commence. GDDs are defined as the days spent when growth and development are proportional to the time spent at a temperature and assume metabolic rate is a linear function of temperature (Neuheimer and Taggart 2007). Because lower temperatures result in eggs requiring a decreased number of GDDs to hatch, there is a curvilinear relationship between incubation temperature and the rate of embryonic development (Brannon 1987). This adaptation helps dampen the effect of yearly variation in temperatures and therefore works to slightly narrow the range in emergence timing (Groot and Margolis 1991).

The rate of development of the alevin stage is similarly directly linked to temperature and therefore emergence is dependent on temperature experiences. The alevin stage lasts for approximately two months for coho (*Oncorhynchus kisutch*), chum (*Oncorhynchus keta*), pink (*Oncorhynchus gorbuscha*) and sockeye (*Oncorhynchus nerka*) salmon and as little as 2-3 weeks for chinook (*Oncorhynchus tshawytscha*) salmon (Groot and Margolis 1991). During the alevin stage, a large yolk sac is used as their sole nutrient source, therefore their energy supply is a fixed quantity (Bams 1969). Due to the lack of an external food supply, alevins that undergo a higher than normal metabolic demand will expend energy otherwise intended for growth (Bams 1969; Ojanguren et al. 1999). Excessive movement during the alevin stage results in elevated metabolic rates and may cause smaller than average fry at the emergence stage (Ojanguren et al. 1999).

Salmonid alevins have been described as photonegative, positively geotactic and thigmokinetic (Noakes 1978). It is these characteristics that keep alevins within the gravel substrate, however, they are still capable of significant sensory and motor responses (Mason 1976). At the time of emergence fry are still negatively phototactic, therefore, emergence typically occurs during the night (Groot and Margolis 1991). Shortly after emergence a shift occurs in the photobehaviour of fry and they become positively phototactic (Mason 1976). It is at this point that fry begin to exhibit feeding behaviour.

Many studies have been conducted to investigate the seasonal timing of fry emergence and the commencement of first feeding. A large part of fry survival is dependent on their successful feeding ability; the most prominent cause of mortality is the starvation of fry (Einum & Fleming 2000). It has been speculated that it may be advantageous for fry to initiate feeding as early as possible during ontogenetic development, as this may enhance early growth and increase the chance of survival (Skoglund and Barlaup 2006). As the transition to exogenous feeding has been found to be gradual rather than a sharp onset, the timing of emergence and prey availability may be crucial in the survival of a juvenile year class (Skoglund and Barlaup 2006). Chironomid larvae and baetid nymphs are known to be the most important food sources for newly emergent salmonid fry, such as brown trout, and their availability is necessary during those first few weeks of emergence (Skoglund and Barlaup 2006; Sánchez-Hernández et al. 2011). Sockeye fry are known to commonly feed on zooplankton such as freshwater shrimp Mysidae (Hyatt et al. 2004).

1.4 Environmental impacts on developing sockeye salmon

Juvenile sockeye salmon are susceptible to many dangers throughout the wintering months of February to April during the alevin stage of their lifecycle (Groot and Margolis 1991). The fragile state of their yolk sac decreases their mobility and increases their susceptibility to risks external to the redd environment as evidenced by the behavioural traits noted above (Noakes 1978) that discourage premature emergence. Consequently, it is generally believed that premature emergence from spawning beds at the alevin stage is likely to be associated with extremely high vulnerability and mortalities associated with threats posed by factors such as turbulent water flow and predators in the above-gravel environment.

The physical environment encountered by sockeye alevin can vary, and is not always representative of historical conditions. The success of a year class is highly dependent on the suitability of the environmental conditions for the given year. Elevated water temperatures, droughts, or floods can be devastating to developing salmon eggs, embryos and alevins (Brett 1971; Lisle and Lewis 1992; Lisle 1989). Typically, a spawning temperature range between 5.6°C – 12.8°C is suitable for salmon, although some populations are clearly adapted to specific environments exhibiting temperatures outside of this range (Brannon et al. 2004).

The physiological responses of salmon are related to the rise and fall of their environmental temperature (Brett 1971). As salmon exhibit life history adaptations that synchronize events with the temperature regime of their environment, the timing of extreme changes to the physical environment is almost more important than the changes themselves (Brannon 1987). Developing salmon may become more vulnerable to

increases in mortality rates when either the upper or lower temperature limits are crossed, (Gunnes 1979). Temperature is not the only environmental factor that can affect alevins; large changes in water currents may also be detrimental to alevin survival.

Elevated discharges can have a devastating effect on the survival rate of eggs and alevin sockeye salmon (*Oncorhynchus nerka*), located within the gravel beds (Hvidsten 1985). High flows exerting sufficient tractive forces are capable of disrupting gravel beds and creating scouring events deep enough to disrupt redds and force premature emergence of alevins. Scour-induced movement of alevins from their protective gravel environment and into the water column is believed to subject alevins to hazards such as: damaging water velocities, exposure to predators, early depletion of yolk sac through excess physical exertion as well as disorientation leading to an inability to return to intragravel positions after water currents subside.

Because *Oncorhynchus nerka* alevins receive 100% of their macronutrients from their yolk sacs they can remain motionless within the gravel bed (Groot and Margolis 1991). Forced emergence of alevins through a large-scale scour event may result energy intended for growth being reallocated to movement. The dramatic change from alevins remaining relatively motionless to excessive movement could cause elevated energy expenditure and leave less energy available for growth, resulting in an undersized/underdeveloped fry (Fast and Stober 1984). Smaller than average fry appear to be susceptible to higher than average mortality rates which may reduce an entire year class (Good et al. 2001). Conversely alevins, by nature, are not suited for long durations of swimming; they are still developing the fins necessary for full mobility. Their swimming abilities are also hindered by the occurrence of a large yolk (Vernier 1969).

Their less than adequate mobility can cause alevins to be extremely susceptible to predation if removed from gravel beds (Vøllestad et al. 2004). Both premature depletion of the yolk sac and carrying of a large yolk sac are clearly adverse to the survival by an alevin within the water column.

1.5 Sockeye salmon in the Okanagan River, BC

There are currently only three remaining populations of sockeye salmon (*Oncorhynchus nerka*) in the Columbia River Basin. The Okanagan River sockeye population is one of those remaining stocks (Hyatt and Rankin 1999, Lawrence 2003). Chinook, coho, chum and steelhead were also indigenous salmon species in the Okanagan Basin, but today they are either locally extinct or found in very low numbers due to the construction of dams, channelization, urban encroachment, water management practices and impacts of invasive species (Glenfir Resources 2006).

The upstream spawning migration limit of sockeye is controlled by the operation of McIntyre Dam, located downstream of Vaseux lake, near Oliver, BC (Hyatt et al. 2003). The majority of the spawning occurs within a 7 km stretch of the Okanagan River (Hyatt et al. 2003). This portion of the river is still in its natural state while the remaining portions of the Okanagan River were channelized and dammed for flood control measures in the mid 1950s (Hourston et al. 1954). Once fry emerge from the gravel, they spend one year of their life rearing in Osoyoos Lake, before beginning their migration to the Pacific Ocean (Hyatt et al. 2003). During their migration to the ocean, an unknown proportion of juvenile sockeye salmon are killed while migrating through hydroelectric dams along the Columbia River (Hyatt et al. 2003).

Due to the snowmelt dominated nature of the Okanagan River system, 90% of the annual inflows occur during a spring freshet between the months of April and June (Hyatt and Stockwell 2010). The rest of the year sees very little inflow. Because there are drastic differences in inflow between seasons, a complex system of water regulation structures and procedures are used to satisfy flood control, irrigation and fisheries management objectives. Water regulation occurs through the use of multiple small dams, water removal and channelization of the river (Glenfir Resources 2006). The channelization work that has occurred along the Okanagan River has caused water to move through the system rapidly rather than being retained on the floodplain (Hyatt and Stockwell 2010). This would normally result in higher freshet flows and lower minimum flows but retention of water in Okanagan Lake helps to offset these impacts by storing freshet flows and releasing water during low flow periods (Glenfir Resources 2006). The Okanagan Lake can store up to 420 million cubic meters of water representing less than half of spring discharge in an above average water year (Glenfir Resources 2006). Moreover, during the spring freshet the amount of water entering the system far exceeds the amount that can be released through the dams (Hyatt and Stockwell 2010). Consequently, in order to avoid the potential for flood-induced property damage, water must be released, in all but drought years, prior to the freshet, during the February to late April interval prior to sockeye alevin emergence as free-swimming fry. Given high levels of uncertainty and an inability to reliably forecast total annual water yields associated with late season accumulations of snowpack, fish-and-water managers are faced with rapidly changing seasonal conditions and conflicting decisions that determine the balance between managing daily to weekly water storage and release to avoid flood-

induced damage to either property or alternately fisheries values (Hyatt and Stockwell 2010).

To elaborate, annual production variations exhibited by juvenile Okanagan River sockeye salmon appear to be influenced considerably by water regulation decisions at a series of low-head dams built and operated to meet flood control, fisheries and other water-use objectives (Hourston et al. 1954, Alexander et al. 2008). Given that the post-hatch to emergence interval of sockeye may take 6-10 weeks, water managers are faced with difficult decisions and high levels of uncertainty for maintaining discharges below levels known to induce redd-scour (scour occurs at $>30 \text{ m}^3/\text{s}$) in the Okanagan River. If these elevated discharges are delayed excessively, risks of river and lakeshore flooding that damage urban and agricultural infrastructure become unacceptably high. Resource managers in the Okanagan currently employ a computer-based decision support application known as the fish-and-water management tools (FWMT) system to assess risks and consequences to both human systems and aquatic ecosystems of daily to seasonal water management decisions (see Alexander et al. 2008, Hyatt et al. 2009 and Hyatt and Stockwell 2010 for details). The FWMT system is comprised of a coupled set of four biophysical models of key relationships (among climate, water, fish and property) used to predict consequences of water management decisions (represented in a fifth decision-rules model) for fish and other water users in the Okanagan valley. A sockeye life history model embedded within the FWMT system explicitly considers the influence of human as well as naturally-induced flood-and-scour events on annual variations in fry production of Okanagan sockeye salmon. Two key assumptions of this sockeye life history model are that (1) all eggs and (2) all alevins scoured during flood events ultimately suffer mortality. An assumption that egg mortality will reach 100% during

major flood-and-scour events is likely reasonable, but is unlikely to be true of alevins throughout the entire several week period of development from the point of hatching to just prior to fry emergence. However, the absence of any published information on the development of ecological competence of sockeye alevins at various points between egg hatch and fry emergence necessitated this assumption. I am directly testing this assumption using lab studies with *Oncorhynchus nerka*

This project aims to better understand the development of ecological competence of Okanagan sockeye salmon between the point of egg hatch and subsequent point(s) of volitional emergence. Specifically, I will determine, to what extent and at what size can alevins respond effectively to ecological challenges associated with premature emergence due to redd scour. To test the ability of alevins to swim, feed and avoid predators, a series of trials was created to test the ecological competence level of alevins at various weeks of life from hatch to volitional emergence. The purpose of this project is to better understand the fitness of alevins after forced emergence has occurred. This was done by observing the survival rate of alevins during the course of a 60-minute simulated elevated discharge event (hereafter termed an SEDE) in addition to observations of their behaviour in a series of fitness tests conducted immediately after alevin exposure to an SEDE. Alevins were subjected to fitness tests to determine: their aptitude to rebury into the gravel bed, predator avoidance, exogenous feeding and swimming performance. Testing was conducted through time to determine the relationship of fitness and alevin development. The general hypothesis was that as alevins mature, their ability to successfully survive an SEDE would increase along with their abilities to execute specific behaviours that would enhance their survival in epibenthic or water column habitats.

2 Methods and materials:

The study organisms used for this project were sockeye salmon collected from the Okanogan River ($49^{\circ}11'0''$ N / $119^{\circ}33'0''$ W), a tributary of the Columbia River, located in southern British Columbia, along the Canada/USA border. During the month of October, sockeye salmon spawn in the river in their natal spawning ground near the city of Oliver (this part of the river is one of the few non-channelized parts of the river) located 986 km from the Columbia River mouth and 277 m above sea level (Figure 2.1). Fry typically begin to emerge mid-April and then migrate approximately 15-20 km downstream to rear in Osoyoos Lake (Hyatt et al. 2003).

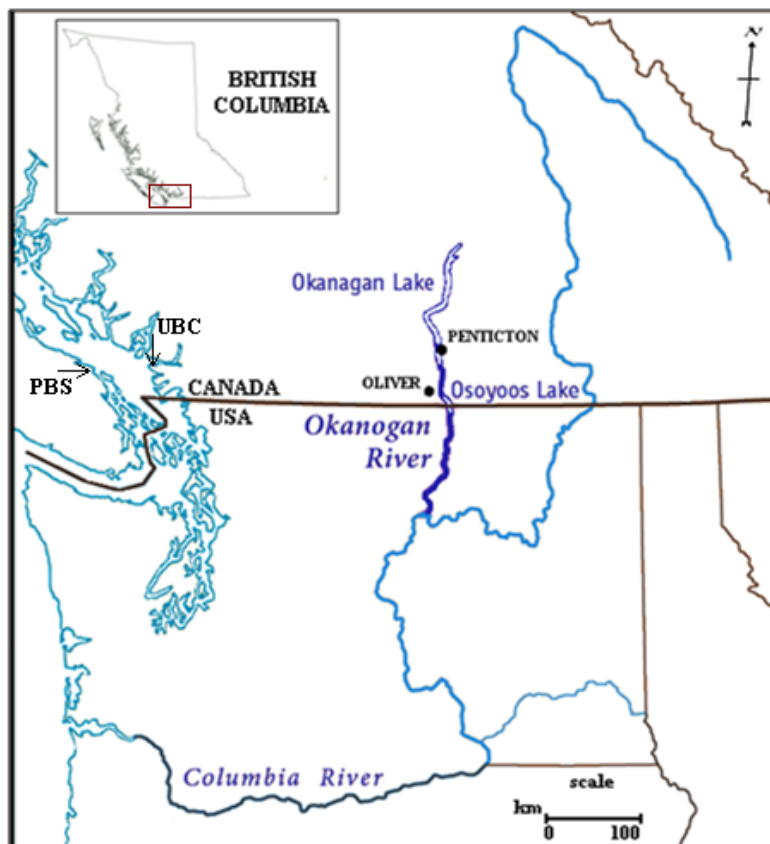


Figure 2.1: Features of the study area and relative location within British Columbia (inset). Laboratory location abbreviated: Pacific Biological Station (PBS). (Adapted from: http://en.wikipedia.org/wiki/Okanogan_River) Scale is approximate.

On October 16, 2008, with the assistance of the Okanagan Nation Alliance Fisheries Department (ONAFD), beach seining was conducted at the Okanagan River spawning grounds to capture reproductively mature sockeye salmon. Ten male and ten female adult sockeye salmon were chosen at random and removed from the beach seine catch. Ripeness was assessed through the use of gentle abdominal pressure in the dorsal to ventral direction. The easy ejection of eggs or milt signified a sufficient degree of ripeness for a given sockeye adult to serve as a source of eggs or sperm.

Fish were immediately euthanised through a cerebral concussion administered with a wooden mallet. Adults were briefly submerged in an iodine/water solution before gills were split to allow the removal of blood. Milt was extracted through abdominal pressure and contained in small individual Whirl-Paks before placement on ice. Egg removal consisted of separating the abdominal cavity and extracting the skin. Eggs were deposited into sterile plastic containers before placement on ice. Great care was taken to avoid water or blood contamination of gametes. Three sub-samples consisting of 10 eggs from each female were weighed (± 0.01 g) to calculate average individual egg mass. Egg diameters were also recorded (± 0.01 mm).

Gametes were flown to the Pacific Biological Station in Nanaimo, BC. Fertilization took place using the protocol of Patterson et al. (2004). Crosses consisted of one female separately fertilized by two males and each male separately fertilizing two females. The crosses resulted in 10 genetically separate families and 10 families related by one parent.

Fertilized eggs from each family were deposited into separated partitions within Heath trays for incubation. Each Heath tray consisted of four families, two females

crossed with four males. Water temperatures were maintained at 4°C through regulated pumping. Assessment of egg development and Heath tray maintenance were completed by Bill Damon of Fisheries and Oceans Canada throughout the winter months.

2.1 Simulated elevated discharge experiment:

2.1.1 General methods:

I assessed the mortality rate of sockeye alevins during 60-minute simulated elevated discharge events (SEDEs) as a measure of their likely ability to survive scour events. Alevin mortality was defined as having occurred when operculum movement ceased for greater than one minute. Mortality was evaluated for each of six 10 minute intervals during the 60-minute SEDE. Experimental trials were always initiated by exposing 10 randomly selected alevins of the same genetic family to a SEDE. Three genetically separate families were used (three replicates). SEDE experiments were completed at weekly intervals to measure the change in alevin mortality rates over time relative to their stage of development. SEDE experiments took place in an oval fibreglass tank with 119 cm x 58 cm x 43 cm dimensions (Figures 2.2 & 2.3) at the Pacific Biological Station. The experiments took place from March 4, 2009 to April 23, 2009.

2.1.2 Trial:

SEDE experiments were initiated at 7 weeks after eggs hatch and carried on until alevins were 11 weeks post-hatch. It was intended that the younger alevins be tested as well, but unforeseen circumstances delayed the commencement of the experiments.

Water was pumped and directed through a 4 cm perforated PVC capped pipe (Figure 2.2) into an oval fibreglass tank that served as the SEDE “arena”. The water was removed through a perforated 10 cm center drainpipe. The drainpipe was wrapped in 907 μm wire mesh to ensure alevins did not escape from the tank. The flow of water entering the tank was set at a rate equal to the rate of removal of water through the drainpipe to ensure the maintenance of a constant water level. A timer was used to measure consecutive 10-minute intervals, and at each interval the flow of water in the tank was reduced and the survival status of each alevin was checked. All viable alevins were returned to the tank and SEDE conditions were reinstated, any alevin deemed to be moribund was removed from the experiment. The experiment continued until alevins had been exposed to 60 minutes of elevated discharge or all alevins were deceased. Average velocity of water circulating in the experimental apparatus was retrospectively measured using a frame-by-frame video play back of the SEDE after it was determined the mechanical flow meter initially used was defective. Average velocity associated with SEDE’s was determined to be $\sim 2.2 \text{ m/s}$ ($\pm 0.3 \text{ m/s}$) or in average alevin body length of $2.5 \text{ mm} \sim 880 \text{ bl/s}$ ($\pm 120 \text{ bl/s}$).

Upon completion of each SEDE any remaining viable alevins were euthanised using MS-222. All alevins used in the experiment were measured for length ($\pm 0.1 \text{ mm}$), total wet mass and wet mass of yolk sac ($\pm 0.01 \text{ g}$). Mass of yolk sac was determined by weighing the alevin after the yolk sac had been surgically removed after euthanasia. The mass of the yolk sac was removed from the total mass to determine the mass of the sac alone. The size and degree of development of an alevin during an elevated discharge event may play an important role in determining whether or not it is physically able to survive the high velocity currents as well as other risk factors previously stated. As age

and size of salmon have been found to be strongly linked together in juvenile salmon, age in weeks may be used as a determinant of size during the dramatic growth period of *O. nerka* alevins (Ricker 1981).

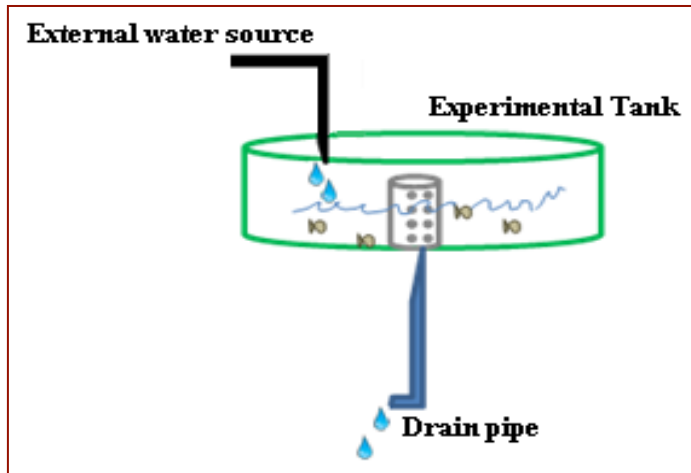


Figure 2.2: Schematic of the experimental apparatus used to create SEDEs.

2.2 Bury experiment:

I assessed the ability of alevins to return to the cover of gravel (“bury”) after being subjected to an SEDE lasting 30-minutes. SEDEs took place as described above. The water was removed through a perforated 10 cm center drainpipe. The drainpipe was wrapped in 907 μm wire mesh to ensure alevins were not removed from the tank. The internal velocity of water was set at a rate equal to the rate of removal of water through the drainpipe to ensure the maintenance of the water level within the tank. Velocity was retrospectively measured using a frame-by-frame video play back of the SEDE after it was determined the mechanical flow meter initially used was defective. A SEDE consisted of 10 randomly selected alevins of the same genetic family. At the end of the 30-minute SEDE all viable alevins were removed from the tank with a dip net and transferred into an 8 L tank containing 5 cm of river rocks, ranging from approximately 2.5 cm to 4.0 cm in size, and 8°C water. Alevins were placed into the tank and left for 60

minutes. As the tank contained non-circulating water, temperatures were monitored and recorded. The alevins' behaviour was recorded with a JVC GZ-MS100RU memory camcorder. The playback of the video was used to determine the length of time an individual alevin required to achieve concealment within the gravel. Complete concealment was defined as the total lack of visibility of the alevin from the surface. A control test was conducted using 10 alevins not subjected to a SEDE prior to entering the tank. The experiment was repeated three times a week for five weeks.

Upon completion of each SEDE the remaining viable alevins were euthanised using MS-222. All alevins used in the experiment were measured for length (± 0.1 mm), total mass and mass of yolk sac (± 0.01 g). Mass of yolk sac was determined by subtraction using masses of the alevin both before and after the yolk sac had been surgically removed.

The values taken from the time to bury test were divided into two sections. The alevins that were able to bury within the allotted 60-minute time period were classified as viable. Alevins that were either unable to bury within the time period or dead from exposure to the SEDE, were classified as deceased for the purpose of this experiment.

2.3 Statistical analysis:

Data from the SEDE experiments were not transformed before conducting separate ANOVA analyses. Mortality was reported as the proportion of the total number of alevin deceased (out of 10 alevins original placed in the SEDE) at each given time interval. The ANOVA analysis was used to determine the significance of alevin age in weeks (Age) and SEDE length in minutes (Time) as factors in determining alevin

survival during a SEDE event. Following the ANOVA analysis a Bonferroni correction was used on all Age and Time data. A Bonferroni-corrected alpha of 0.005 was used. Size was used as a covariate in the SEDE experiments. The size variables used were: fork length (mm), mass (g), and yolk mass (g). All three were analysed separately against the mortality rates of the alevins associated with SEDE exposure and used as covariates for both Age and Time. The data collected from the viable alevins in the rebury test were transformed using $y = 2 \cdot \arcsin \sqrt{x}$. The data were then analysed using an ANOVA. The ANOVA was used to determine the significance of Age on the length of time alevins took to rebury into the gravel after exposure to a 30 minute SEDE, when compared to alevins not subjected to a 30 minute SEDE. The data from the deceased alevins in the bury test were analysed separately and were not transformed prior to the ANOVA analysis. The ANOVA was used to determine the effect of alevin Age on the mortality rates of alevins during a 30 minute SEDE as well as their ability to rebury within the gravel subsequent to the SEDE. The data collected from the feeding experiment were analysed using an ANOVA test.

The Bonferroni-corrected alpha was used in these analyses to help minimize the chances of Type I errors occurring due to the use of multiple comparisons. But as these tests have multiple confounding factors, it has been stated that the use of Bonferroni corrections when dealing with behaviour ecology can lead to a substantial reduction in the statistical power of rejecting an incorrect H_0 (Nakagawa 2004). We therefore have recorded the statistical significance of each factor using Bonferroni corrections, but have referenced the typical alpha of 0.05 for data interpretation provided in the discussion.

2.4 Supplementary experiments:

The additional experiments were conducted to determine various other sockeye alevin's abilities. An experiment to examine the potential for early exogenous feeding on *Daphnia pulex* before the complete absorption of their yolk sac was carried out, but the results were not found to be significant (Appendix A). An experiment to determine the swimming abilities of alevins was conducted. The results found no evidence of ability to maintain position within the water column (Appendix A). A final experiment was carried out to examine the reaction time for alevins to potential threat of predation. The results were inconclusive (Appendix A).

3 Results:

3.1 Simulated elevated discharge experiment:

The results of the SEDE experiment indicated the age of the alevin to have a significant effect on their survival ($F_{4,20} = 15.65$, $P < 0.0001$). Alevins at 9 and 10 weeks after hatch, were 10% more likely to survive a 60-minute SEDE than alevins at 7 weeks after hatch, during the SEDE experiment ($P = 0.041$, $P = 0.017$, respectively) and alevins at week 11 were 23% more likely to survive than alevins at week 7 and week 8 ($P = 0.0007$, $P = 0.003$, respectively) (Figure 3.1). Alevins at 11 weeks after hatch were also able to survive 13% more than alevins at week and 9 ($P = 0.035$) (Figure 3.1). There were no significant differences in mortality rates between groups of alevins for which age differed by only one week. For example, survival of alevins at week 8 was not significantly different from alevins at either week 7 or week 9. Significant differences were found only between weeks 7 and 11 and between weeks 8 and 11, when using the restricted Bonferroni-corrected alpha of 0.005.

Age was a significant factor in alevin survival during the SEDE experiments, however, it was the duration of exposure to the SEDE that appeared to have the most impact on the survival rate of the alevins ($F_{5,20} = 109.17$, $P < 0.0001$). There were significant differences in mortality rates between all six 10-minute time periods during the one hour trial ($P < 0.05$ for all pair-wise combinations, Figure 3.1). The largest change in mortality rates occurred between the 30 and 40 minute intervals of a given SEDE trial, with an average of 27.3% increase in mortality. The second largest change in mortality rates occurred between the 50 and 60 minute periods with a 19.3% increase.

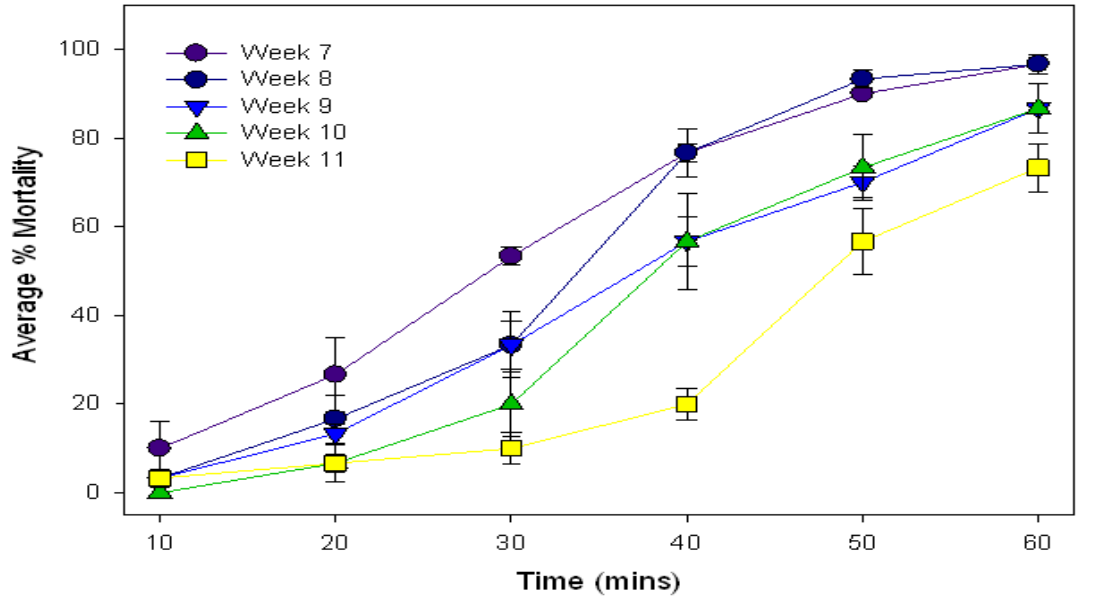


Figure 3.1: SEDE experiment. Cumulative mortality rates of sockeye salmon alevins over 60-minute simulated SEDE trials conducted every week (n = 3 per week) until volitional emergence at 11 weeks. Each trial contained 10 alevin sockeye salmon. Symbols indicate means with 95% CI.

All time periods were significantly different ($P < 0.003$) except between the 10 and 20 minute and between the 50 and 60 minute periods which no longer differed statistically ($P = 0.036$ and $P = 0.018$, respectively), when using the Bonferroni correction of 0.0033.

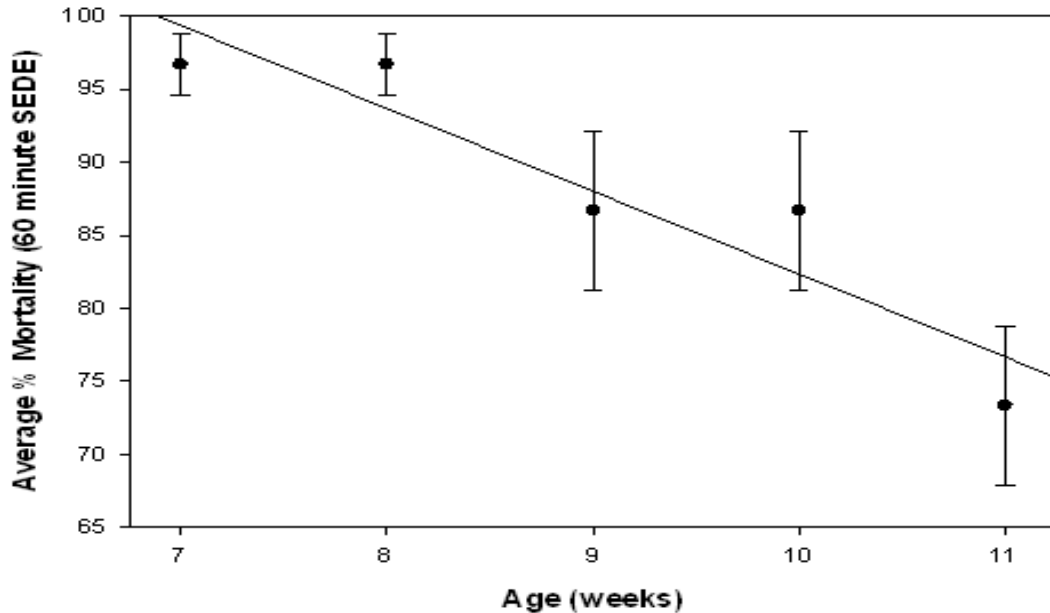


Figure 3.2: Regression for the cumulative mortality rates of sockeye salmon alevins during 60-minute SEDE trials conducted every week ($n = 3$ per week) until volatile emergence at 11 weeks after hatch. Each trial contained 10 alevin sockeye salmon. Symbols indicate means with 95% CI.

The results indicate a strong linear decrease in mortality rates of alevins subjected to 60 minute SEDEs with increasing alevin age in weeks (Percent mortality = $-5.667 \text{ weeks} + 139$, $R^2 = 0.871$, $P = 0.021$) (Figure 3.2). Every two weeks a significant drop in mortality rates occurred. Alevins at week 7 and 8 showed a mortality rate of 97% after 60 minutes, which dropped to 87% in weeks 9 and 10, before dropping again to 73% by week 11.

Size can affect mortality rates, hence size was considered as a covariate in a further analysis of the 60-minute SEDEs. The size measures were fork length (mm), total mass (g) and mass of yolk sac (g) for the SEDE experiments (Figure 3.3). The use of fork length as a covariate in a General Linear Model (GLM). The interaction between fork length and survival following SEDE exposure was not found to be significant ($P =$

0.497), and neither was the covariate ($P = 0.579$). Therefore, none of the LS means (weeks 7-11) were significantly different from one another ($P > 0.005$).

Mass, and yolk mass were used as covariates in a GLM for the SEDE data. The interactions between survival rates and size were not statistically significant (all with $P > 0.32$), and neither was the covariate when either mass or yolk sac were used ($P = 0.700$ and $P = 0.140$). Therefore, none of the Least Square Means (LSM) of the ages (weeks 7-11) were significantly different from one another ($P > 0.005$ for all combinations).

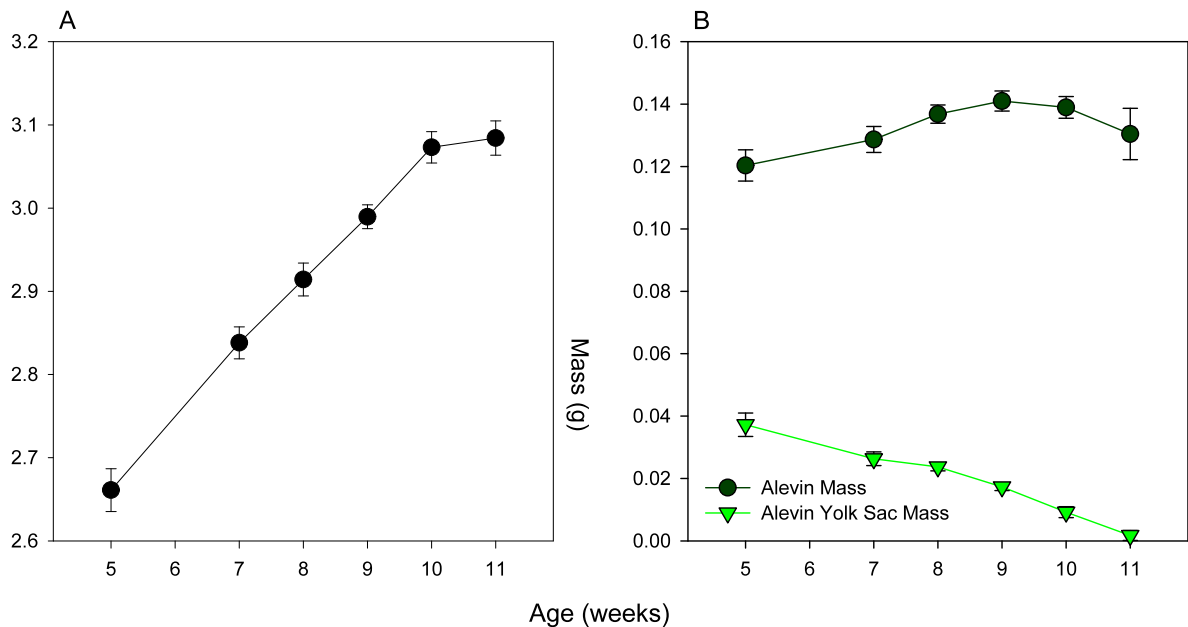


Figure 3.3: The fork length (A), and mass and yolk sac mass (B) of all tested alevins were measured to the nearest 0.1 mm and 0.01 g. Mass was recorded as total wet mass of alevin. Symbols indicate means with 95% CI, $n = 42, 28, 29, 26, 19$ for each week in sequential order.

3.2 Bury experiment:

An experiment was performed to determine the amount of time alevins took to completely rebury within the gravel bed after being subjected to a 30-minute SEDE (Figure 3.4). All alevins that died during the SEDE or did not bury completely within the

gravel in a 60-minute period were considered to be deceased and were therefore analyzed separately (Figure 3.5).

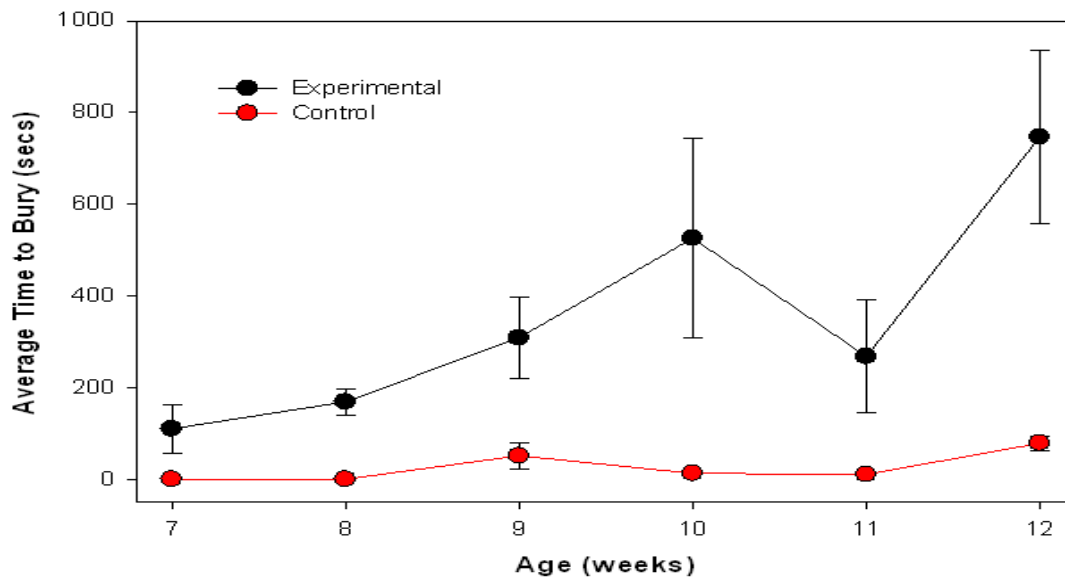


Figure 3.4: The time in which individual alevin sockeye salmon completely buried within a simulated gravel bed. Each trial contained 10 alevin ($n = 3$ per week). Alevins were subjected to a 30 minute SEDE prior to placement in an aquarium containing a 5 cm deep gravel bed. Controls were carried out where alevins were not previously subjected to an SEDE event. Symbols indicate means with 95% CI.

The analysis for the alevins that were successful at reburying in gravel indicated that age in weeks is not a strong variable determining for determine the alevins ability to rebury after exposure to an SEDE. There were no significant differences due to age ($F_{5,12} = 1.33, 12, P = 0.3165$) (Figure 3.4), however, there was a significant group-to-group variation within each age. This may have been due to the fact that three different families were used for each group and the different families showed varied responses ($P = 0.022$). There were also a strong differences found between groups ($P = 0.0003$). The groups developed at different rates and were therefore at different physical stages.

There was still a visible trend that as age increased the amount of time for alevins to bury increased exponentially ($R^2 = 0.346$) except during week 11 where the length of time dropped dramatically (Figure 3.4). The control group reacted considerably differently from the treatment group ($F_{1,11} = 10.93$, $P < 0.007$), as all alevins were able to bury in the gravel within a few seconds to a minute. At week 12, some alevins were buttoned up (emergent) and therefore not as quick to bury.

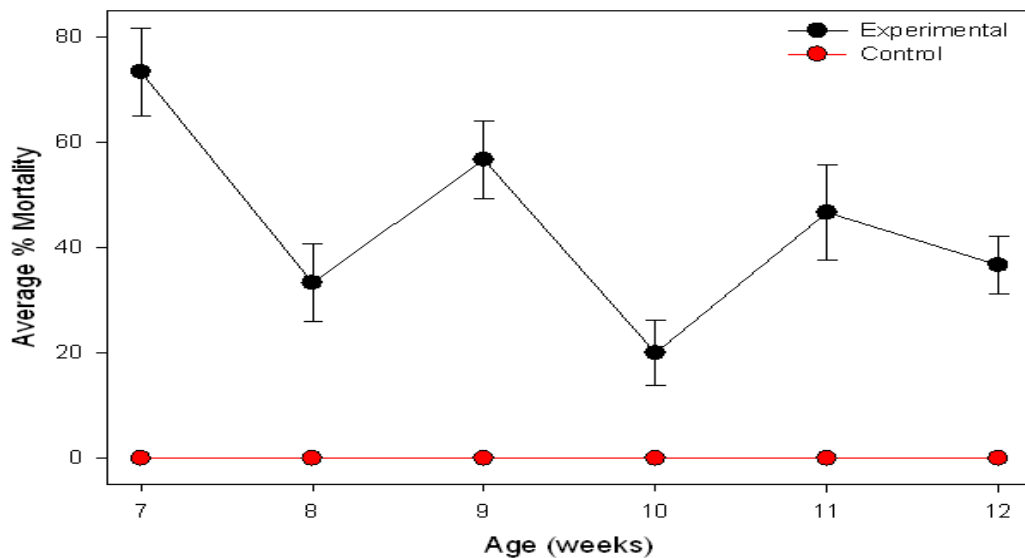


Figure 3.5: Comparison of cumulative mortality rates of sockeye salmon alevins exposed to a 30-minute SEDE versus unexposed control groups of alevins. For the purpose of this experiment mortality is classified as either failure to completely conceal in the gravel after 60 minutes or dead from exposure to the SEDE. Individual alevins were given 60 minutes to completely bury within a 5 cm deep simulated gravel bed before being classified as deceased. Each trial contained 10 alevins ($n = 3$ per week). Symbols indicate means with 95% CI.

The mortality analysis indicates that age in weeks was not a significant variable ($F_{5,12} = 2.43$, $P = 0.096$) influencing survival. However, there remains the suggestion of a trend for total mortality of alevins to decrease as the weeks progressed ($R^2 = 0.457$) (Figure 3.5). The control group was strongly different from the treated group, as none of

the control alevins died during the experiment and all were able to conceal quickly beneath the gravel ($F_{1,5} = 83.80$, $P < 0.0001$).

4 Discussion:

Growth and development were found to increase the ecological competence of alevins over a two-month time period. As alevins matured and developed more prominent physical features (i.e., fins and loss of yolk sac), they became better adapted to survive, recover and reburial after a simulated elevated discharge event (SEDE).

4.1 Simulated elevated discharge experiment:

Alevins of sockeye salmon showed developmental stage-specific survival rates when exposed to an SEDE, but there have been almost no studies conducted on the effects of forced emergence on alevins. Because of the lack of scientific literature on this topic, most of the comparable knowledge comes from the work that has been done on early post-emergent salmonid fry.

During the weeks that sockeye salmon alevins spend beneath the gravel bed they undergo multiple physical changes and pass through five stages based on the development of physical characteristics thereby becoming increasingly better adapted to survive fast or turbulent flows. As they matured their vulnerability to the environment began to decrease slightly. Through development, their fragile yolk sac depletes, their fins develop, their mobility increased, and eventually they buttoned-up and became fry. The results from this experiment lined up with how physical differences between developmental stages affected the alevin's ability to cope with environmental challenges. These experiments showed both age and duration of exposure have significant impacts on the survival rate of alevin sockeye salmon during a SEDE.

During the first week after hatch we found alevin mortality rates in a 60 minute SEDE to be 100% but as they developed, their mortality rates decreased to 57% at five weeks after hatch. This data showed that halfway through their juvenile developmental stages the majority of alevins were able to survive a large scale scour event and that almost 25% of the alevins were able to survive when tested just before the time of volitional emergence. These findings were consistent with those of Ottaway and Clarke (1981), who found the relationship between velocity and fry displacement within the water column to be continually changing. They found that the relationship increased or decreased dependent on the exact stage of fry development. Ottaway and Clarke (1981) conducted an experiment where early emergent salmon and trout were subjected to an abrupt increase in velocities within a simulated channel. Using velocities ranging from 0.10 m/s to 0.73 m/s, they observed that whenever an abrupt change in water velocity occurred an increased number of fry were displaced downstream, but as the fry matured their ability to withstand these velocity changes increased.

With other research showing the sensitivity of post-emergent alevins and fry to elevated water velocities (Ottaway and Clarke 1981; Ottaway and Forrest 1983; Daufresne et al. 2005; Hayes et al. 2010) there was support for a conclusion that the pre-emergent alevins were underdeveloped, negatively phototactic and when forcibly removed from their natural habitat were extremely sensitive to increased velocities and hydraulic forces. A previous study showed mortality of salmon can reach as high as 90% within the first year of life (Hayes et al. 2010). The majority of this loss occurred during incubation and through the first few weeks around emergence. Daufresne et al. (2005) exposed pre-emergent brown trout (*Salmo trutta*) in an artificial channel to various water velocities upon emergence, and found that young brown trout were highly sensitive to

velocity changes during the first few days after emergence. About 80% of these young brown trout were displaced downstream during elevated velocities. Alevins may not be able to combat displacement during flooding events, however, the results indicate that as sockeye alevins developed subsequent to hatching, they will become better adapted to survive challenges posed by elevated discharge and/or forced emergence.

One of the largest causes of alevin mortality during the experiment was the loss of their yolk sac. This only occurred when the alevins were still in the early weeks of their development. Alevins showed the greatest level of vulnerability during the first two stages of development. This was because their yolk sacs were still protruding and their morphological features were underdeveloped (Dill 1997). As it has been found that increasing fish size may cause a decrease in susceptibility to displacement by high flows (Irvine 1986; Heggenes and Traaen 1988), one can infer that the smaller/younger stages of alevin development were more susceptible to mortality from displacement. This was supported by the 90 – 100% mortality observed in a 60-minute SEDE for alevins still in the early weeks of development.

4.2 Ability to rebury after dislodgement:

In contrast to our predictions, the results showed that, as alevins age and develop, they were slower to bury into the gravel. However, the number of alevins to survive SEDEs increased through time. During the rebury test fewer immature alevins were able to rebury, whereas, more mature alevins were more successful. The few alevins that survived the 30-minute SEDE at 7 weeks buried within 3 minutes of being placed in still water, whereas by 10 weeks the alevins averaged 9 minutes to bury. The relationship between the length of time to bury and age differed from the prediction, however, the

relationship between SEDE survival and age remained consistent, SEDE survival increased with increasing age. By the time emergence was reached, the number of alevins to survive and rebury after a SEDE was twice the number it was at 7 weeks.

The conflicting results of age and ability to quickly bury may have been due to the lack of stimulus in the still water tank. The lack of current within the tank coupled with the lack of predatory chemical cues within the current may have affected the behavioural responses of the alevins. Various studies have found that alevins of brook charr (*Salvelinus fontinalis*) and Atlantic salmon (*Salmo salar*) were capable of detecting the chemical cues of a predator while within the gravel and able to delay emergence as a consequence (Mirza and Chivers 2001; Jones et al. 2003). This ability to detect predatory chemical cues may materialize at a later stage of alevin development, but more research needs to be conducted to fully determine the extent of their abilities.

The requirement of redistributing energy from growth and development to increased metabolic rates needed for movement may have caused alevins to limit unnecessary swimming and therefore avoided burying into the gravel until preserved predatory threats made it unavoidable. If further developed alevins were capable of recognizing the lack of a predatory threat in the experimental tanks, they may have delayed exerting excessive energy for burying after exposure to an SEDE until a recovery period had passed. This was reinforced through the control groups' consistently rapid response to rebury, and demonstrates the delay in reburying by the test group must therefore have been a consequence of the SEDE exposure. This ability to recognize the presence or lack of presence of a predatory threat coupled with the immense amount of energy utilized during exposure to an SEDE may explain the inconsistency in the data

between the ages as well as between the test (exposed to SEDE) and control (no exposure) alevins. Future studies will need to be conducted to further understand the discrepancies in burying times.

The results from the time-to-bury experiment were unexpected, however, the mortality rates were as predicted and consistent with our SEDE experiment. As the alevins matured they were better equipped to survive a 30 minute SEDE and their aptitude to conceal themselves within the gravel bed improved. Their ability to successfully endure a SEDE and retain enough energy to conceal themselves from predators was vital. A previous study found predation after a scour event increased remarkably, as predators such as *Cottus asper* (prickly sculpin) were able to feed effortlessly on exposed sockeye alevin (Foote and Brown 1998).

4.3 Remaining questions:

The experiments conducted in this study have just begun to touch on many questions that need to be answered in regards to the ability for alevins to survive forced emergence; whether it is the ability to survive a flood event, or to survive within the water column after a forced emergence from an alternate cause, such as disruptions to the redd from terrestrial predators. Additional research needs to be conducted to determine the outcome of alternate flood scenarios.

These experiments dealt solely with one flow rate for a set amount of time. The impact a large-scale flood event can have on an ecosystem is dependent on many variables, such as, the amount of water released (in an anthropogenically induced flood), velocity of the water, the composition of the river bed, etc. Taking these factors into

account when conducting new elevated discharge experiments may further our understanding of the potential impacts of floods on forcibly removed alevins. A complementary study should be conducted where alevins are in artificial redds prior to forced emergence by a SEDE. This may help determine if the actual act of forced removal from the redd has an impact on alevin survival rates.

All new SEDE experiments should include an assessment of the alevin's ability to rebury in the gravel upon the conclusion of the SEDE. The experimental design of these future experiments should be as close to a natural setting as possible, as the lack of predator cues and natural indicators may have confounded these results.

4.4 Implications and management:

The results of these experiments indicate that there are stages in alevin development where the ability to survive a SEDE increases. Alevins showed an approximately 95% mortality rate in weeks 7 and 8, while in weeks 9 and 10 the mortality rate was approximately 87% and in week 11 the mortality rate decreased to 75%.

The multitude of factors necessary to determine the risk level to sockeye salmon are continuously being evaluated by the fish and water managers of the Okanagan River system (Hyatt et al. 2009). Monthly snow-pack analyses are conducted, as well as water surveys, and bi-monthly fish and water risk scenarios are ran (Hyatt and Stockwell 2010). The information gathered is used to determine both the amount and the time water is released into the stream system as well as the potential risks this may have on alevins. The increase in knowledge towards an alevins ability to successfully navigate a scour-

event forced emergence may greatly impact these decisions. Fish and water managers may now attempt to delay releases until alevins are capable of surviving early emergence when forced into releasing water at potentially threatening levels. The need for water release from Okanagan Lake can be unavoidable, but the knowledge gained from these experiments allow water managers a leeway they did not previously have. There is now evidence to suggest that while developing alevins are continuously becoming better adapted to survive elevated flows, there are divisions where there are very little improvements between weeks. Water managers may determine it acceptable to release water to produce potentially dangerous levels when necessary if the alevins are found to be between one of these stages.

References

- Alexander, C.A.D., Hyatt, K., and Symonds, B. (eds). 2008. The Okanagan fish/water management tool: Guidelines for apprentice water managers (v.2.1.000). Prepared for the Canadian Okanagan Basin Technical Working Group, Kamloops, BC and Douglas County Public Utility District, Wenatchee, WA. p130 .
- Bain, M.B., Finn, J.T., and Booke, H.E. 1988. Streamflow regulation and fish community structure. *Ecology* **69** 382–392.
- Bams, R.A. 1969. Adaptations of sockeye salmon associated with incubation in stream gravels, p. 71–87. *In*: T.G. Northcote [ed.]. Symposium on salmon and trout in streams. H.R. MacMillan Lectures in Fisheries. Institute of Fisheries, University of British Columbia, Vancouver, BC.
- Brannon, E.L. 1987. Mechanisms stabilizing salmonid fry emergence timing p. 120-124. *In* H.D. Smith, L. Margolis, and C.C. Wood [ed.] Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Canadian Special Publication of Fisheries and Aquatic Sciences. **96**.
- Brannon, E.L., Powell, M.S., Quinn, T.P., and Talbot, A. 2004. Population structure of Columbia River Basin chinook salmon and steelhead trout. *Reviews in Fisheries Science*. **12**(2): 99–232.
- Brett, J.R. 1971. Energetic responses of salmon to temperature. A study of some thermal relations in the physiology and freshwater ecology of sockeye salmon (*Oncorhynchus nerka*). *Integrative and Comparative Biology* **11**: 99–113.
- Collins, J.P., Young, C., Howell, J., and Minckley, W.L. 1981. Impact of flooding in a Sonoran desert stream, including elimination of an endangered fish population (*Poeciliopsis o. occidentalis*, *Poeciliidae*). *The Southwestern Naturalist* **26**: 415–423.
- Dill, P. 1997. A study of shore-spawning kokanee salmon (*Oncorhynchus nerka*) incubation and emergence, Okanagan Lake - 1996 BROOD In Okanagan Lake Action Plan Year 1 (1996-97) and Year 2 (1997-98) Report (pp. 258-274). Fisheries Project Report No. RD 73, 1998. Province of British Columbia Ministry of Fisheries - Fisheries Management Branch.
- Death, R.G. 2010. Disturbance and riverine benthic communities: What has it contributed to general ecological theory? *River Research and Applications* **26**: 15–25.
- Dudgeon, D., Arthington, A.H., Gessner, M.O., Kawabata, Z-I., Knowler, D.J., Lévêque, C., Naiman, R.J., Prieur-Richard, A-H, Soto, D, Stiassny, M.L.J., and Sullivan, C.A. 2006. Freshwater biodiversity: importance, threats, status and conservation challenges. *Biological Reviews of the Cambridge Philosophical Society* **81**: 163–182.

- Daufresne, M., Capra, H., and Gaudin, P. 2005. Downstream displacement of post-emergent brown trout: effects of development stage and water velocity. *Journal of Fish Biology* **67**: 599-614.
- Einum, S., and Fleming, I.A. 2000. Selection against late emergence and small offspring in Atlantic salmon (*Salmo salar*). *Evolution* **54**: 628-639.
- Farley, A.L. 1979. Atlas of British Columbia: People, environment and resource use. University of British Columbia Press, Vancouver, B.C. 139 p.
- Fast, D.E., and Stober, Q.J. 1984. Intragravel behavior of salmonid alevins in response to environmental changes. University of Washington Fisheries Research Institute **8414**: 104.
- Field-Dodgson, M.S. 1988. Size characteristics and diet of emergent chinook salmon in a small, stable, New Zealand stream. *Journal of Fish Biology* **32**: 27-40.
- Foote, C.J., and Brown, G.S. 1998. Ecological relationship between freshwater sculpins (genus *Cottus*) and beach-spawning sockeye salmon (*Oncorhynchus nerka*) in Ilimna Lake, Alaska. *Canadian Journal of Fisheries and Aquatic Science* **55**: 1524-1533.
- Glenfir Resources. 2006. Plan of study for renewal of the international joint commission's Osoyoos Lake orders. 158p. Available at: http://www.ijc.org.rel/boards/osoyoos/final_pos_060811.pdf.
- Good, S.P., Dodson, J.J., Meekan, M.G., and Ryan, D.A.J. 2001. Annual variation in size-selective mortality of Atlantic salmon (*Salmo salar*) fry. *Canadian Journal of Fisheries and Aquatic Science* **58**: 1187-1195.
- Gottesfeld, A.S., Hassan, M.A., Tunnicliffe, J.F., and Poirier, R.W. 2004. Sediment dispersion in salmon spawning streams: the influence of floods and salmon redd construction. *Journal of the American Water Resources Association* **40**: 1071-1086.
- Gray, L.J. and Fisher, S.G. 1981. Postflood recolonization pathways of macroinvertebrates in a lowland Sonoran Desert. *American Midland Naturalist* **106**: 249-257.
- Groot, C. and Margolis, L. 1991. Pacific salmon life histories. University of British Columbia Press, Vancouver, BC.
- Gunnes, K. 1979. Survival and development of Atlantic salmon eggs and fry at three different temperatures. *Aquaculture* **16**: 211-218.
- Hampton, S.E., Romare, P., and Seiler, D.E. 2006. Environmentally controlled Daphnia spring increase with implications for sockeye salmon fry in Lake Washington, USA. *Journal of Plankton Research* **28**: 399-406.

- Harrell, H.L. 1978. Response of the Devil's River (Texas) fish community to flooding. *Copeia* **1978**: 60–68.
- Hassan, M.A., Church, M., Lisle, T.E., Brardinoni, F., Benda, L., and Grant, G.E. 2005. Sediment transport and channel morphology of small, forested streams. *Journal of the American Water Resources Association* **41**: 853-876.
- Hayes, J.W., Olsen, D.A., and Hay, J. 2010. The influence of natural variation in discharge on juvenile brown trout population dynamics in a nursery tributary of the Motueka River, New Zealand. *New Zealand Journal of Marine and Freshwater Research* **44**: 247-269.
- Heggenes, J., and Traaen, T. 1988. Downstream migration and critical water velocities in stream channels for fry of four salmonid species. *Journal of Fish Biology* **32**: 717-727.
- Heming, T.A., McInerney, J.E., Alderdice, D.F. 1982. Effect of temperature on initial feeding in alevins of chinook salmon (*Onchorhynchus tshawytscha*). *Canadian Journal Fisheries and Aquatic Sciences* **39**: 1554-1562.
- Hoover, T.M., and Richardson, J.S. 2010. Does water velocity influence optimal escape behaviors in stream insects? *Behavioral Ecology* **21**: 242–249.
- Hourston, R., Clay, C.H., Burridge, E.W., Lucas, K.C., Johnson, D.R., Heg, H.T., McKinley, W.R., Barnaby, J.T., Fulton, L.A., and Gentry, A.A. 1954. The salmon problems associated with the proposed flood control project on the Okanagan River in British Columbia, Canada. A report prepared by the technical staffs of the United States Fish and Wildlife Service, The Washington Department of Fisheries and The Department of Fisheries, Canada No. 109.
- Hvidsten, N.Z. 1985. Mortality of pre-smolt Atlantic salmon, *Salmo salar* L. & brown trout, *Salmo trutta* L., caused by fluctuating water levels in the regulated river Nidelva, central Norway. *Journal of Fish Biology* **27**: 711–718.
- Hyatt, K.D. and Rankin, D.P. 1999. A habitat based evaluation of Okanagan sockeye salmon escapement objectives. Canadian Stock Assessment Secretariat Research Document 99/191. 59p. Available at:
http://www.dfompo.gc.ca/csas/CSAS/English/Research_Years/1999/a99_191e.htm.
- Hyatt, K.D., Stockwell, M.M., and Rankin, D.P. 2003. Impact and adaptation responses of Okanagan River sockeye salmon (*Oncorhynchus nerka*) to climate variation and change effects during freshwater migration: Stock restoration and fisheries management implications. *Canadian Water Resources Journal* **28**: 689–713.
- Hyatt, K.D., and McQueen D.J., Shortreed, K.S., and Rankin, D.P. 2004. Sockeye salmon (*Oncorhynchus nerka*) nursery lake fertilization: Review and summary of results. *Environmental Reviews* **12**: 133-162.

- Hyatt, K.D., Bull, C., and Stockwell, M.M. 2009. Okanagan fish and water tool project assessments: Record of management strategy and decisions for the 2005-2006 fish-and-water year. Canadian Manuscript Report of Fisheries and Aquatic Sciences 2897: ix + 68p.
- Hyatt, K.D., and Stockwell, M.M. 2010. Fish and water management tool project assessments: Record of management strategy and decisions for the 30062007 water year. Canadian Manuscript Report of Fisheries and Aquatic Sciences 2913: ix + 65p.
- Irvine, J.R. 1986. Effects of varying discharge on the downstream movement of salmon fry, *Oncorhynchus tshawytscha* Walbaum. Journal of Fish Biology **28**: 17-28.
- Jackson, R.B., Carpenter, S.R., Dahm, C.N., McKnight, D.M., Naiman, R.J., Postel, S.L., and Running, S.W. 2001. Water in a changing world. Ecological Applications **11**: 1027–1045.
- Jähnig, S.C., Lorenz, A, and Hering, D. 2008. Hydromorphological parameters indicating differences between single- and multiple-channel mountain rivers in Germany, in relation to their modification and recovery. Aquatic Conservation: Marine and Freshwater Ecosystems **18**: 1200–1216.
- Jerolmack, D. and Brzinski III, T.A. 2010. Equivalence of abrupt grain-size transitions in alluvial rivers and eolian sand seas: A hypothesis. Geology **38**: 719–722.
- John, K.R. 1964. Survival of fish in intermittent streams of the Chiricahua Mountains, Arizona. Ecology **45**: 112–119.
- Jones, M., Laurila, A., Peuhkuri, N., Piironen, J., and Seppä, T. 2003. Timing an ontogenetic niche shift: Responses of emerging salmon alevins to chemical cues from predators and competitors. Oikos **102**: 155-163.
- Jurajda, P., Reichard, M., and Smith, C. 2006. Immediate impact of an extensive summer flood on the adult fish assemblage of a channelized lowland river. Journal of Freshwater Ecology **21**: 493–501.
- Lawrence, S. 2003 Sockeye egg and alevin development summary 2003. Okanagan Nation Alliance Fisheries Department Final Report. p11.
- Lisle, T.E. 1989. Sediment transport and resulting deposition in spawning gravels, north coastal California. Water Resource Research **25**: 1303–1319.
- Lisle, T.E., and Lewis, J. 1992. Effects of sediment transport on survival of salmonid embryos in a natural stream: a simulation approach. Canadian Journal of Fisheries and Aquatic Science **49**: 2337–2344.

- Ma, Y., Huang, H.Q., Xu, J., Brierley, G.J. and Yao, Z. 2010. Variability of effective discharge for suspended sediment transport in a large semi-arid river basin. *Journal of Hydrology* **388**: 357–369.
- Mason J.C. 1976. Some features of coho salmon, *Oncorhynchus kisutch*, fry emerging from simulated redds and concurrent changes in photobehavior. *Fishery Bulletin* **74**: 167–175.
- Massee, K.C., Kim, J., Berejikian, B.A., and Hardy, R.W. 2007. Prey selection and efficiency of naïve and experienced juvenile sockeye salmon. *Journal of Fish Biology* **70**: 1213-1223.
- Matthews, W.J. 1986. Faunal structure in an Ozark stream: Stability, persistence and a catastrophic flood. *Copeia* **1986**: 388–397.
- Michener, W.K., and Haeuber, R.A. 1998. Flooding: natural and managed disturbances. *Bioscience* **48**: 677–680.
- Mirza, R.S., and Chivers, D.P. 2001. Are chemical alarm signals conserved within salmonid fishes? *Journal of Chemical Ecology* **27**: 1641–1655.
- Moyle, P. B., and Leidy, R. A. 1992. Loss of biodiversity in aquatic ecosystems: evidence from fish faunas. Pages 128- 169 in P. L. Fielder and S. A. Jain, editors. *Conservation biology: the theory and practice of nature conservation, preservation and management*. Chapman and Hall, New York, New York, USA.
- Nakagawa, S. 2004 A farewell to Bonferroni: the problems of low statistical power and publication bias. *Behavioral Ecology* **15**: 1044-1045.
- Neuheimer, A.B., and Taggart, C.T. 2007. The growing degree-day and fish size-at-age: The overlooked metric. *Canadian Journal of Fisheries and Aquatic Science* **64**: 375–385.
- Noakes, D.L.G. 1978. Ontogeny of behavior in fishes: a survey and suggestions, p. 103-125. *In*: G.M. Burghart and M. Bekoff (eds.). *The development of behavior: comparative and evolutionary aspects*. Garland Publishing, New York, NY.
- Ojanguren, A.F., Reyes-Gavilán, F.G., and Muñoz, R.R. 1999. Effects of temperature on growth and efficiency of yolk utilization in eggs and pre-feeding larval stages of Atlantic salmon. *Aquatic International* **7**: 81–87.
- Ottaway, E.M., and Clarke, A. 1981. A preliminary investigation into the vulnerability of young trout (*Salmo trutta L.*) and Atlantic salmon (*Salmo salar L.*) to downstream displacement by high water velocities. *Journal of Fish Biology* **19**: 135–145.
- Ottaway, E.M., and Forrest, D.R. 1983. The influence of water velocity on the downstream movement of alevins and fry of brown trout, *Salmo trutta L.* *Journal of Fish Biology* **23**: 221-227.

- Patterson, D.A., MacDonald, J. S., Hinch, S.G. Healey, M.C., and Farrell, A.P. 2004. The effect of exercise and captivity on energy partitioning, reproductive maturation and fertilization success in adult sockeye salmon. *Journal of Fish Biology* **64**: 1039–1059.
- Poole, G.C. 2010. Stream hydrogeomorphology as a physical science basis for advances in stream ecology. *Journal of the North American Benthological Society* **29**:12–25.
- Power, M.E., Parker, M.S., and Dietrich, W.E. 2008. Seasonal reassembly of a river food web: Floods, droughts, and impacts of fish. *Ecological Monographs* **78**: 263–282.
- Quinn, T.P., Doctor, K., Kendall, N., and Rich, H.B., Jr. 2009. Diadromy and the life history of sockeye salmon: nature, nurture, and the hand of man. *In American Fisheries Society Symposium 69: Challenges for Diadromous Fishes in a Dynamic Global Environment*, 18–21 June 2007, Halifax, Nova Scotia. *Edited by* A.J. Haro, K.L. Smith, R.A. Rulifson, C.M. Moffitt, R.J. Klauda, M.J. Dadswell, R.A. Cunjak, J.E. Cooper, K.L. Beal, and T.S. Avery. American Fisheries Society, Bethesda, Md. In press.
- Ricker, W.E. 1981. Changes in the average size and average age of Pacific salmon. *Canadian Journal of Fisheries and Aquatic Science* **3**: 1636–1656.
- Rosgen, D.L. 1994. A classification of natural rivers. *Catena* **22**: 169–199.
- Sánchez-Hernández, J., Vieira-Lanero, R., Servia, M.J., and Cobo, F. 2011. First feeding diet of young brown trout fry in a temperate area: disentangling constraints and food selection. *Hydrobiologia* **663**: 109–119.
- Schael, D.M., Rudstam, L.G., and Post J.R. 1991. Gape limitation and prey selection in larval yellow perch (*Perca flavescens*), freshwater drum (*Aplodinotus grunniens*), and black crappie (*Pomoxis nigromaculatus*). *Canadian Journal of Fisheries and Aquatic Sciences* **48**: 1919–1925.
- Skoglund, H., and Barlaup, B.T. 2006. Feeding pattern and diet of first feeding brown trout fry under natural conditions. *Journal of Fish Biology* **68**: 507-521.
- Sponseller, R. A., Grimm, N. B., Boulton, A. J., and Sabo J. L. 2010 Responses of macroinvertebrate communities to long-term flow variability in a Sonoran Desert stream. *Global Change Biology* **16**: 2891–2900.
- Tew, K.S., Han, C.C., Chou, W.R., and Fang, L.S. 2002. Habitat and fish fauna structure in a subtropical mountain stream in Taiwan before and after a catastrophic typhoon. *Environmental Biology of Fishes*. **65**: 457–462.
- Tregnaghi, M., Marion, A., Coleman, S. and Tait, S. 2010. Effect of flood recession of scouring at bed sills. *Journal of Hydraulic Engineering* **136**: 204–213.

- Uehlinger, U., and Naegeli, M.W. 1998. Ecosystem metabolism, disturbance, and stability in a prealpine gravel bed river. *Journal of the North American Benthological Society* **17**: 165–178.
- Valett, H.M., Hakenkamp, C.C., and Boulton, A.J. 1993. Perspectives on the hyporheic zone: integrating hydrology and biology. *Journal of the North American Benthological Society* **12**: 40–43.
- Velsen, F.P.J. 1980. Embryonic development in eggs of sockeye salmon, *Oncorhynchus nerka*. Canadian Special Publications of Fisheries and Aquatic Sciences **49**: 1-19.
- Vernier, J-M. 1969. Chronological table of the embryonic development of rainbow trout, *Salmo gairdneri* Rich. 1836. *Annales d'embryologie et de morphogenèse*. 2: 495-520. (Translated from French by Fisheries Marine Service. Translation Series number. 3913, 1976)
- Vøllestad, L.A., Peterson, J. and Quinn, T.P. 2004. Effects of freshwater and marine growth rates on early maturity in male coho and chinook salmon. *Transactions of the American Fisheries Society* **133**: 495–503.
- Vörösmarty, C.J., McIntyre, P.B., Gessner, M.O., Dudgeon, D., Prusevich, A., Green P., Glidden, S., Bunn S.E., Sullivan, C.A., Liermann, C.R., and Davies, P.M. 2010. Global threats to human water security and river biodiversity. *Nature* **467**: 555–561.
- Wainwright, P.C. and Richard, B.A. 1995. Predicting patterns of prey use from morphology of fishes. *Environmental Biology of Fishes* **44**: 97–113.
- Wallace, J.C. and Aasjord, D. 1984. An investigation of the consequences of egg size for the culture of Arctic charr, *Salvelinus alpinus* (L.). *Journal of Fish Biology* **24**: 427-435.
- Wang, Z.Y. 1999. Experimental study on scour rate and river bed inertia. *Journal of Hydraulic Research* **37**: 17–37.
- Wang, X. and Pullar, D. 2005. Describing dynamic modeling for landscapes with vector map algebra in GIS. *Computers & Geosciences* **31**: 956–967.
- Williams, D.D. and Hynes, H.B.N. 1976. The recolonization mechanisms of stream benthos. *Oikos* **27**: 265–272.
- Wolman, M.G., and Miller, J.P. 1960. Magnitude and frequency of forces in geomorphological processes. *Journal of Geology* **68**: 54–74.
- Young, R.G., Wilkinson, J., Hay, J., and Hayes, J.W. 2010. Movement and mortality of adult brown trout in the Motupiko River, New Zealand: Effects of water temperature, flow, and flooding. *Transactions of the American Fisheries Society* **139**: 137–146.

Appendix A

A.1 Predator avoidance experiment:

I assessed the ability of sockeye alevins to avoid predation from a simulated predator after being subjected to a 30-minute SEDE. This experiment attempted to determine if alevins, prematurely exposed to the water column, possessed the ecological competence to recognize and avoid potential predatory threats. This is an important ecologically relevant aspect of this study as the threats presented to alevins after a scour event may be as lethal as a scour event itself if the alevins are not equipped to survive predation. The predator experiment was initiated using the same SEDE apparatus and protocol as described above for the bury test. In addition, a simulated predator was constructed using a 10 cm plastic circle painted black with non-toxic waterproof paint (Hoover and Richardson 2010). The black circle was fastened to metal wires to use as a handle.

Ten randomly selected alevins of the same genetic family were subjected to a 30-minute SEDE. Upon completion of the SEDE all alevins were removed using a dip net and placed in a 20 L tank containing a five cm deep substrate composed of small river rocks. The simulated predator was placed 15 cm from the top of the tank and moved left and right along the long-axis of the tank. Presentation of the simulated predator was maintained for 30 minutes or until all alevins had completely buried within the gravel. The behaviour of each alevin was recorded for one hour with a JVC GZ-MS100RU memory camcorder. A control experiment took place using 10 alevins not previously subjected to a SEDE. Predator experiments occurred each week for seven weeks using three randomly chosen genetically separate families.

The data collected from the predator avoidance experiments were inconclusive as the alevins showed no response to the simulated predator over the 7-week period.

The lack of predator avoidance results from our study make it imperative that further research be conducted to determine whether or when forcibly removed alevins develop the ability to recognize potential threats as well as avoid predation. The absence of the alevin's reaction to the visual cues the simulated predator provided may have been due to the absence of supplementary natural stimuli within the experimental tank, whether it be chemical, auditory or tactile. Further studies need to be conducted with either an enhanced simulated predator or an actual live predator.

A.2 Exogenous feeding experiment:

I assessed the ability of sockeye alevins to initiate and or successfully prey upon the zooplankton *Daphnia pulex*. This experiment was conducted in an attempt to determine if alevins were capable of supplementing their nutritional intake by initiating feeding prior to completing yolk sac absorbance. If alevins utilized an excessive amount of energy swimming subsequent to a forced early emergence, the fixed energy content of their yolk sac may not be sufficient to ensure normal growth and development in which case the ability to capture and process supplemental prey would be a benefit. The feeding experiment consisted of the same initial set up as the Bury Test. *Daphnia pulex* were cultivated "in-house" for experimental use.

To ensure the survival of one alevin at the end of a SEDE, five alevins were exposed to a 30 minute SEDE in the experimental arena. Immediately following exposure to the SEDE, one randomly chosen alevin was placed in an 2 L tank. Upon the

introduction of the alevin to the tank, 100 *Daphnia pulex* were added. The behaviour of each alevin was recorded for one hour with a JVC GZ-MS100RU memory camcorder. Alevins were removed from the tank and euthanized with MS-222. The stomachs of each alevin were dissected and the contents were recorded. Controls for the experiment were conducted using alevins not subjected to SEDEs prior to feeding. The experiment was repeated three times a week for five weeks.

Upon completion of each SEDE the remaining viable alevins were euthanized using MS-222. All alevins used in the experiment were measured for length (± 0.1 mm) total wet mass and wet mass of yolk sac (± 0.01 g) as described above for the 2009 trials.

The feeding test indicated that there were no significant differences between alevins of the control and the treatment groups ($P = 0.245$), and there were no significant differences between the different ages after hatch ($P = 0.476$). The alevins that had been subjected to a SEDE did not respond any differently to the presence of *Daphnia pulex* than the control alevins that were not exposed to an SEDE (Figure 3.8).

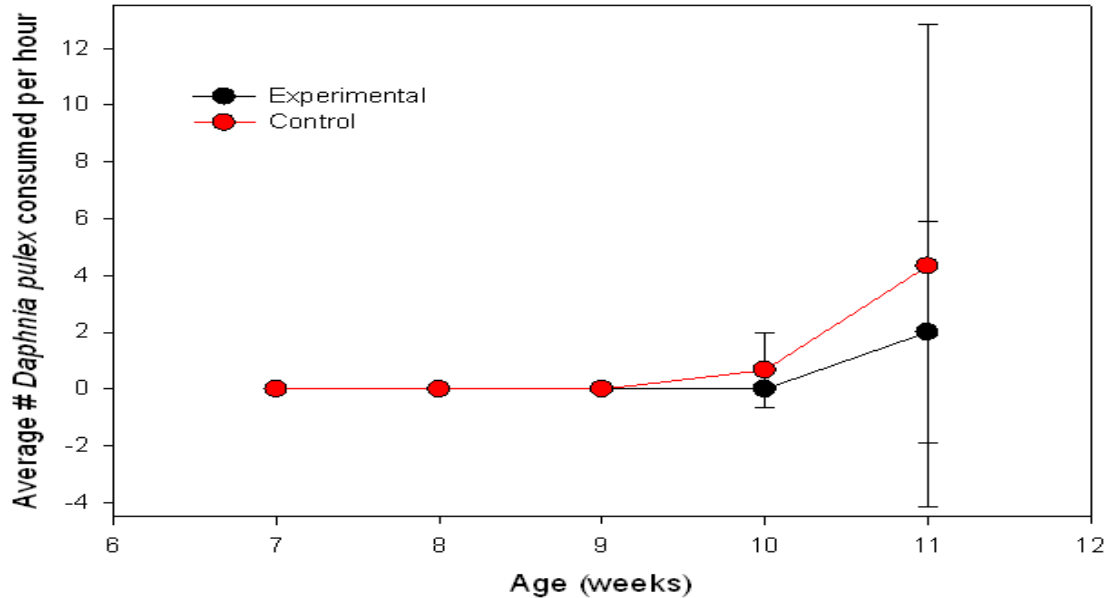


Figure A.1: Comparison of exogenous feeding responses exhibited by sockeye alevins exposed to an SEDE versus those of an unexposed control group. The experiment commenced 7 weeks after hatch and ceased upon volitional emergence at 11 weeks (n = 3 per week). Controls were carried out where alevins were not previously subjected to an SEDE. Bars represent 95% CI.

The onset of exogenous feeding typically occurs when the yolk sac is depleted by at least 70% (Skoglund and Barlaup 2006). A previous study found food in the stomachs and intestines of pre-emergent fry of brown trout, confirming that feeding can occur prior to emergence from the gravel and while yolk remains (Skoglund and Barlaup 2006). Predation can occur during the early developmental period of juvenile salmon, however, there are physical constraints that will limit alevins ability to successfully predate certain taxa. Previous studies found the size of the mouth gape imposed limitations on diversifying the feeding behaviour of alevins and small fry (Schael et al. 1991; Wainwright and Richard 1995; Sánchez-Hernández et al. 2011). Visual constraints of newly hatched alevin due to an incomplete development of their visual system can impede the capture of diverse preys, although studies suggest that capture of some taxa

appears possible at a very early life stage (Sánchez-Hernández et al. 2011). Motor abilities of alevins peak at the end of yolk sac absorption, therefore their swimming performance may not be adequate prior to absorption to capture particularly fast moving prey (Sánchez-Hernández et al. 2011). The need to transfer energy from the yolk sac to growth for successful development plays an important role in avoiding early alevin mortality, death before full absorption of the yolk sac, and pin-head mortality, and death caused by an inadequate yolk supply (Wallace and Aasjord 1984).

Sockeye salmon alevins were able to begin feeding prior to emergence; however, they did not appear to be able to supplement the loss of energy caused by excessive movement. Previous studies have shown that prey consumed prior to the loss of their yolk sac caused no apparent benefit on growth or survival (Heming et al. 1982; Skoglund and Barlaup 2006). Early feeding by salmon has been termed ‘precocious feeding’ as a result of the lack of energy transfer, as alevin feces have been found to contain fully intact chironomid larvae and other prey items (Heming et al. 1982). Pre-emergent feeding still exhibits secondary benefits to the fish through increased prey capture rate, post-emergence, as feeding is a learned behaviour through trial and error (Heming et al. 1982; Skoglund and Barlaup 2006). The alevin’s lack of ability to supplement their diet during excessive swimming has the potential to cause starvation and ultimately mortality. Whereas previous studies have looked at pre-emergent feeding exclusively within the redd (Wallace and Aasjord 1984; Schael et al. 1991; Wainwright and Richard 1995; Skoglund and Barlaup 2006; Sánchez-Hernández et al. 2011), our experiment dealt with a scenario where excessive movement caused by forced emergence may cause alevins to absorb their yolk sacs earlier than anticipated. There are no previous studies dealing with this situation, and as such it is currently unknown if precocious feeding is still an issue

with forced emergence or if alevins are able to begin digesting prey items early upon depletion of their energy source. Although, findings by Skoglund and Barlaup (2006) suggest that fry emerging after depleting their yolk sac initiated feeding more quickly than those that emerge with a portion of their yolk sac still remaining.

The findings from this study do not support the idea of early onset of feeding, however, as none of the alevins forced into excessive movement through a SEDE showed any interest in feeding prior to natural emergence, we believe this to be a result of insufficient testing. Our findings showed the alevins in the control group, not subjected to excessive movement, began feeding one week earlier than the experimental alevins that were subject to excessive movement. One of the reasons that may have limited the alevins' ability to capture *Daphnia pulex* at earlier developmental stages was that the size of the prey was too large for the gape of the alevins mouths. *Daphnia* sp. are one of the preferred prey of juvenile sockeye salmon during summer and autumn months (Hampton et al. 2006; Masee et al. 2007), however, alevins may not have developed gapes wide enough to capture the larger zooplankton species until they reach later stages of development. Field-Dodgson (1988) found that emerging salmon feed on prey that coincided with their mean mouth breadth (MMB) of 0.22 cm and a mean fork length (MFL) of 3.35 cm. The typical sizes of prey consumed are relatively narrow and correspond to approximately half the MMB of the fry. The alevins in our feeding studied reached an MFL of 3.06 cm at week 10, and 3.03 cm at emergence in week 11 (Figure 5.1). MMB was not recorded during this study and we were therefore unable to compare. *Daphnia pulex* are typically between 0.02 and 0.5 cm in length, and as a result the alevins may be incapable of capturing the prey until just before emergence.

The contradiction between our results and our prediction, i.e., that alevins exposed to increased movement will initiate early feeding, may be due to the time scale in which the experiments were conducted. Alevins were only exposed to extraneous movement once immediately prior to their exposure to *Daphnia pulex*. It has been previously suggested that the low feeding rates observed among the alevins are most likely due to low feeding motivation or appetite, as their yolk sacs supply is still intact (Skoglund and Barlaup 2006). Therefore, until the yolk sac had actually been depleted, alevins did not begin to supplement their diet with prey.

The experiments conducted on exogenous feeding by early emergent alevins were only preliminary. These experiments should be repeated with an increased amount of time between forced movement (i.e., SEDE) and with exposure to prey items included. Such an experimental design may provide alevins a recovery period from the SEDE and initiate an interest in feeding. A complementary study should be conducted where alevins are repeatedly forced into extraneous movement until their yolk sacs have been depleted before exposure to potential prey occurs. This would help determine the earliest point in alevin development where they become capable of successfully hunting prey.